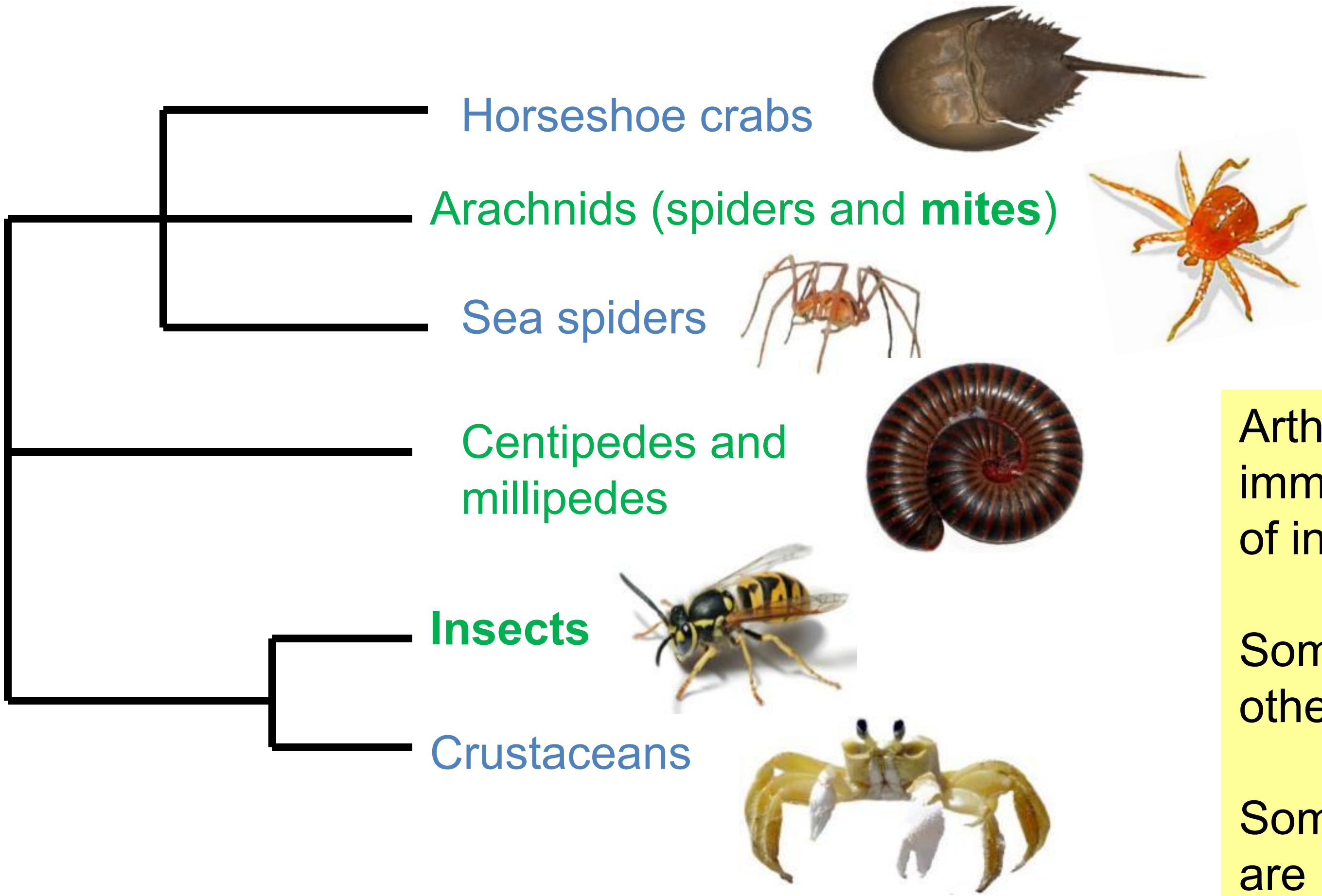
Plants and Arthropods

Friends or Foes?

www.plantcell.org/cgi/doi/10.1105/tpc.111.tto811

What are arthropods?



Arthropods are an immense, diverse group of invertebrates

Some are terrestrial and others aquatic

Some **mites** and **insects** are major herbivores that can cause extensive damage to living plants

Arthropods cause crop yield losses of ~10 - 30% every year

- How do arthropods damage plants?
- How do plants defend themselves from herbivores?
- How do herbivores cope with plant defenses?
- How do plants establish mutualistic interactions with arthropods including pollinators and their herbivores' natural enemies?

Photo by Scott Bauer
USDA

Lecture outline

1. **400 million years of living together**
2. **Basic conflict – herbivory**

   Plant defense and herbivore counter-measures
   - Constitutive defenses
   - Induced defenses
   - Secondary metabolites in defense
3. **Alliance #1** – Carnivorous and / or parasitoid arthropods
   - Herbivore-induced volatiles guide foraging carnivores to prey
   - Domatia and extrafloral nectar can accommodate carnivores
4. **Alliance #2** – Pollinators
   - Physiological compatibility between plants and pollinators
   - Controlling pollen and nectar theft

A long-term, complicated relationship

The basic conflict: plants are food for herbivorous arthropods

M. sexta eating *N. attenuata*

Alliance #1: Predatory or parasitic arthropods protect plants from herbivore damage

M. sexta after attack by predator

Alliance #2: Most angiosperms rely upon arthropods for successful reproduction

Nicotiana attenuata **pollinated by** ***Manduca sexta*** **moth**

Photo credits: Danny Kessler; R.J. Reynolds Tobacco Company Slide Set, Bugwood.org; Wu, J., Hettenhausen, C., Meldau, S. and Baldwin, I.T. (2007). Herbivory rapidly activates MAPK signaling in attacked and unattacked leaf regions but not between leaves of *Nicotiana attenuata*. Plant Cell. 19: 1096-1122.

The evolution of herbivory

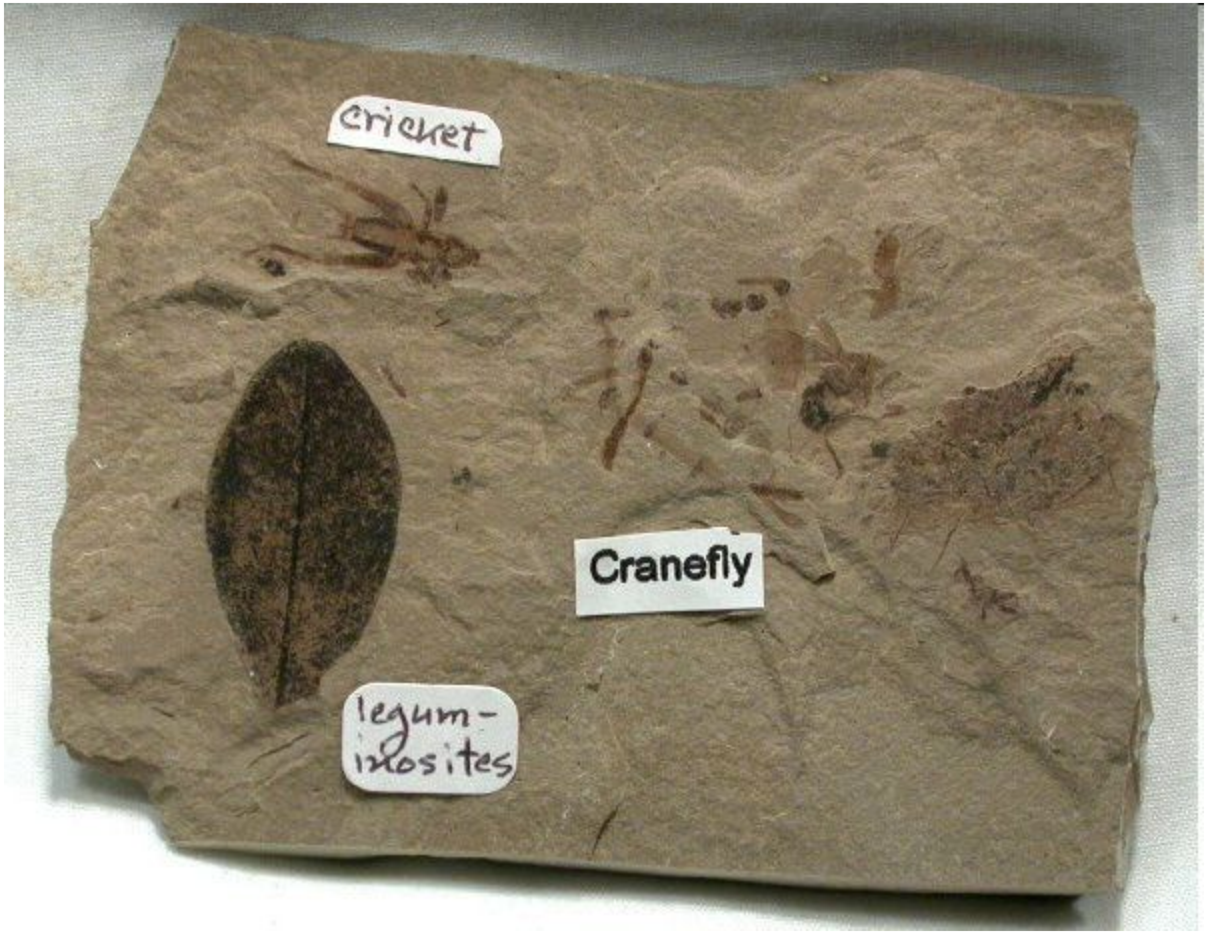
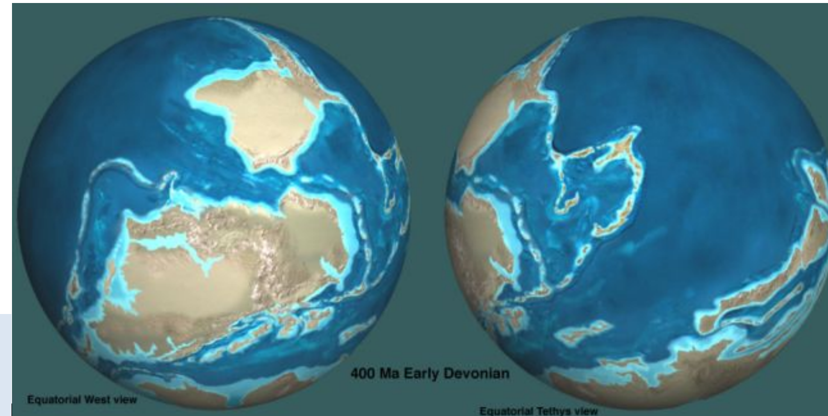


Photo credit: [Fossil mall]

400 million years ago the world was very different

The land was mostly barren, continents were far from their present locations, and the atmosphere, flora and fauna were vastly different than today



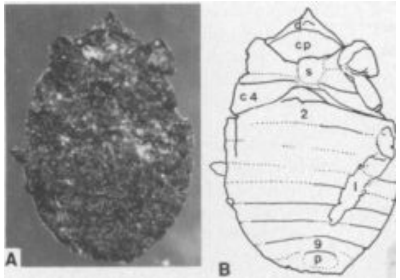
Earth 400 million years ago

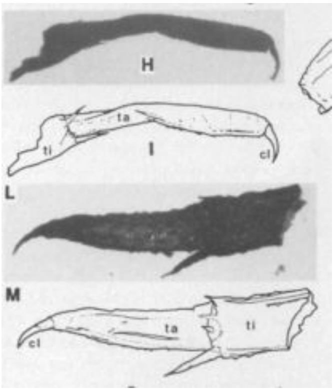
Map copyright Ron Blakey and Colorado Plateau Geosystems, Inc.

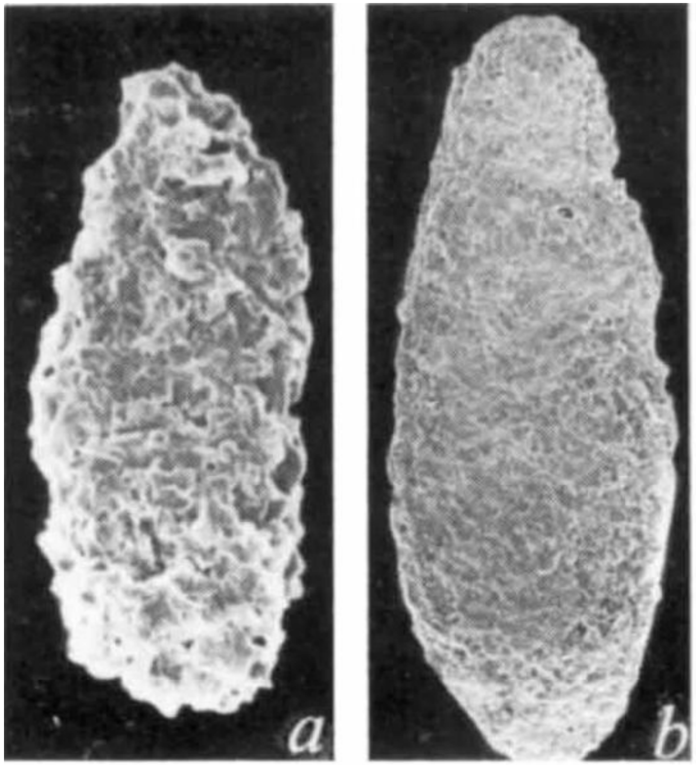
400 million year-old fossils show evidence of herbivory

Fossils of early plants

Fossils of early terrestrial arthropods







Fossilized feces (coprolites) showing ingested plant material

Image credit: [Miguasha National Park]Image credit: Miguasha National Park; Jeram, A.J., Selden, P.A. and Edwards, D. (1990). Land Animals in the Silurian: Arachnids and Myriapods from Shropshire, England. Science. 250: [658-661] reprinted with permission from AAAS. Edwards, D., Selden, P.A., Richardson, J.B. and Axe, L. (1995). Reprinted by permission from Macmillan Publishers Ltd: Coprolites as evidence for plant-animal interaction in Siluro-Devonian terrestrial ecosystems. Nature. 377: [329-331].

Plants and arthropods share 400 million years of evolution

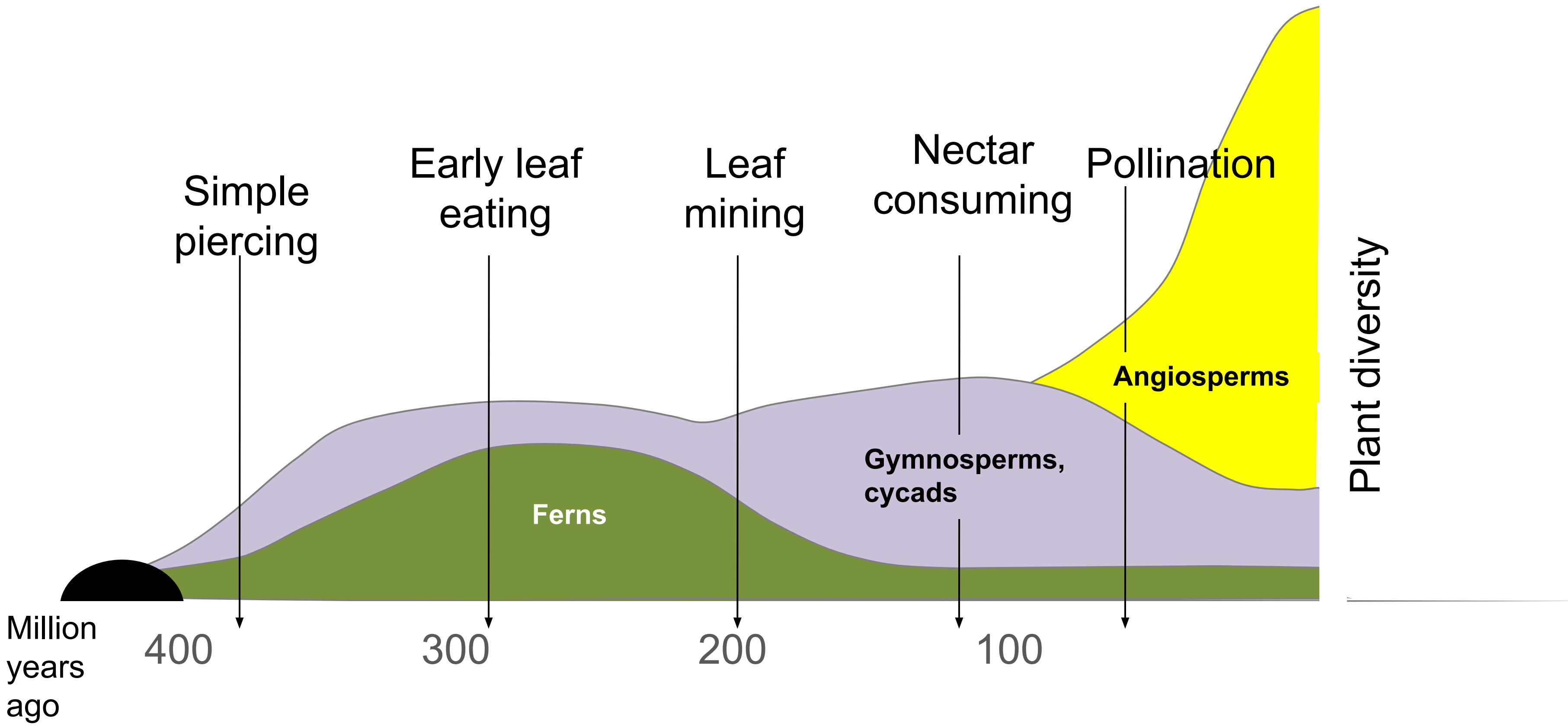


Image derived from : L. Shyamal Image derived from : L. Shyamal based on work by Bruce Tiffney

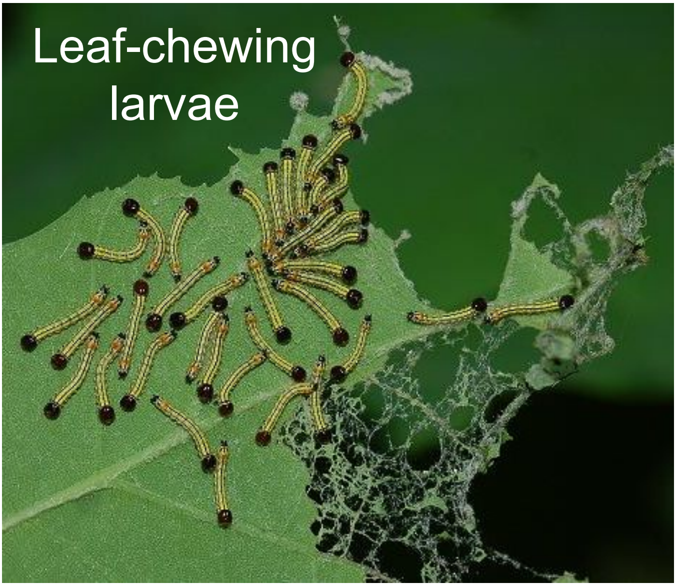
The ongoing conflict: Herbivory

Phloem-sucking aphids

Mesophyll-grazing leaf miners

Mesophyll-suc king mites

Root-vascular cylinder sucking nematodes



Plants produce energy from photosynthesis; animals are hungry and eat plants (or they eat plant-eaters)

Photo credits: Sate Al AbbasiPhoto credits: Sate Al Abbasi; David CappaertPhoto credits: Sate Al Abbasi; David Cappaert, Michigan State University, Bugwood.org; University of MissouriPhoto credits: Sate Al Abbasi; David Cappaert, Michigan State University, Bugwood.org; University of Missouri. Published by MU Extension,Photo credits: Sate Al Abbasi; David Cappaert, Michigan State University, Bugwood.org; University of Missouri. Published by MU Extension, all rights reserved. William WergiPhoto credits: Sate Al Abbasi; David Cappaert, Michigan State University, Bugwood.org; University of Missouri. Published by MU Extension, all rights reserved. William Wergi; John R. MeyerPhoto credits: Sate Al Abbasi; David Cappaert, Michigan State University, Bugwood.org; University of Missouri. Published by MU Extension, all rights reserved. William Wergi; John R. Meyer

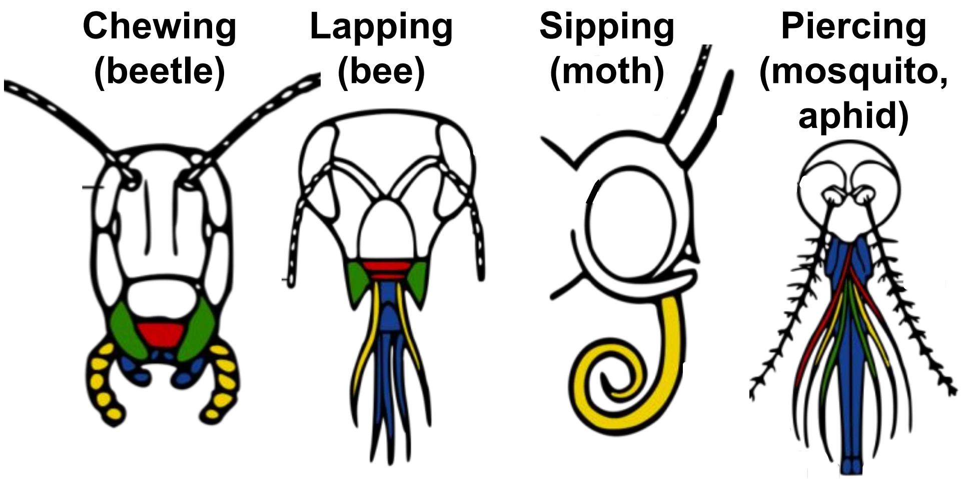
Plants respond differently to different types of feeding behaviour

Chewing insects cause extensive wounding, and some partially digest their food outside their bodies by regurgitation

Piercing arthropods have needle-like stylets that pierce tissues and then suck nutrients out

Photo credits: Sate Al AbbasiPhoto credits: Sate Al Abbasi; John R. Meyer, North Carolina State University;

Piercing-sucking and chewing may have evolved more than once



Chewers and suckers are found among both carnivores and herbivores

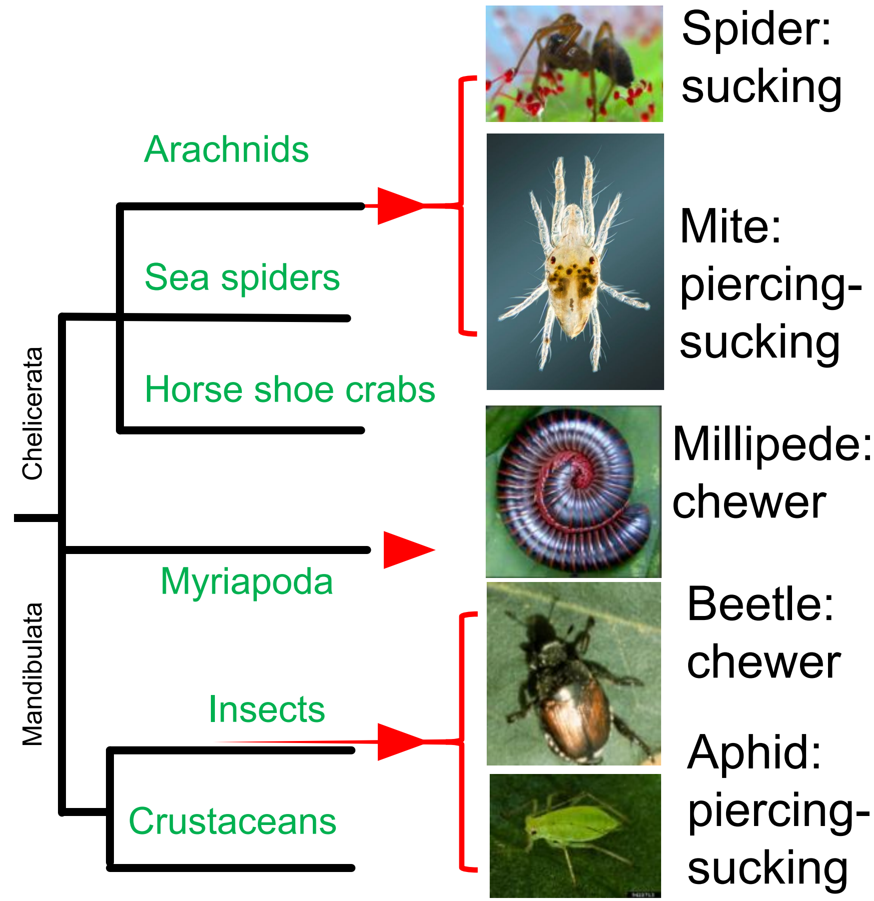
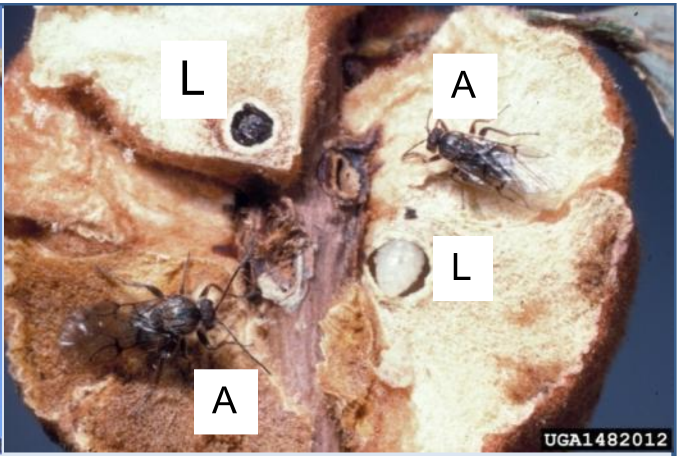


Photo credits: Jan van Arkel (IBED; University of Amsterdam); R.J. Reynolds Tobacco Company Slide SetPhoto credits: Jan van Arkel (IBED; University of Amsterdam); R.J. Reynolds Tobacco Company Slide Set, Bugwood.org; Scott Bauer, USDA Agricultural Research Service, Bugwood.org

Some arthropods form galls

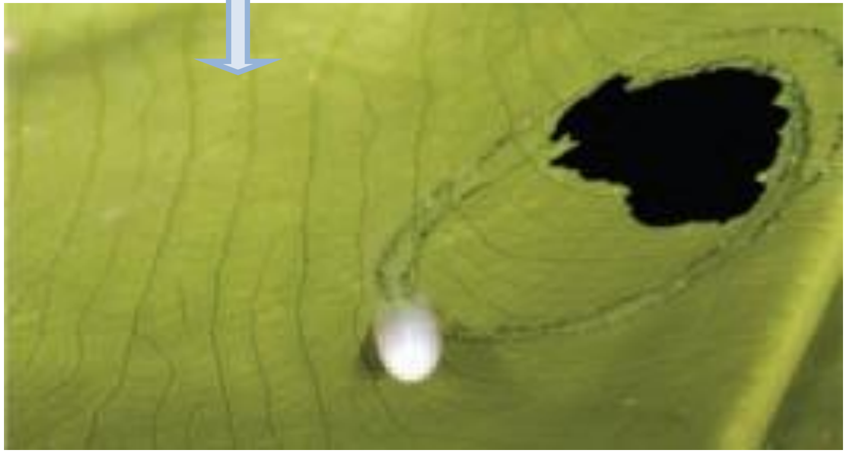


Gall on oak caused by cynipid gall wasp; opened gall showing adults (A) and larvae (L)

Galls are localized tissue proliferations induced by arthropods, which lay their eggs in them, or pathogens. Insects and some pathogens form galls by manipulating plant hormones. Galls are often more nutritious and less defended than other tissues, but it is not yet understood how this occurs

Clemson University Clemson University - USDA Cooperative Extension Slide Series; Milan ZubrikClemson University - USDA Cooperative Extension Slide Series; Milan Zubrik, Forest Research Institute, Slovakia; Gyorgy CsokaClemson University - USDA Cooperative Extension Slide Series; Milan Zubrik, Forest Research Institute, Slovakia; Gyorgy Csoka, Hungary Forest Research Institute; Milan ZubrikClemson University - USDA Cooperative Extension Slide Series; Milan Zubrik, Forest Research Institute, Slovakia; Gyorgy Csoka, Hungary Forest Research Institute; Milan Zubrik, Forest Research Institute, Slovakia; Sturgis McKeever, Georgia Southern University, Bugwood.org

Constitutive plant defenses and herbivore countermeasures



Aplosonyx leaf beetle cutting a circular trench on a leaf of *Colocasia*

Labidomera clivicollis cutting a trench through the leaf tissue to avoid ingesting sticky, toxic latex

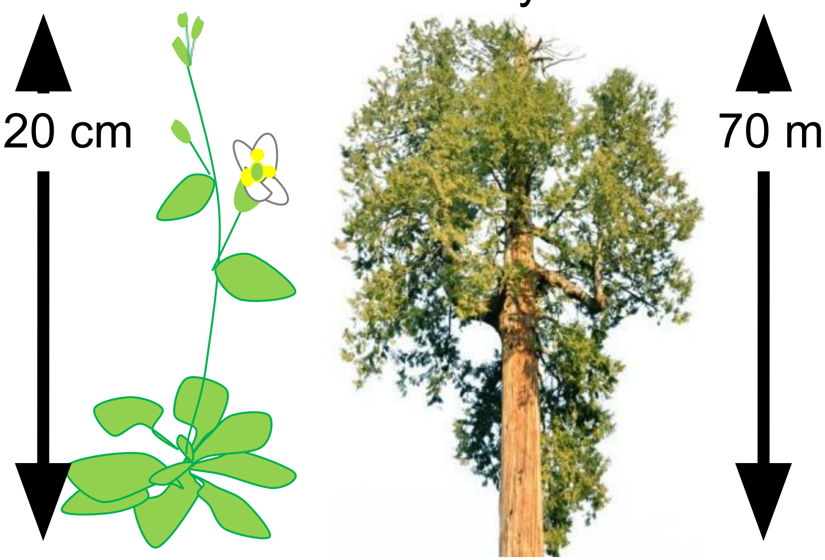
Photo scopyright Chris DarlingPhoto scopyright Chris Darling; Dussourd, D., and Eisner, T. (1987). Vein-cutting behavior: insect counterploy to the latex defense of plants. Science 237: 898-901 reprinted with permission of AAAS; .

Plants and plant tissues vary in their degree of defensiveness

Plant ***apparency*** matters – short-lived, ephemeral plants may invest less energy in defense than long-lived, highly apparent ones do

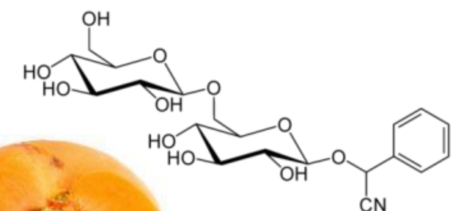
Lifespan: ~2 months

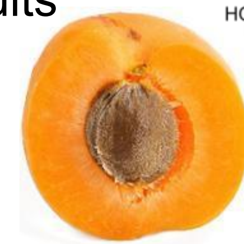
Lifespan: 1000 years

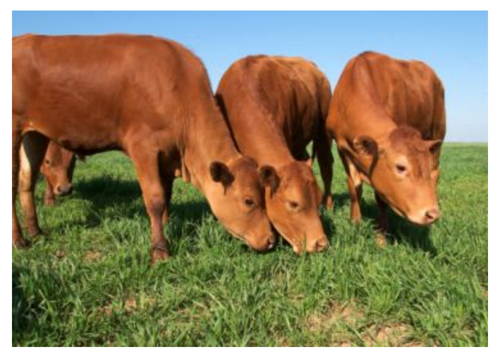


Nutritional value also matters – nutrient-rich tissues including seeds are often heavily defended

Seeds of apricots and related fruits contain toxins such as amygdalin







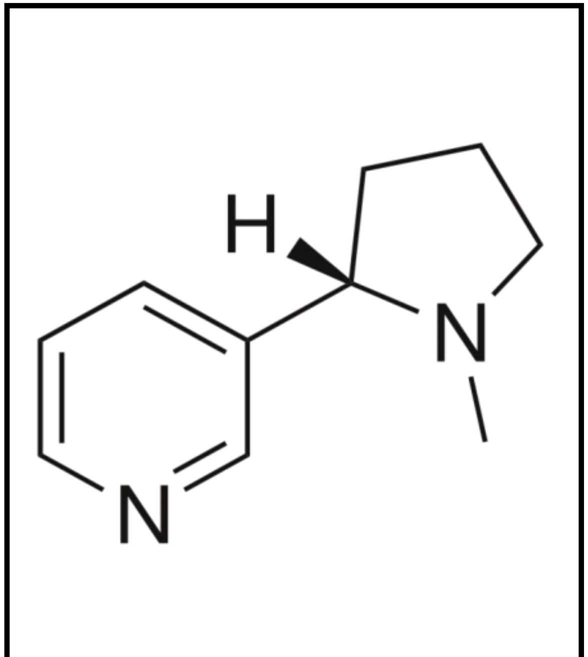
Herbivores preferentially consume nutrient-rich plant material

Photo credit Stephen Ausmus

Plants have evolved many ways to defend against herbivory

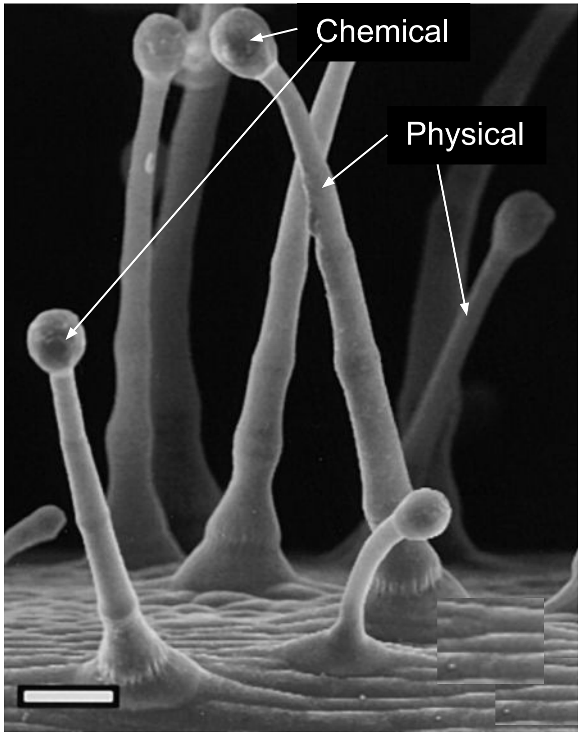
Physical

Chemical



Nicotine

Both



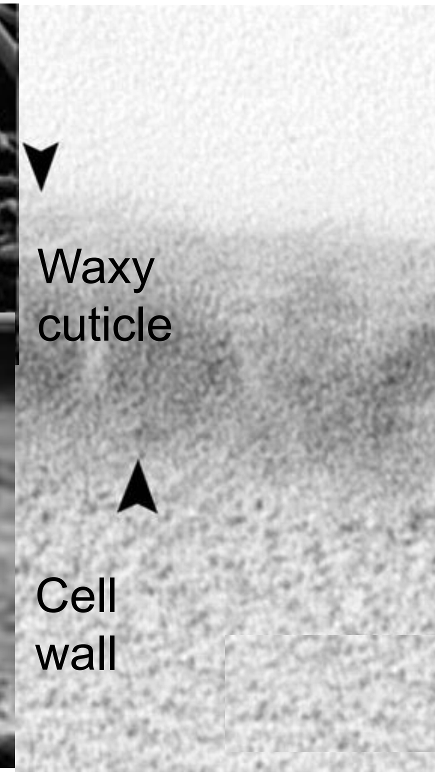
Ranger, C.M., and Hower, A.A. (2001). Glandular morphology from a perennial alfalfa clone resistant to the potato leafhopper. Crop Sci. 41: 1427-1434.

Physical defenses against herbivory

Thorns

Trichomes (hairs)

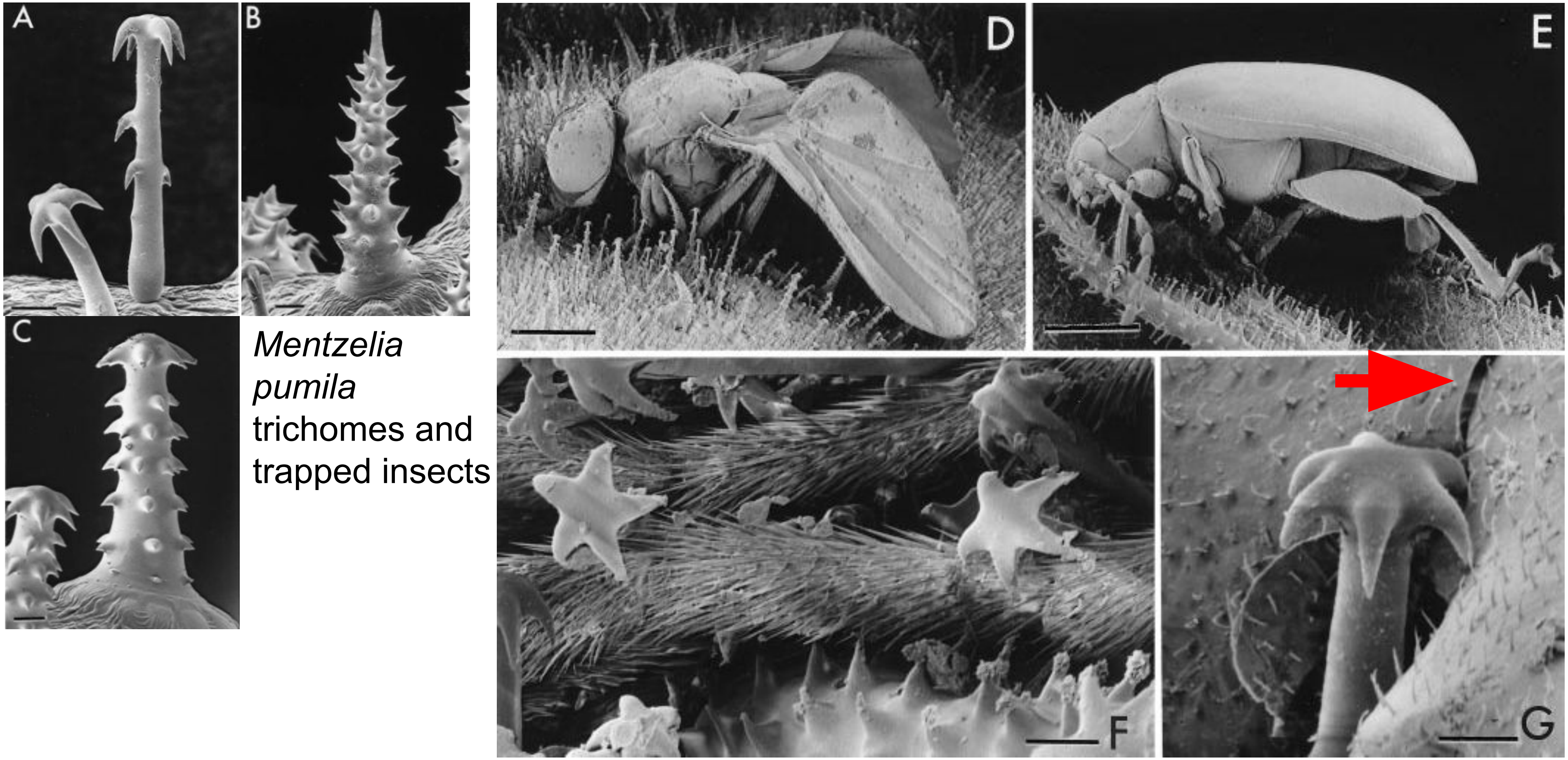
Wax and wall



Latex and resin

Cardoso, M.Z. (2008). Herbivore handling of a Plant's trichome: the case of *Heliconius charithonia* (L.) (Lepidoptera: Nymphalidae) and *Passiflora lobata* (Killip) Hutch. (Passifloraceae). Neotropical Entomology 37: [247-252](247-252).

From an arthropod's perspective trichomes can be lethal

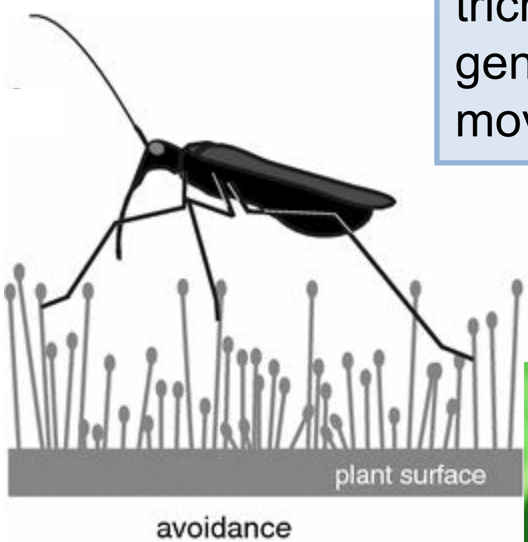


Mentzelia pumila trichomes and trapped insects

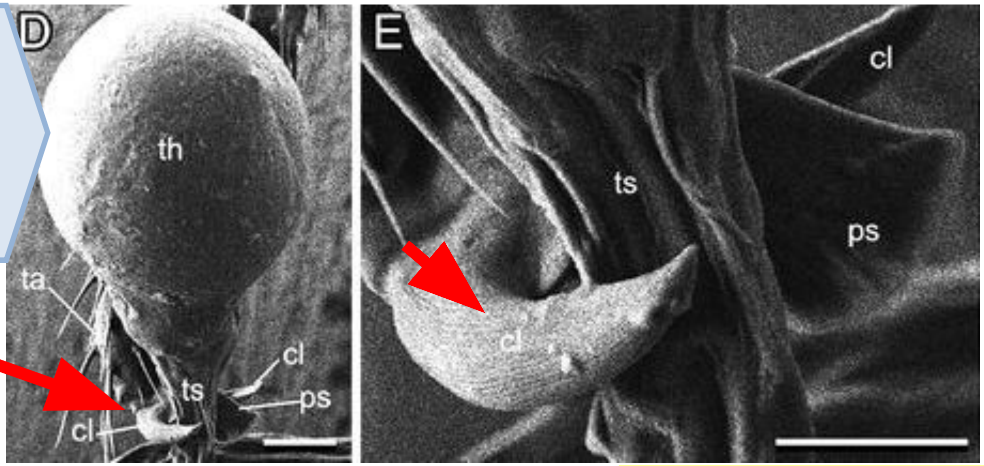
Eisner, T., Eisner, M. and Hoebeke, E.R. (1998). When defense backfires: Detrimental effect of a plant's protective trichomes on an insect beneficial to the plant. Proc. Natl. Acad. Sci. USA 95**:** 4410-4414, copyright National Academy of Sciences, USA.

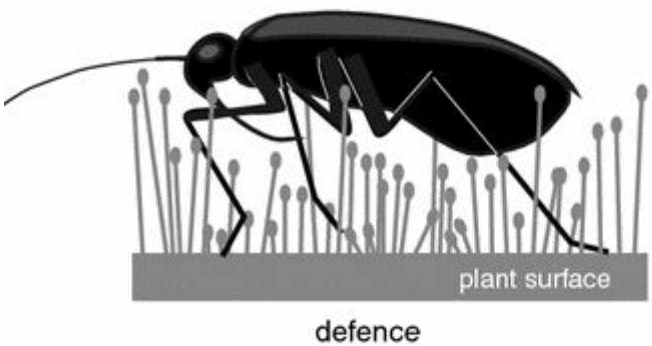
Some arthropods avoid sticky trichomes or push past them

Claws grab onto trichome stalks to generate force for movement



Long legs help rise above sticky materials





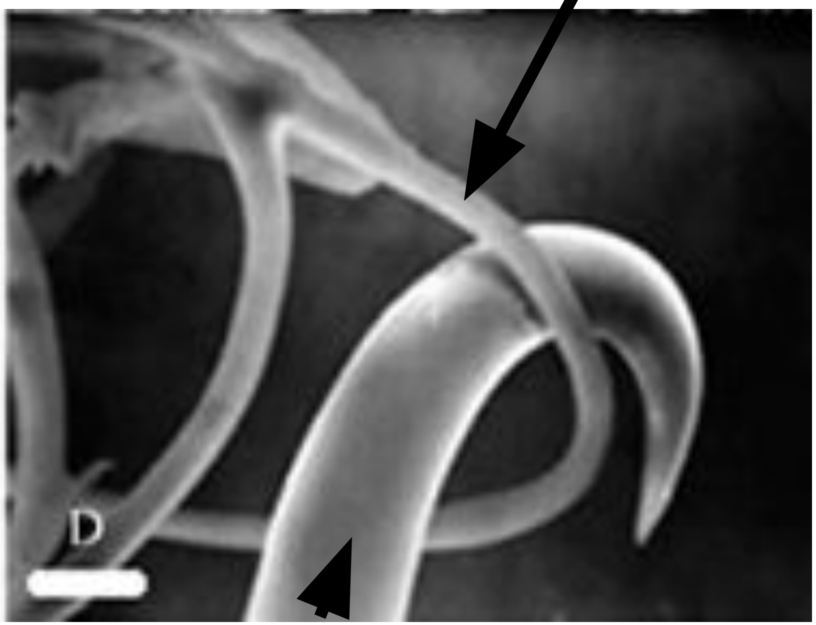
Force and non-stick coatings help push past sticky materials

Voigt, D. and Gorb, S. (2010). Locomotion in a sticky terrain. Arthropod-Plant Interactions. 4: 69-79Voigt, D. and Gorb, S. (2010). Locomotion in a sticky terrain. Arthropod-Plant Interactions. 4: 69-79; Russ Ottens, University of Georgia, Bugwood.org.

Some arthropods cover trichomes with silk or bite off the hooked ends

The hooked trichomes of a passionflower have been bitten off and covered with silk

Larval silk

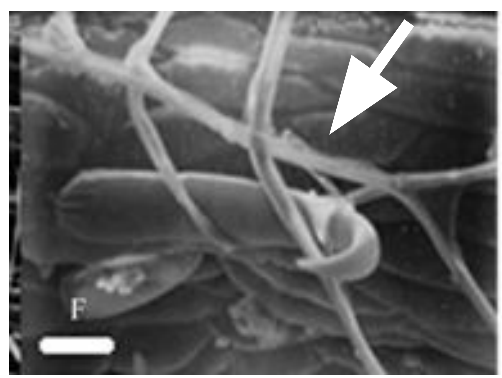


Trichome tip

Passion flower

Zebra Longwing larvae

Trichome tied down by silk



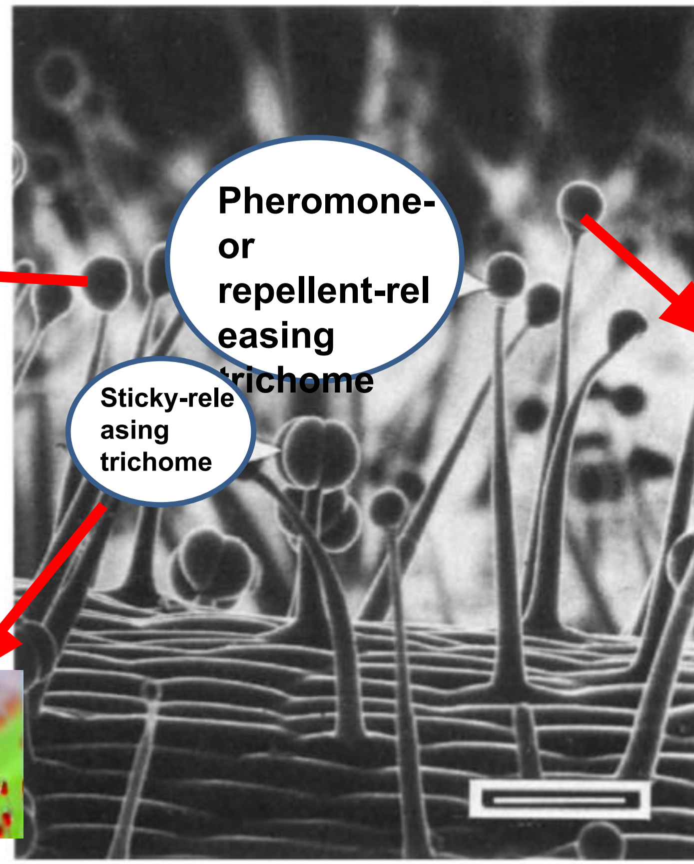
Trichome tip bitten off

Photo copyright Dale Clark; Cardoso, M.Z. (2008). Herbivore handling of a Plant's trichome: the case of *Heliconius charithonia* (L.) (Lepidoptera: Nymphalidae) and *Passiflora lobata* (Killip) Hutch. (Passifloraceae). Neotropical Entomology 37: 247-252.

Trichomes can release chemical deterrents to arthropods

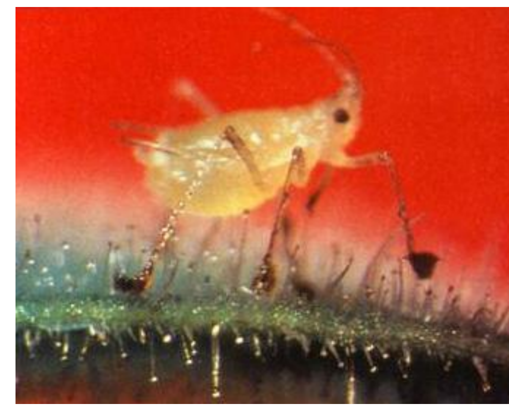
Tomato (*Solanum lycopersicum)*

Tomato trichomes produce chemicals repellent to whiteflies



Many trichomes produce sticky substances

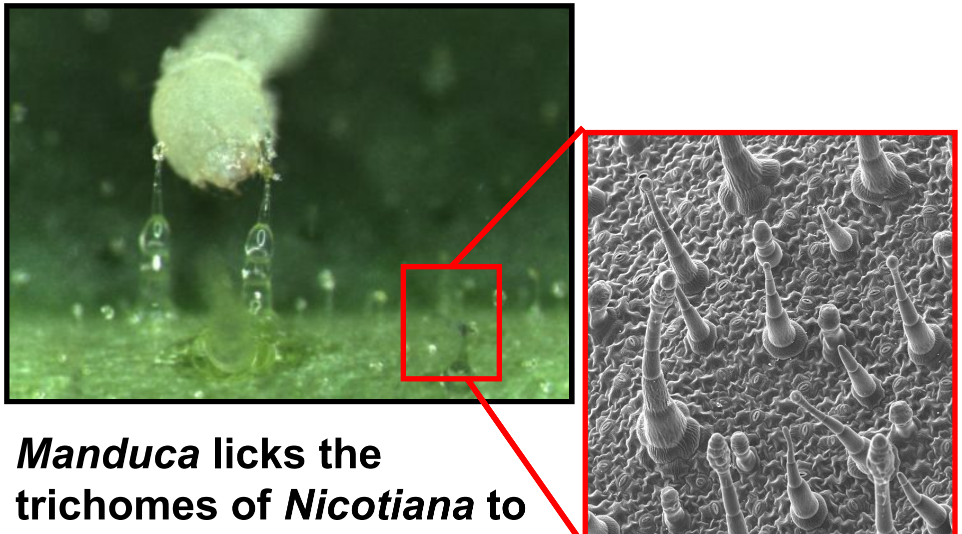
Wild-potato (*Solatium berthaultii)*



Wild-potato trichomes produce aphid alarm pheromones

Reprinted by permission from Macmillan Publishers Ltd. from Gibson, R.W., and Pickett, J.A. (1983). Wild potato repels aphids by release of aphid alarm pheromone. Nature 302: 608-609.

Sometimes freshly hatched caterpillars "lick" the sugars off trichomes …



Manduca licks the trichomes of *Nicotiana* to eat the acyl-sugars these secrete

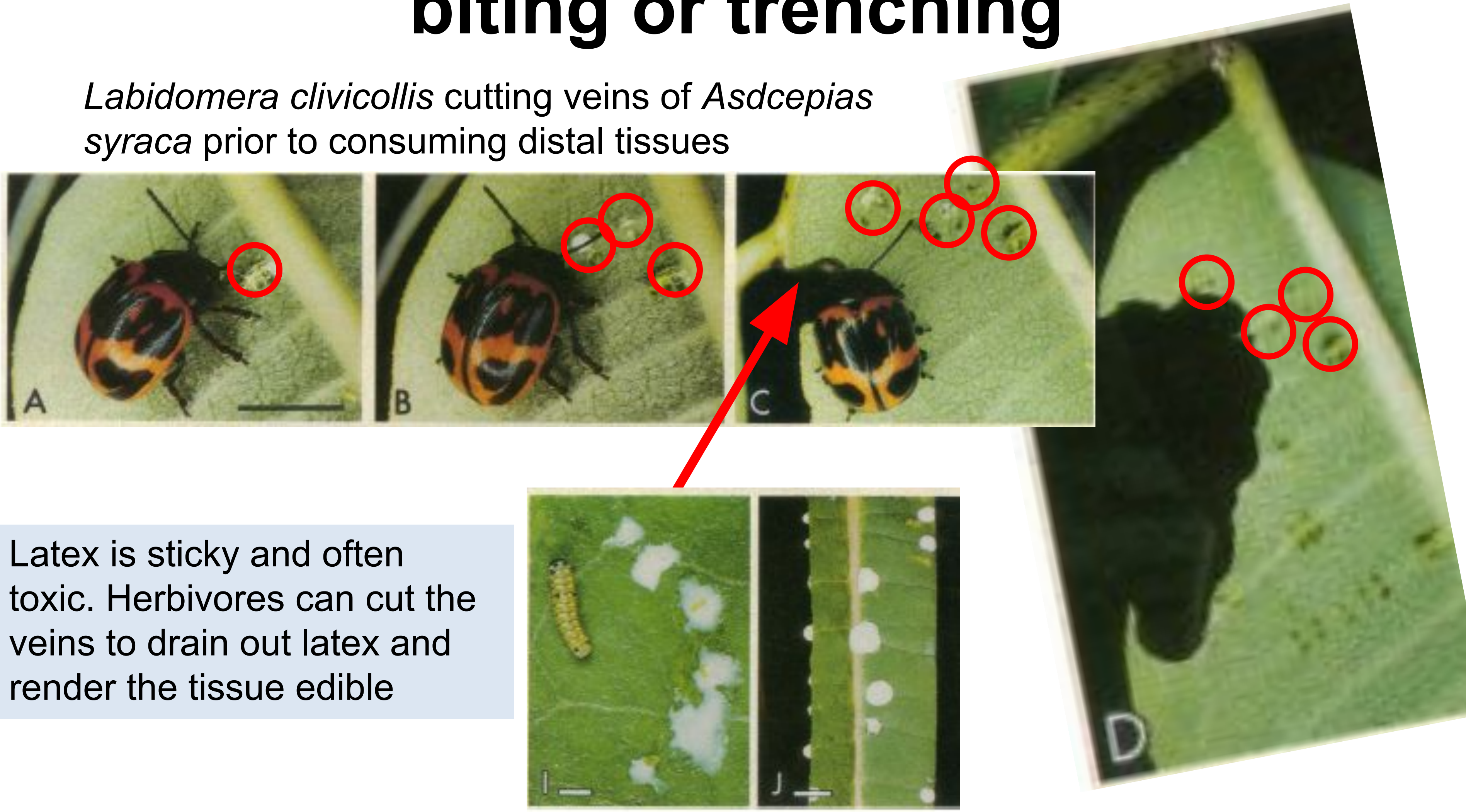
The ant *Pogonomyrmex rugosus* forages using the smell of those same volatile acyclic fatty acids

… but this gives them a "smell" that betrays them to their enemies

Photo credits: Alex Weinhold and Ian BaldwinPhoto credits: Alex Weinhold and Ian Baldwin; Weinhold, A. and Baldwin, I.T. (2011). Trichome-derived O-acyl sugars are a first meal for caterpillars that tags them for predation. Proc. Natl. Acad. Sci. 108: 7855-7859Photo credits: Alex Weinhold and Ian Baldwin; Weinhold, A. and Baldwin, I.T. (2011). Trichome-derived O-acyl sugars are a first meal for caterpillars that tags them for predation. Proc. Natl. Acad. Sci. 108: 7855-7859; Louisa Howard, Dartmouth University

Latex can be avoided through vein biting or trenching

Labidomera clivicollis cutting veins of *Asdcepias syraca* prior to consuming distal tissues



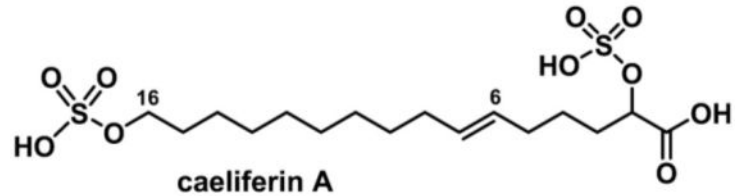
Latex is sticky and often toxic. Herbivores can cut the veins to drain out latex and render the tissue edible

Dussourd, D., and Eisner, T. (1987). Vein-cutting behavior: insect counterploy to the latex defense of plants. Science 237: 898-901 reprinted with permission of AAAS.

Induced defenses and herbivore countermeasures

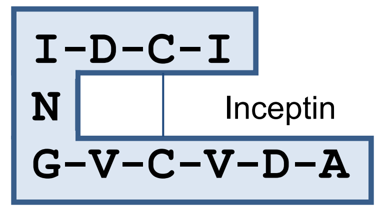
Perception of herbivory

Biting and wounding damage



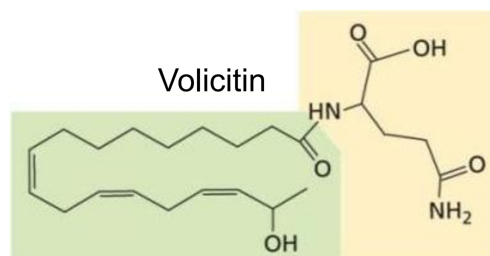
caeliferin A

Piercing and saliva

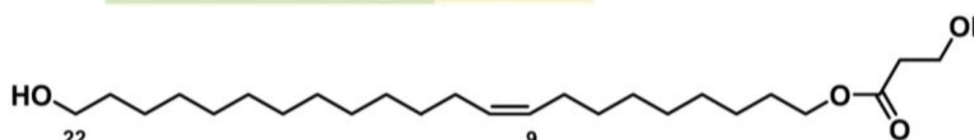


Oral secretions and regurgitant

Volicitin



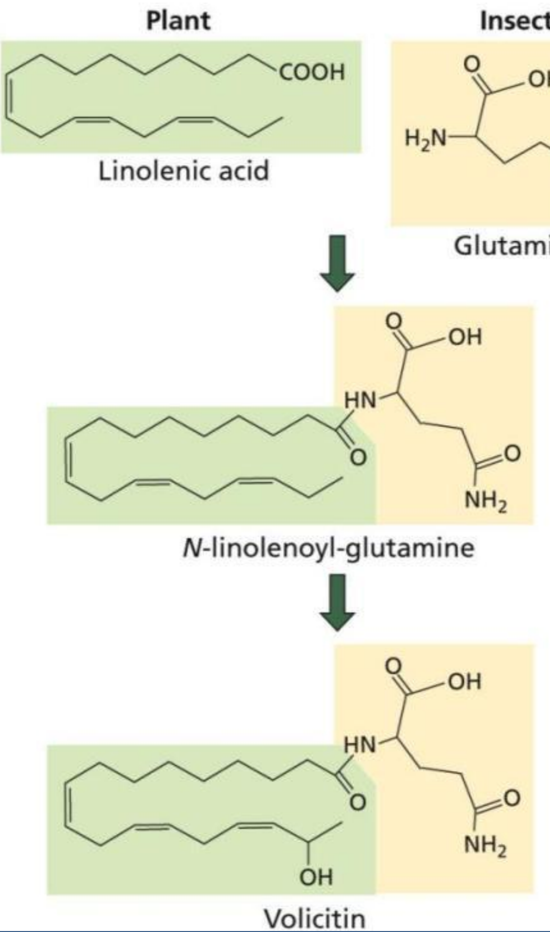
Egg laying damage and secretions



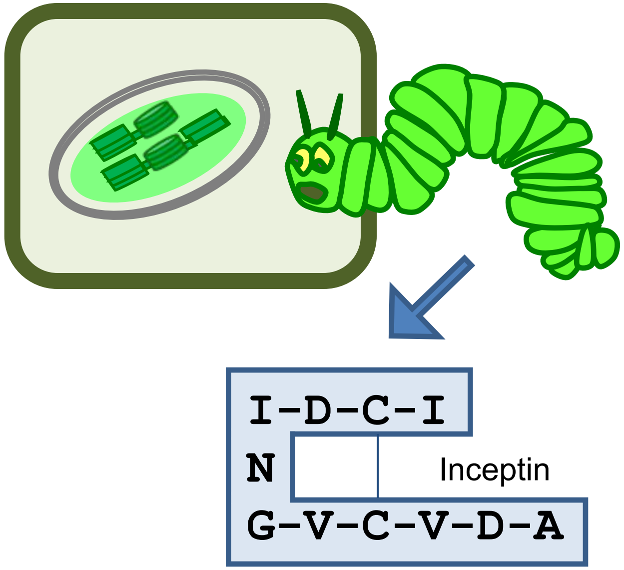
bruchin A

Phillip RobertsPhillip Roberts, USDA Forest ServicePhillip Roberts, USDA Forest Service University of Georgia, Bugwood.org; Mithöfer, A. and Boland, W. (2008). Recognition of herbivory-associated molecular patterns. Plant Physiology. 146: 825-831; .

Volicitin and inceptin are herbivory-specific compounds

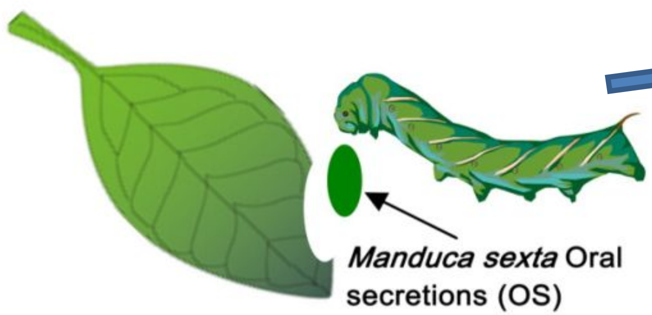


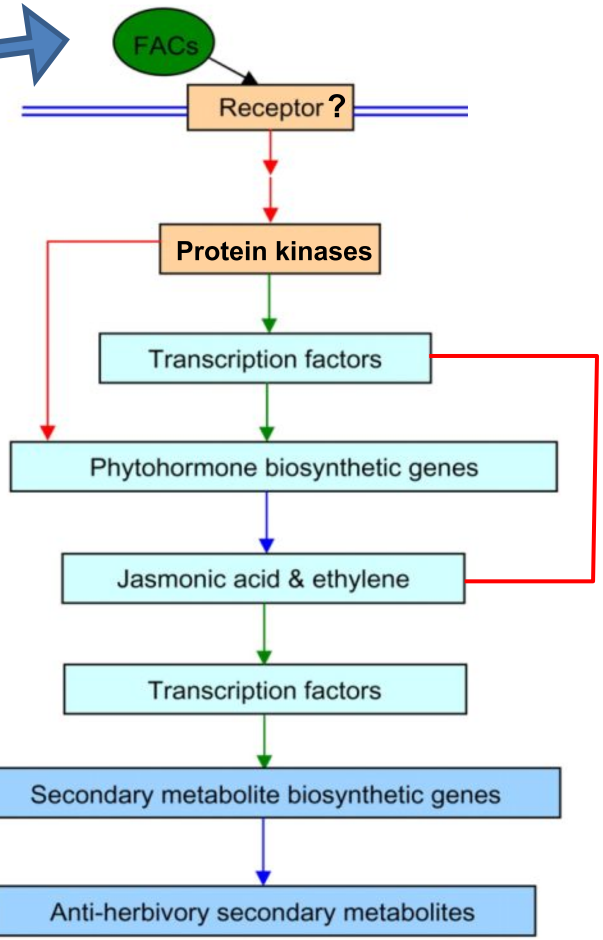
Volicitin is produced from the conjugation of a plant-derived fatty acid conjugated to glutamine in the herbivore midgut, then regurgitated onto plant tissues



Inceptin is a peptide derived from proteolytic cleavage by the insect of a chloroplastic ATP synthase from the plant

Herbivory-specific compounds induce plant defenses



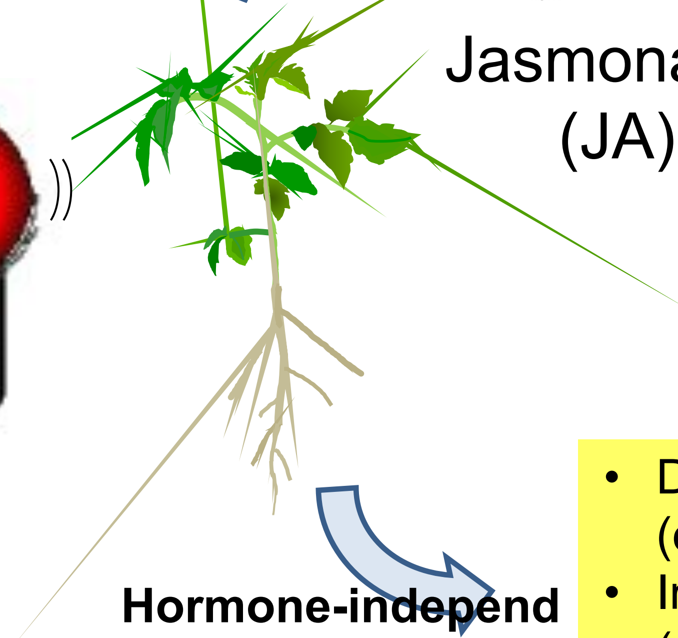


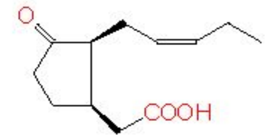
The fatty-acid conjugates (FACs) and other herbivore signals induce expression of secondary metabolite biosynthetic genes and other defense & repair genes

Wu, J., Hettenhausen, C., Schuman, M.C. and Baldwin, I.T. (2008). A comparison of two *Nicotiana attenuata* accessions reveals large differences in signaling induced by oral secretions of the specialist herbivore *Manduca sexta*. Plant Physiology. 146: 927-939.

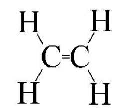
Many induced defense responses are mediated by hormones

Hormone dependent signaling

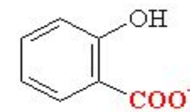




Jasmonate (JA)



Ethylene (ET)



Salicylate (SA)

Hormone-independent signaling

- Direct responses (e.g. toxins)
- Indirect responses (e.g. predator attraction)

Phillip RobertsPhillip Roberts, USDA Forest Service University of Georgia, Bugwood.org

Infestation induces expression of defense-associated genes

Plants respond to the type of herbivory – different herbivores induce different subsets of genes. In general, infested plants induce synthesis or accumulation of toxins, anti-nutritives, and damage repair compounds

Photo credits: Sate Al AbbasiPhoto credits: Sate Al Abbasi; John R. MeyerPhoto credits: Sate Al Abbasi; John R. Meyer, North Carolina State University; Mites Photo credits: Sate Al Abbasi; John R. Meyer, North Carolina State University; Mites CopyrightPhoto credits: Sate Al Abbasi; John R. Meyer, North Carolina State University; Mites Copyright 1993 to 2011 University of Missouri. Published by MU Extension, all rights reserved.

Herbivory induces direct and indirect defenses locally and systemically

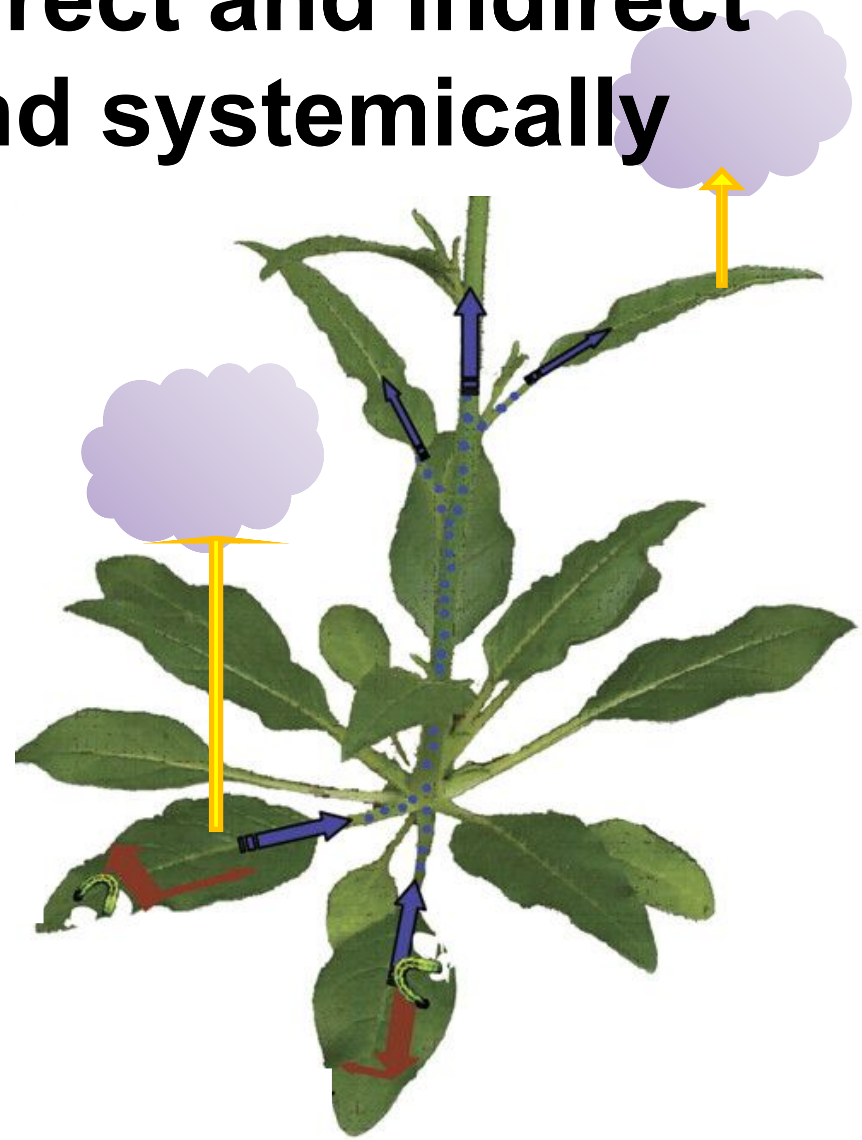
Local signals and hormone accumulation

Induction of **direct** defenses (e.g. alkaloids and other toxins, proteinase inhibitors)

Induction of volatiles that attract natural enemies of herbivores (**indirect** defenses)

Long distance signals and systemic responses

Induction of **direct** defenses (e.g. alkaloids and other toxins, proteinase inhibitors) albeit later and often less strong



Wu, J., Hettenhausen, C., Meldau, S., and Baldwin, I.T. (2007). Herbivory rapidly activates MAPK signaling in attacked and unattacked leaf regions but not between leaves of *Nicotiana attenuata*. Plant Cell 19: 1096-1122.

Some herbivores can suppress induced plant defense responses

Tetranychus urticae

T. urticae ***induces*** tomato defenses and its fitness on tomato is ***moderate***

Tetranychus evansi

T. evansi ***suppresses*** induced defenses in tomato and is a ***serious*** pest on it

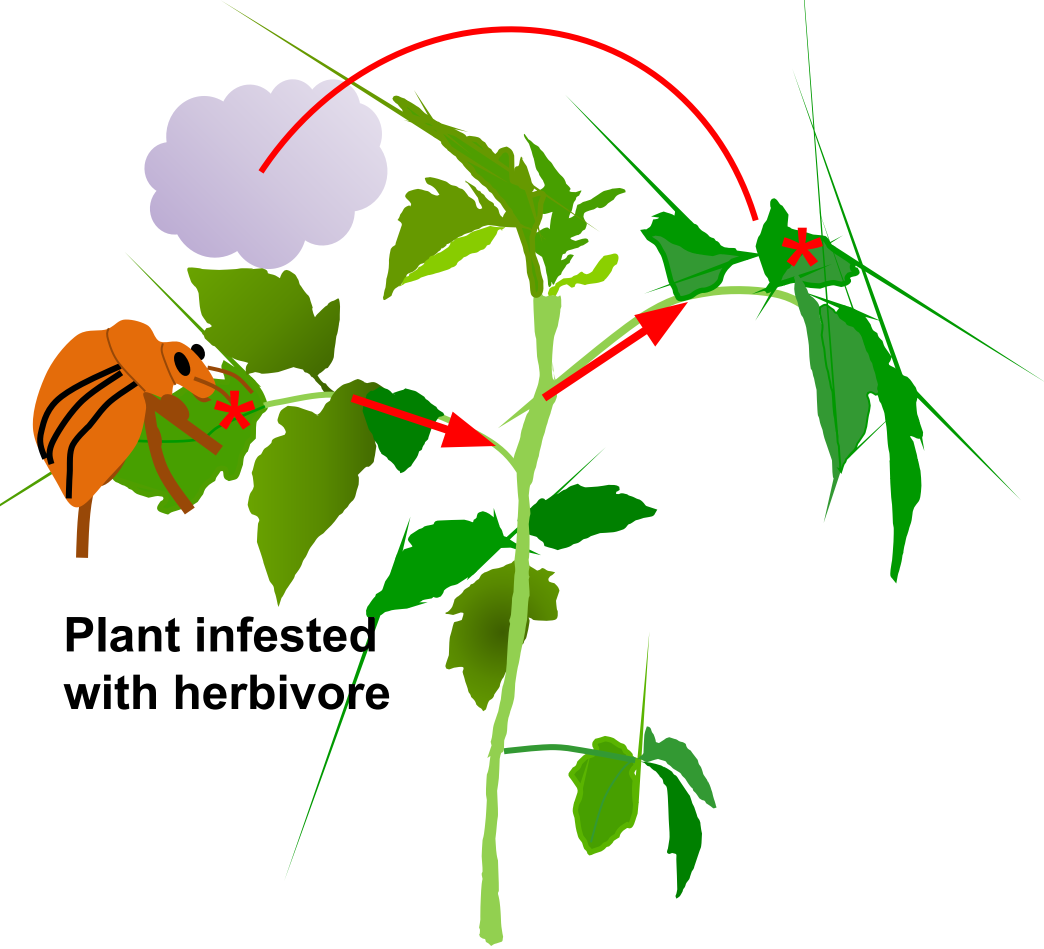
T. urticae and *T. evansi* together

The ***fitness*** of *T. urticae* ***increases*** in the presence of *T. evansi*

Some, but not all, spider mite species suppress or delay plant defenses

Photo: Jan van Arkel (IBED; University of Amsterdam)

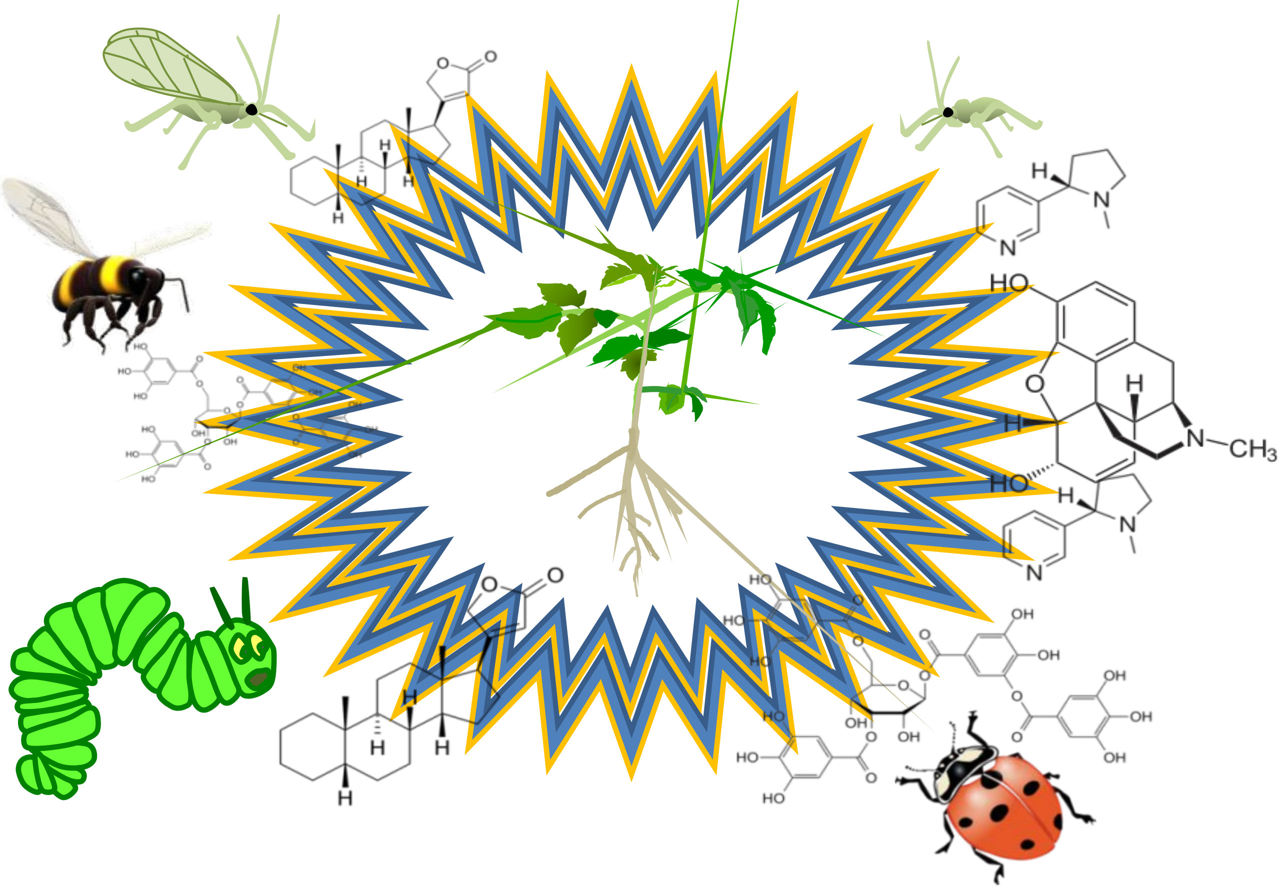
Summary: defenses are induced locally and some also systemically



Systemic signals are molecules that can move through vascular tissues and are related to jasmonate and salicylate. Also volatile hormones (ethylene) and possibly derivatives (methyl jasmonate and methyl salicylate) contribute to the systemic response

Green, T.R., and Ryan, C.A. (1972). Wound-induced proteinase inhibitor in plant leaves: A possible defense mechanism against insects. Science 175: 776-777.

Defensive chemicals and herbivore countermeasures



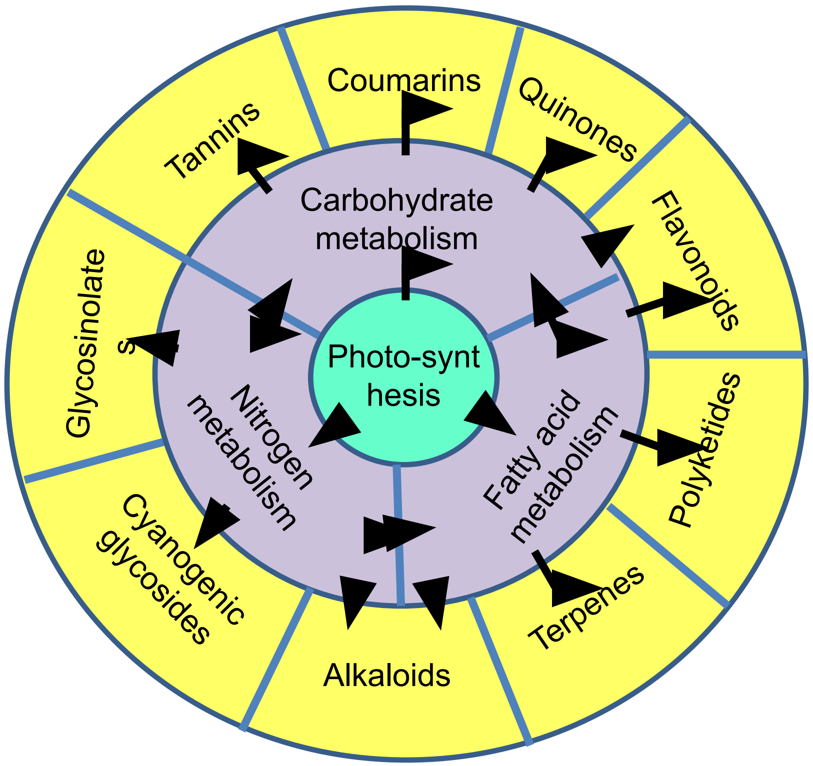
- Plants produce >100.000 compounds
- 80% of the known natural compounds have a botanical origin
- Many of these chemicals function in defense

The raison d'être of secondary plant substances "is to repel and attract insects" – Fraenkel 1959

Some defense compounds are “secondary metabolites”

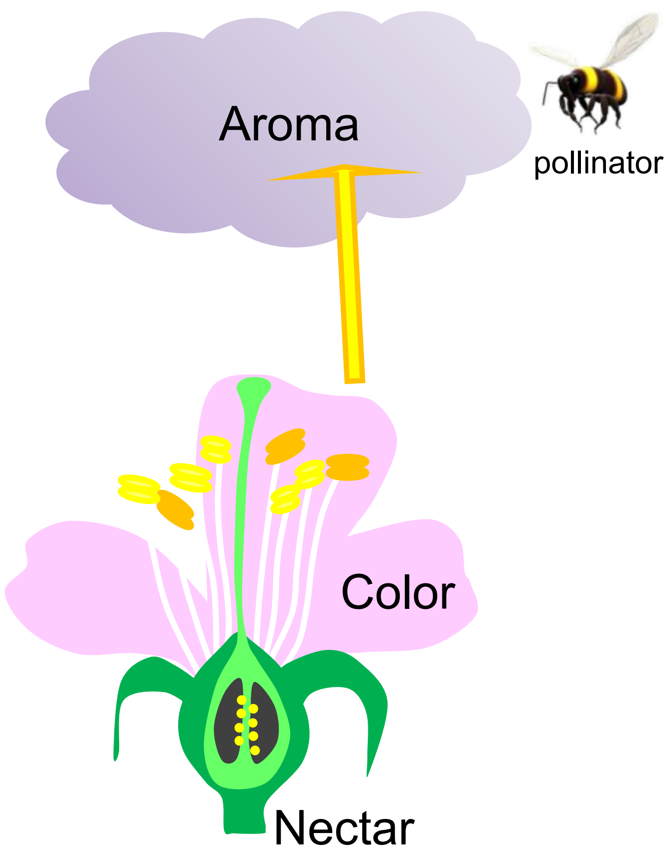
Primary metabolites: amino acids, sugars, nucleotides, lipids → found throughout the plant kingdom

Secondary metabolites: defense and attractant functions, phylogenetically restricted



Redrawn from Hartmann, T. (1996). Diversity and variability of plant secondary metabolism: a mechanistic view. Entomologia Experimentalis et Applicata 80: 177-188.

Some secondary compounds attract pollinators, predators or parasitoids



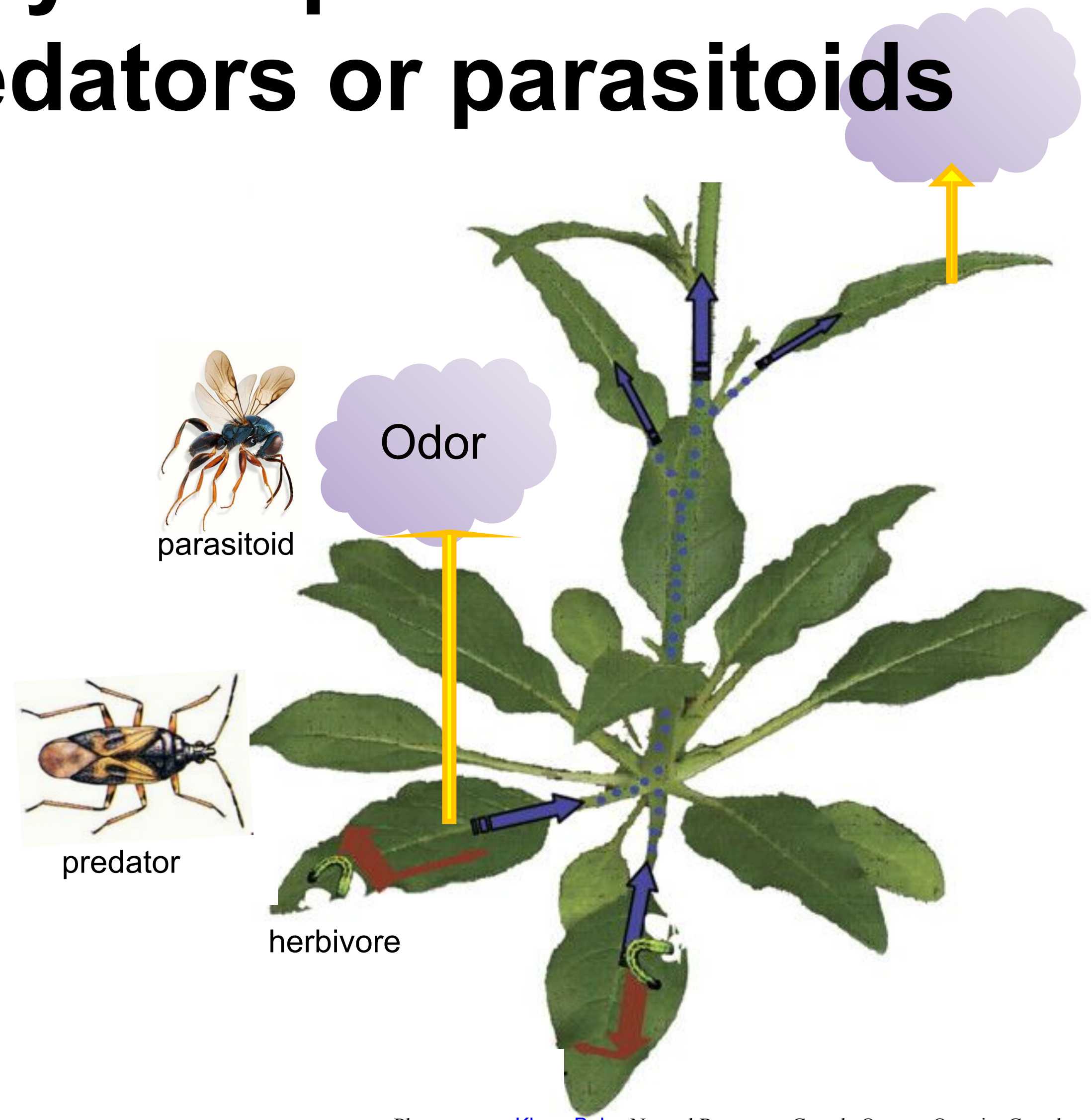
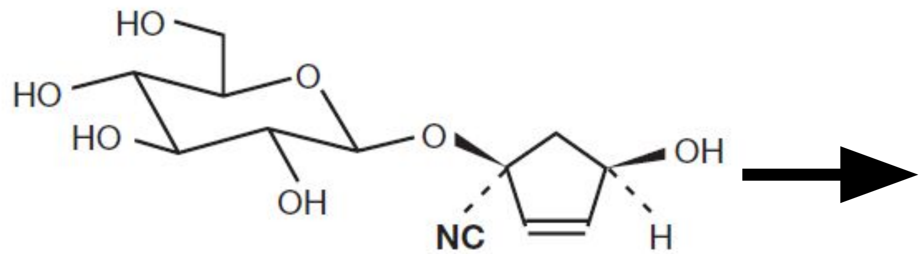


Photo source: [Klaus Bol](#)te, Natural Resources Canada Ottawa, Ontario, Canada

Other compounds are toxic, or can be converted to toxins, or are anti-nutritive

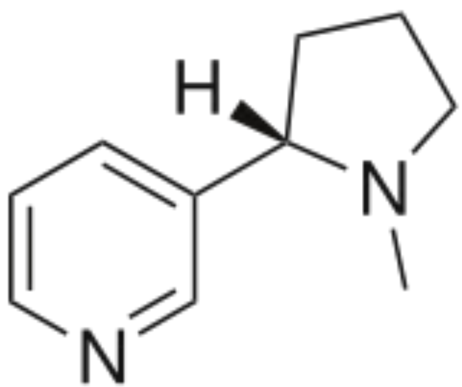
A cyanogenic glycoside that releases toxic cyanide

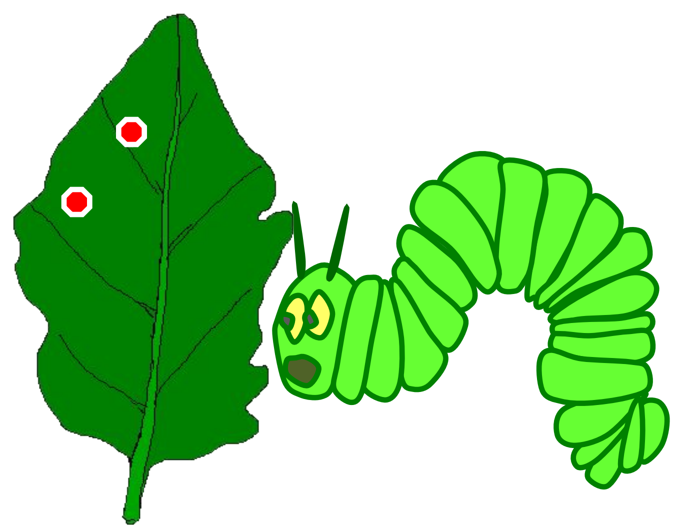


HC≡N

Cyanide

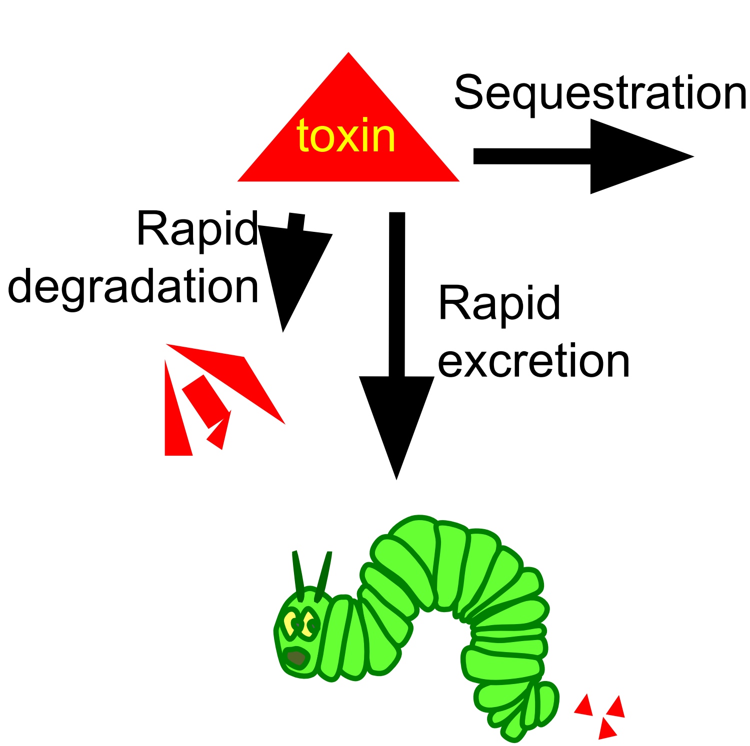
Nicotine, a toxin found in tobacco and its relatives





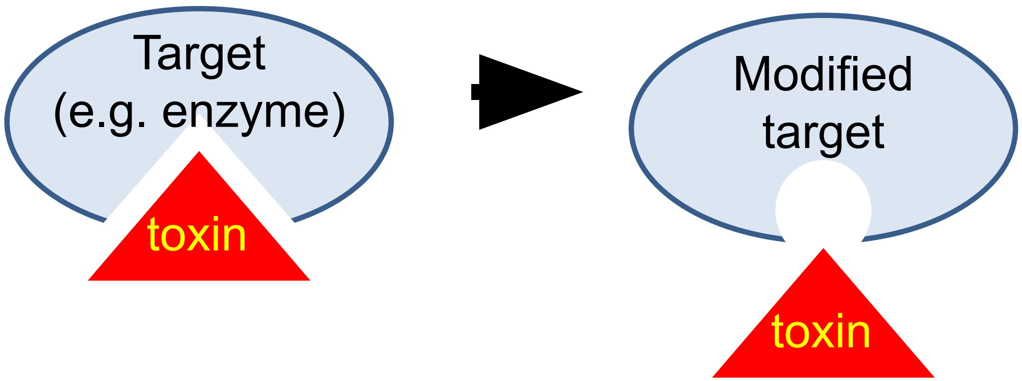
Anti-nutritives interfere with herbivores' digestion or assimilation of nutrients, impairing their growth, development and reproduction

Some herbivores have evolved tolerance to plant toxins



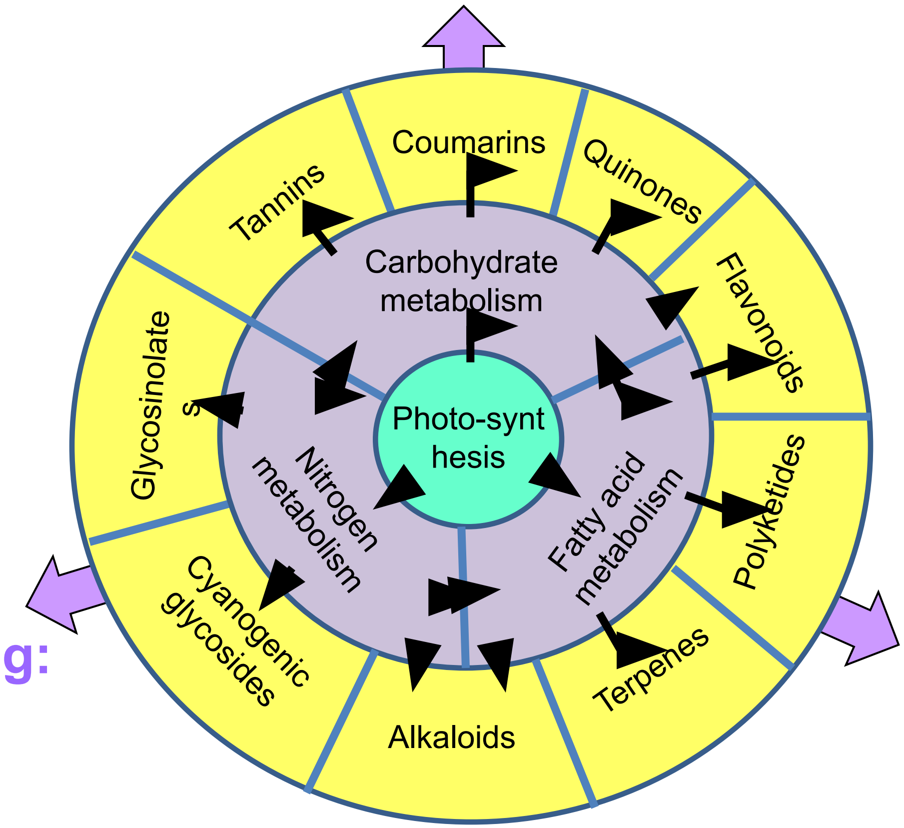
Herbivores can tolerate plant toxins through ***degradation***, ***excretion*** and ***sequestration*** (through chemical modification and storage in specialized glands).

In some cases the target enzyme has been modified to now be unaffected by the toxin



Defensive secondary metabolites can be roughly divided in three groups

Phenolic: e.g. Flavonoids; Salicylic acid; Lignins etc



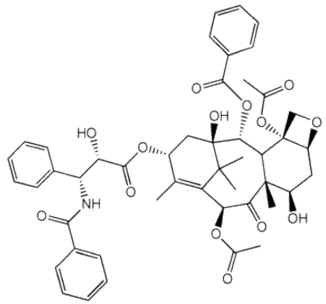
Nitrogen containing:
e.g. Alkaloids
Glucosinolates

Terpenoids:
e.g. Limonoids
Saponins
Pinene

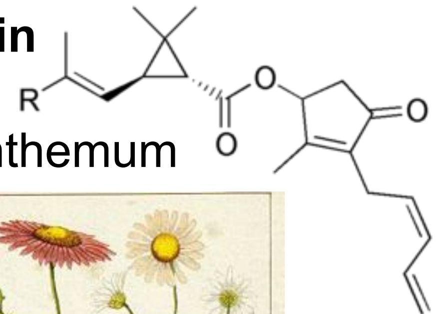
Redrawn from Hartmann, T. (1996). Diversity and variability of plant secondary metabolism: a mechanistic view. Entomologia Experimentalis et Applicata 80: 177-188.

Phenolics and terpenes include medicines, insecticides and irritants

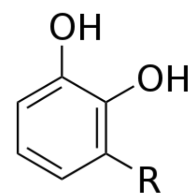
Taxol
From
Pacific
yew tree



Pyrethrin
From
Chrysanthemum



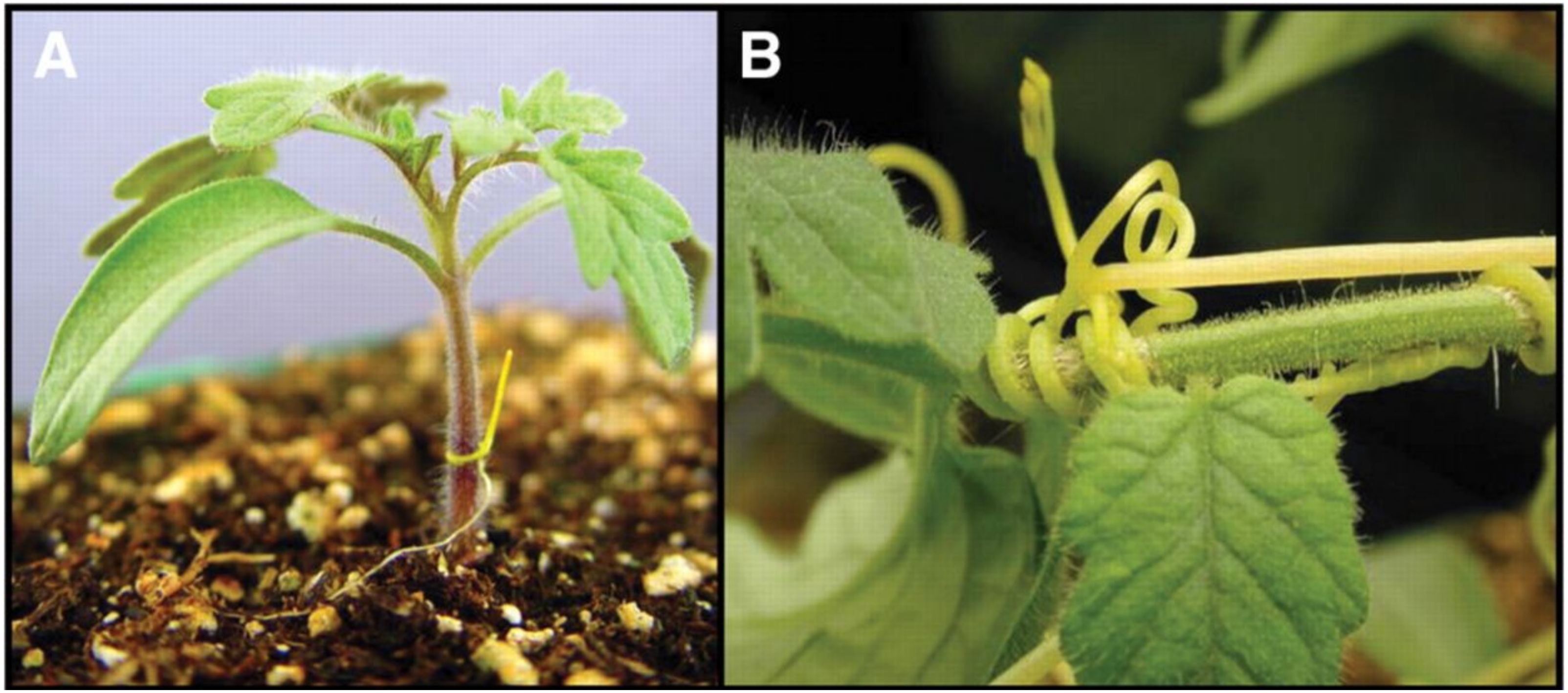
And at least 10,000 more, many uncharacterized…



Urushiol
From poison ivy

Photo credit: Dave Powell, USDA Forest Service, Bugwood.org

Parasitic plants also sense volatile terpenoids produced by hosts…

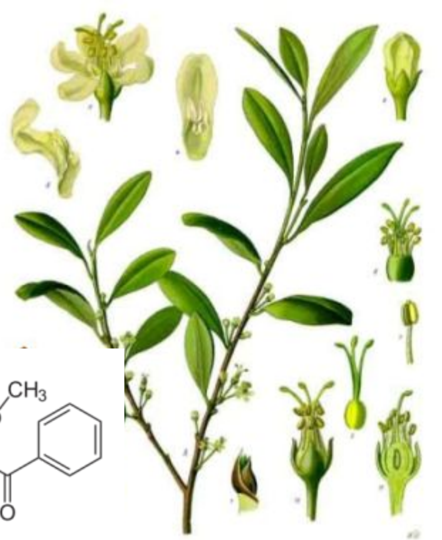


Cuscuta pentagona (dodder) grows towards a tomato plant, but shows the same response to volatiles collected from the tomato

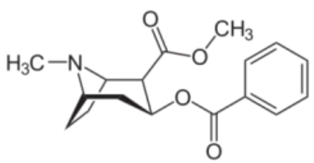
Runyon, J.B., Mescher, M.C. and De Moraes, C.M. (2006). Volatile chemical cues guide host location and host selection by parasitic plants. Science. 313: 1964-1967 reprinted by permission from AAAS.

Alkaloids contain nitrogen and include stimulants and narcotics

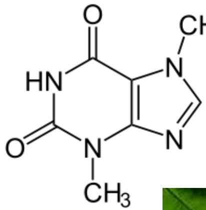
Coca



Cocaine



Theobromine

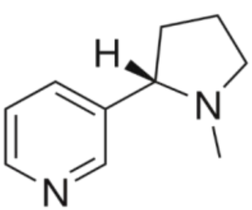


Cacao

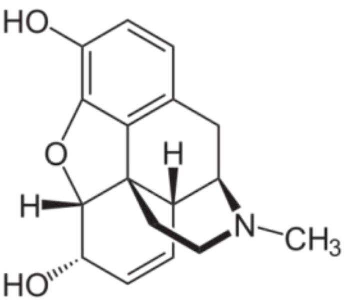
Coffee

caffeine

Nicotine



Tobacco



Morphine

Opium Poppy

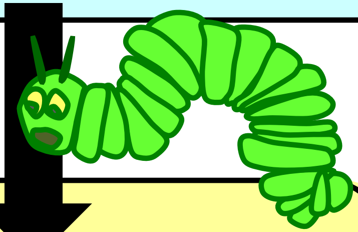
Glucosinolates are typical for the Cabbage (Brassicaceae) Family

Myrosinases and glucosinolates are stored in separate plant cells…

Glucosinolates

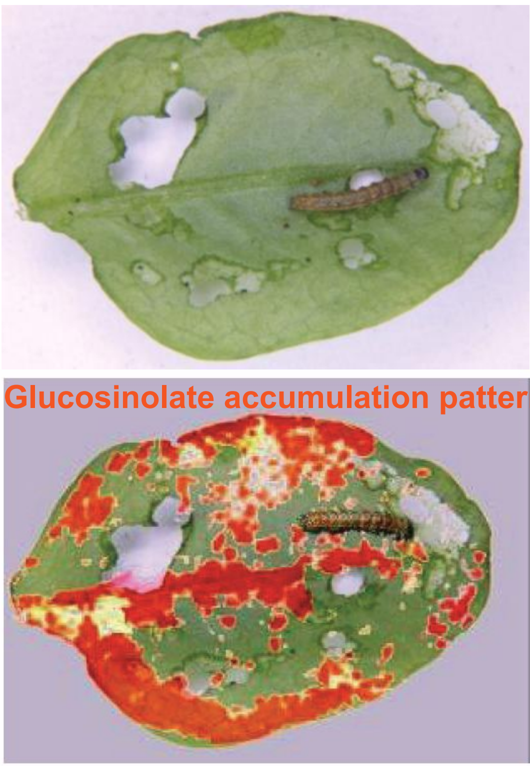
Myrosinases

…..until the cells are broken and mixed, for example by herbivore damage



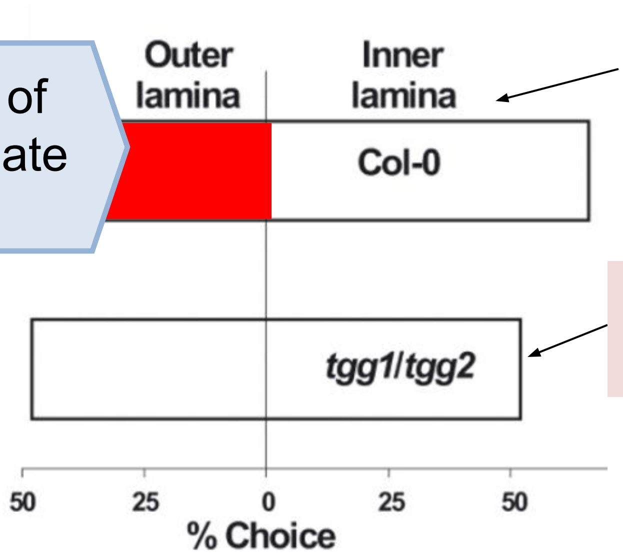
Various toxic and distasteful breakdown products

Helicoverpa armigera (the cotton bollworm) avoids tissues with high concentrations of glucosinolates



Glucosinolates accumulate in midveins and the outer parts of the leaf blade. Bollworms selectively eat the middle of the blade on normal plants but not on mutant plants that that do not accumulate glucosinolates.

Less herbivory of high-glucosinolate tissue



Col-0 = Normal glucosinolate producing ecotype

Tgg1/2 = Glucosinolate deficient mutant

Shroff, R., Vergara, F., Muck, A., Svatoš, A. and Gershenzon, J. (2008). Nonuniform distribution of glucosinolates in *Arabidopsis thaliana* leaves has important consequences for plant defense. Proc. Natl. Acad. Sci. USA 105: 6196-6201.

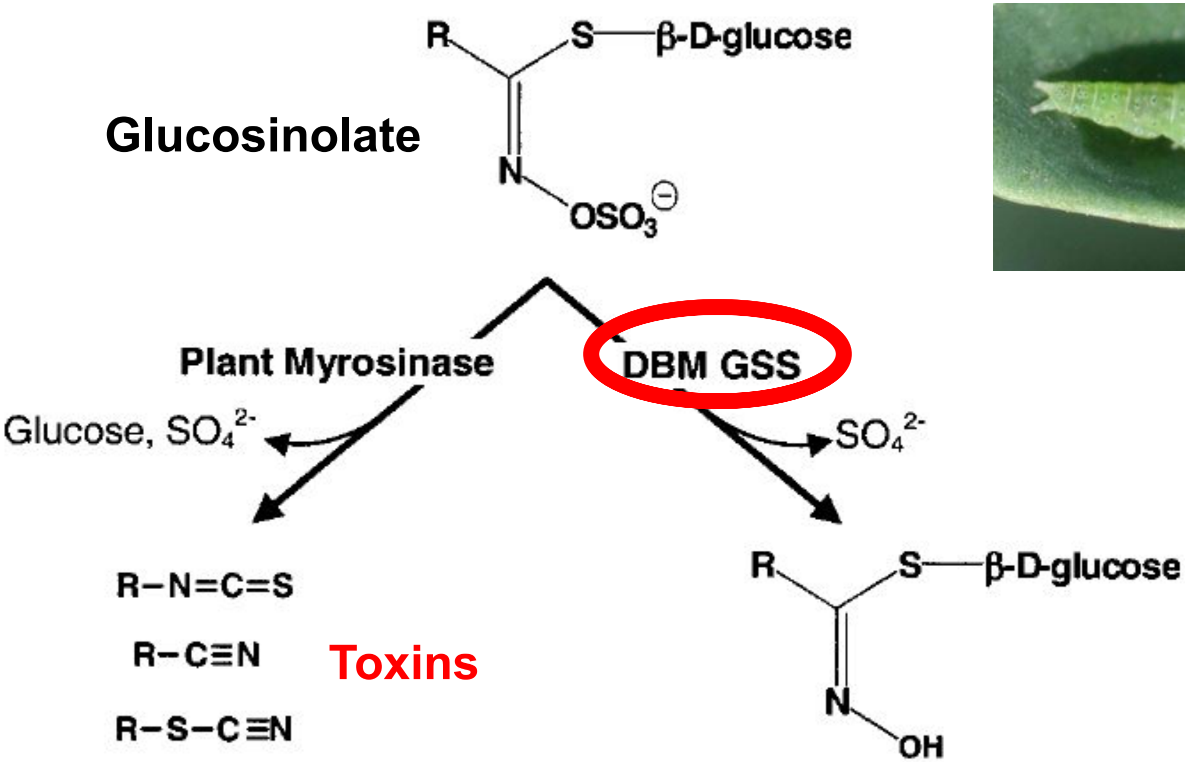
Most herbivores avoid Brassicaceae but some can eat it

Green peach aphid (*Myzus persicae*) feeding on cabbage

Cabbage looper (*Trichoplusia ni*) feeding on crucifers, damage, and adult form

Image credits (all Bugwood.org): Whitney CranshawImage credits (all Bugwood.org): Whitney Cranshaw, Colorado State University; David CappaertImage credits (all Bugwood.org): Whitney Cranshaw, Colorado State University; David Cappaert, Michigan State University; Keith NaylorImage credits (all Bugwood.org): Whitney Cranshaw, Colorado State University; David Cappaert, Michigan State University; Keith Naylor; David CappaertImage credits (all Bugwood.org): Whitney Cranshaw, Colorado State University; David Cappaert, Michigan State University; Keith Naylor; David Cappaert, Michigan State University; David JonesImage credits (all Bugwood.org): Whitney Cranshaw, Colorado State University; David Cappaert, Michigan State University; Keith Naylor; David Cappaert, Michigan State University; David Jones, University of Georgia; David Riley, University of Georgia.

The diamondback moth has an enzyme that eliminates glucosinolates

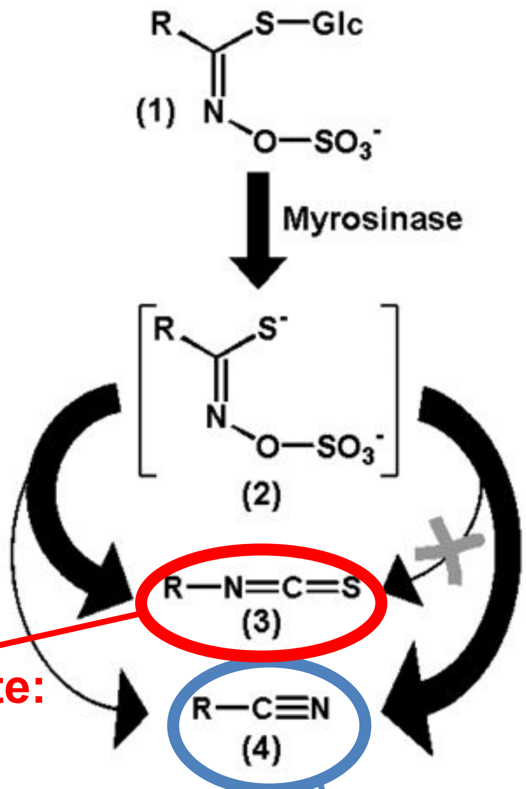


Plutella xylostella

The diamondback moth sulfatase (DBM GSS) enzyme removes the glucosinolate's sulfate group such that myrosinase does not recognize the glucosinolate anymore

Ratzka, A., Vogel, H., Kliebenstein, D.J., Mitchell-Olds, T. and Kroymann, J. (2002). Disarming the mustard oil bomb. Proc. Natl. Acad. Sci. USA. 99: 11223-11228Ratzka, A., Vogel, H., Kliebenstein, D.J., Mitchell-Olds, T. and Kroymann, J. (2002). Disarming the mustard oil bomb. Proc. Natl. Acad. Sci. USA. 99: 11223-11228; Russ Ottens, University of Georgia, Bugwood.org

Cabbage white butterfly larvae convert glucosinolates into less-toxic products



NSP – nitrile-specifying protein

Standard product isothiocyanate: more toxic

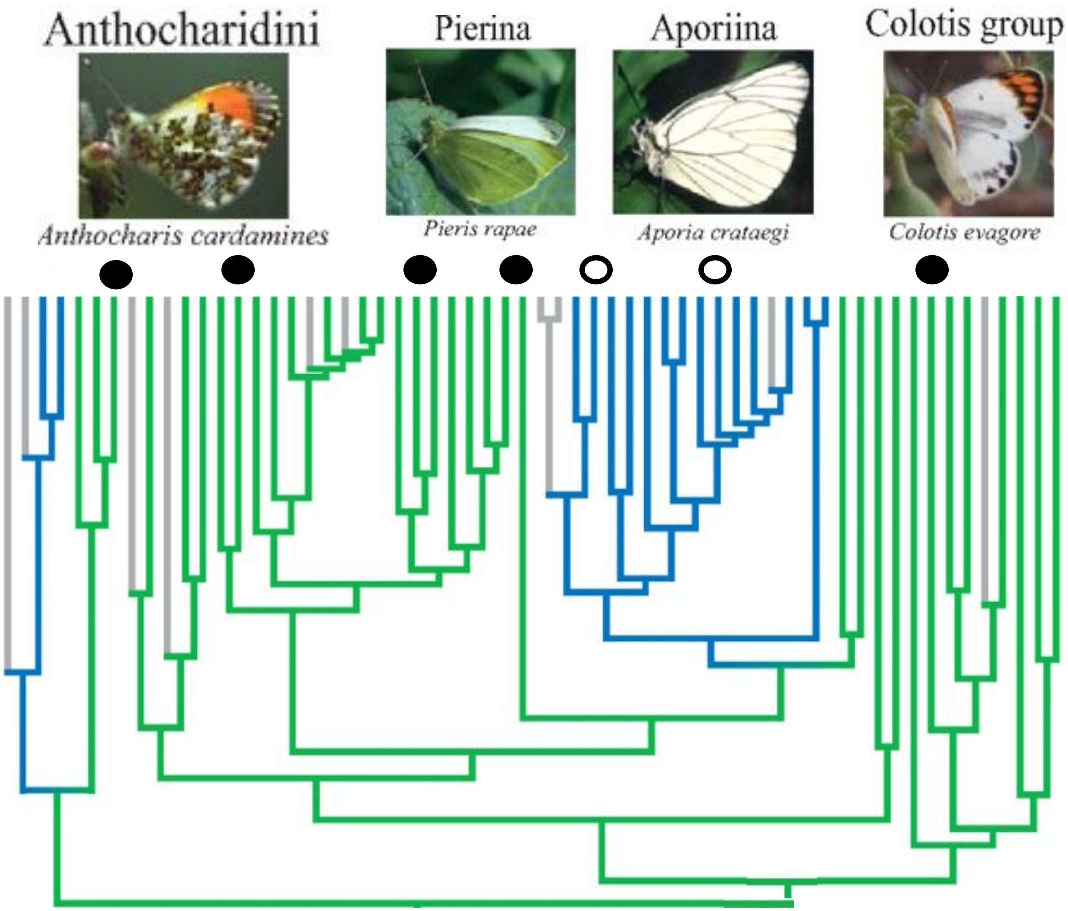
Nitrile: less toxic

It sequesters the glucosinolates as protection against predators

Adult form

Wittstock, U., Agerbirk, N., Stauber, E.J., Olsen, C.E., Hippler, M., Mitchell-Olds, T., Gershenzon, J., and Vogel, H. (2004). Successful herbivore attack due to metabolic diversion of a plant chemical defense. Proc. Natl. Acad. Sci. USA 101: 4859-4864Wittstock, U., Agerbirk, N., Stauber, E.J., Olsen, C.E., Hippler, M., Mitchell-Olds, T., Gershenzon, J., and Vogel, H. (2004). Successful herbivore attack due to metabolic diversion of a plant chemical defense. Proc. Natl. Acad. Sci. USA 101: 4859-4864; David Cappaert, Michigan State University, Bugwood.org

NSP production has been lost in some related butterflies

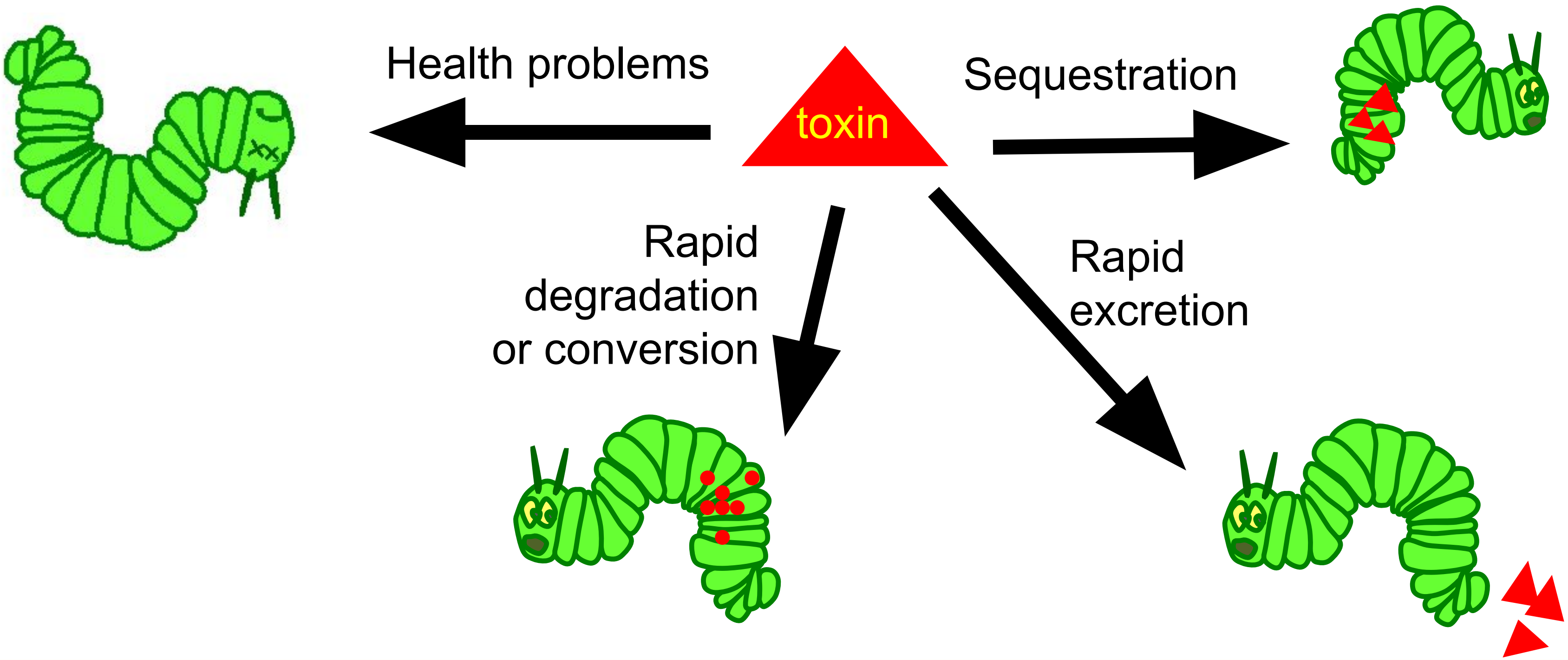


Glucosinolate feeding has been lost in some lineages (blue bars). Black dots indicates NSP, white dots indicates absence of NSP

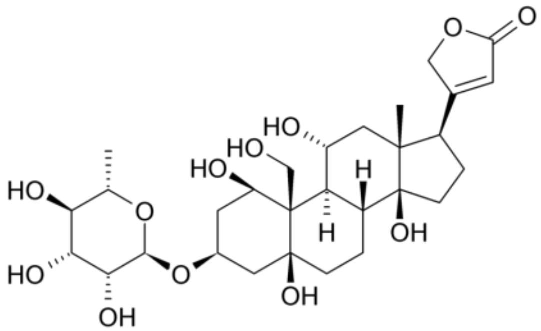
Origin of NSP detoxification scheme ~ 80 million years ago

Wheat, C.W., Vogel, H., Wittstock, U., Braby, M.F., Underwood, D., and Mitchell-Olds, T. (2007). The genetic basis of a plant–insect coevolutionary key innovation. Proceedings of the National Academy of Sciences 104: 20427-20431.

Summary: ingested secondary defense compounds can be toxic but sometimes herbivores have adapted



Case study: Milkweeds and monarch butterflies



Milkweed (*Asclepias syriaca*) produces latex that contains a toxic alkaloid ouabain

Ouabain binds to the Na^+, K^+ ATPase and interferes with its function

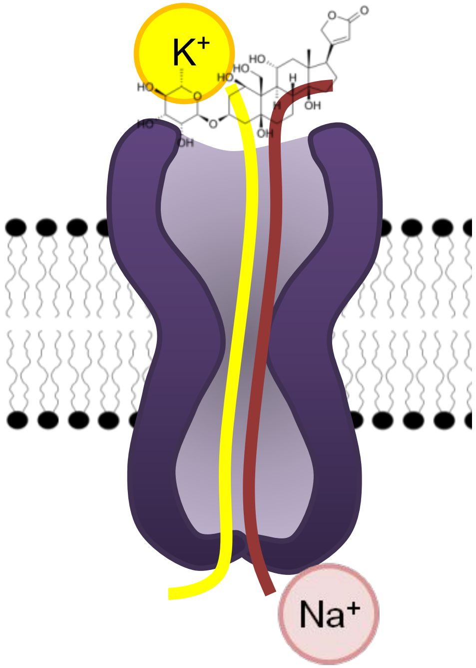
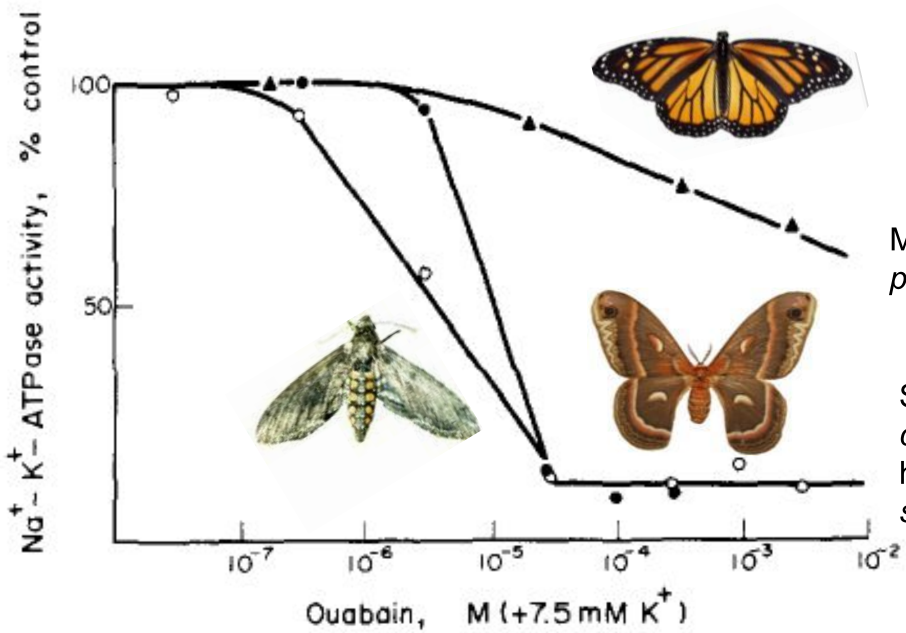


Photo credits: Kenneth Dwain HarrelsonPhoto credits: Kenneth Dwain Harrelson, Steven Katovich, USDA Forest Service, Bugwood.org

The Na$^+$, K$^+$ ATPase from monarch butterfly larvae is insensitive to ouabain



Monarch *Danaus plexippus* (insensitive)

Silkmoth *Hyalophora cecropia,* Tobacco hornworm *Manduca sexta* (sensitive)

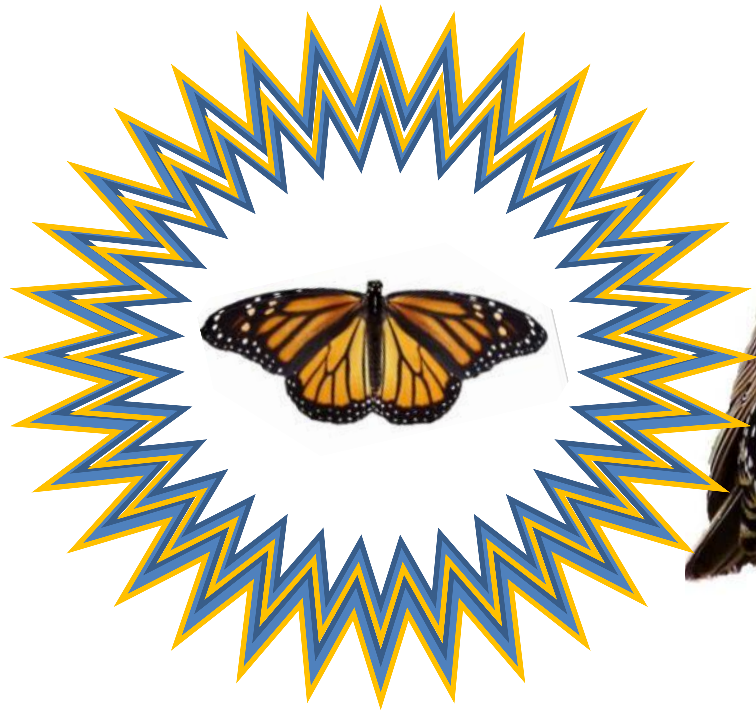
ASN → HIS

An amino acid substitution in the Na$^+$, K$^+$ ATPase confers ouabain insensitivity to monarchs

Reprinted from Vaughan, G.L., and Jungreis, A.M. (1977). Insensitivity of lepidopteran tissues to ouabain: Physiological mechanisms for protection from cardiac glycosides. J. Insect Physiol. 23: 585-589, with permission from Elsevier.

Monarch butterflies avoid predation through ouabain accumulation

Some butterflies mimic the monarch's colors to avoid predation



Viceroy butterfly – nontoxic but protected by mimicry

Some predators have become tolerant of the monarch's ouabain

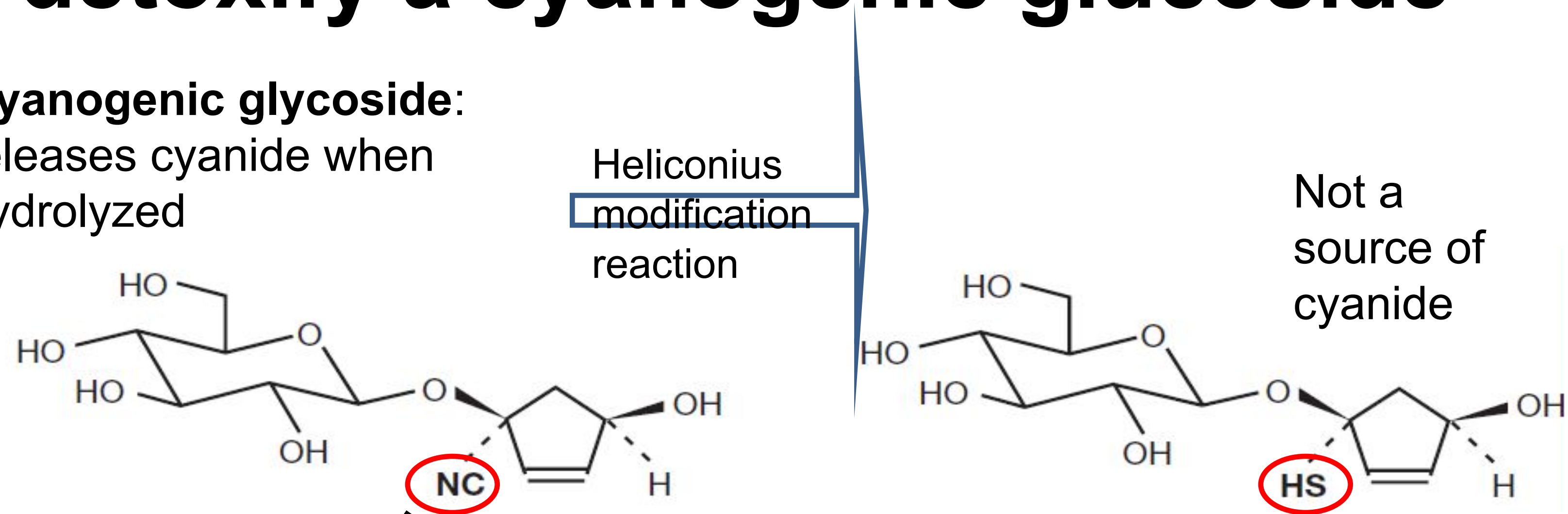
Case study: *Heliconian* butterflies and passion flowers

South American *Heliconian* butterflies were collected and studied as early as the 17th century, and provided the basis for ideas about mimicry

Maria Sybilla Merian 1705; William M. CieslaMaria Sybilla Merian 1705; William M. Ciesla, Patricia M. Ciesla, Forest Health Management International, Bugwood.org

Some Heliconius butterflies can detoxify a cyanogenic glucoside

Cyanogenic glycoside: releases cyanide when hydrolyzed

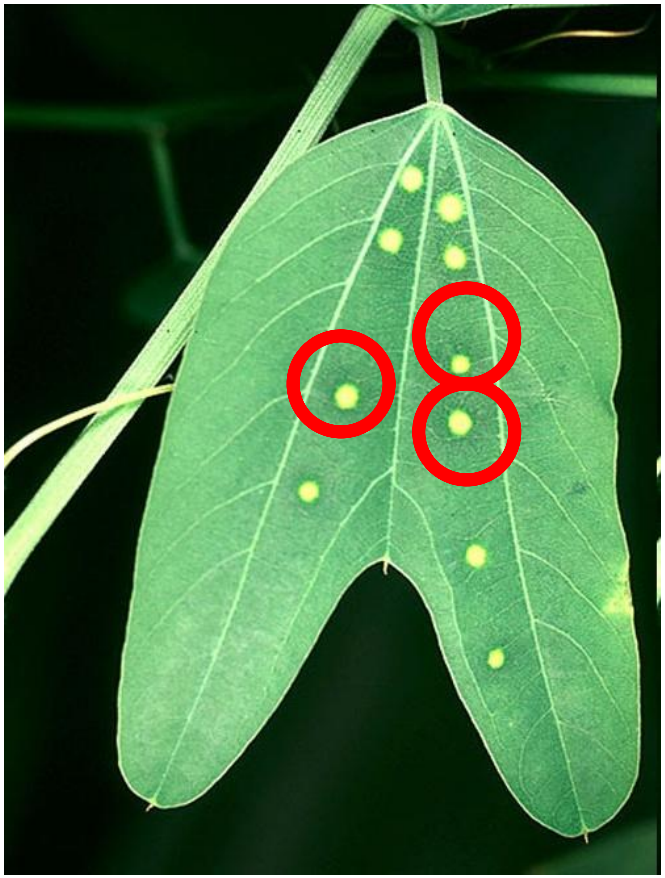


HC≡N

Toxic cyanide

The larvae of more than 60 species of *Heliconius* butterflies are specialized feeders of *Passiflora* and are tolerant of their various secondary metabolites

Passionflower plants make structures that resemble butterfly eggs



Female butterflies prefer to lay their eggs on an unoccupied leaf to protect their young from cannibals and hence avoid leaves with ‘fake’ eggs

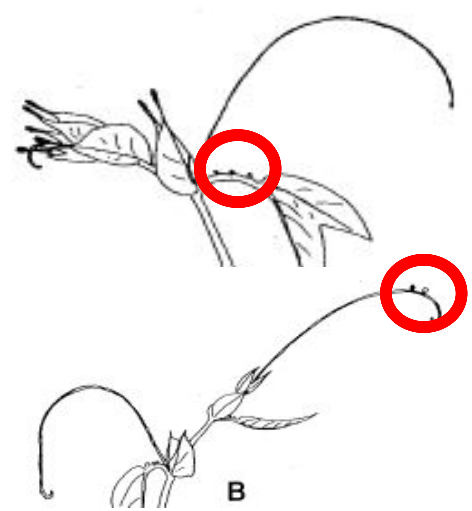
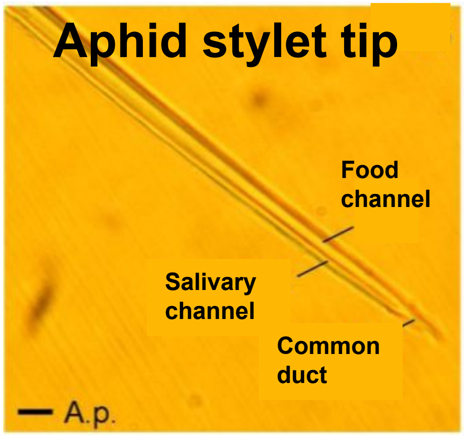
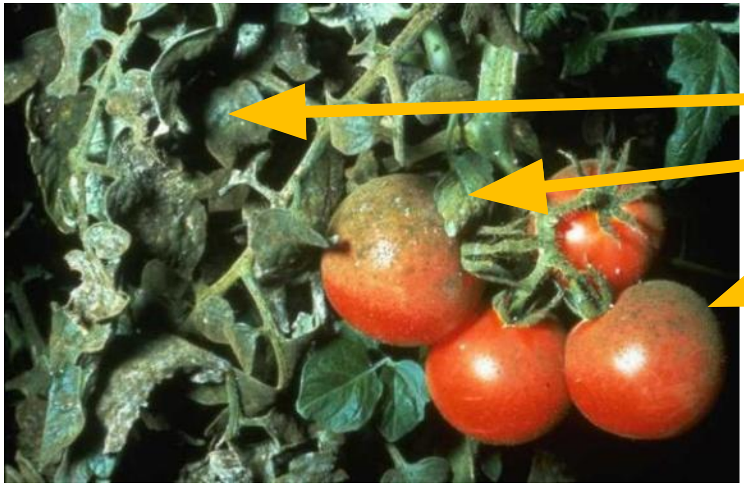


Photo copyright Missouri Botanic GaPhoto copyright Missouri Botanic Garden; Williams, K.S. and Gilbert, L.E. (1981). Insects as selective agents on plant vegetative morphology: Egg mimicry reduces egg laying by butterflies. Science. 212: 467-469Photo copyright Missouri Botanic Garden; Williams, K.S. and Gilbert, L.E. (1981). Insects as selective agents on plant vegetative morphology: Egg mimicry reduces egg laying by butterflies. Science. 212: 467-469 reprinted with permission from AAAS; Jerry A. Payne, USDA Agricultural Research Service, Bugwood.org

Case study: Aphids and whiteflies, phloem-feeding insects



Phloem-feeding insects are major agricultural pests. They insert stylets into phloem, depleting the host plant of nutrients and spreading disease.

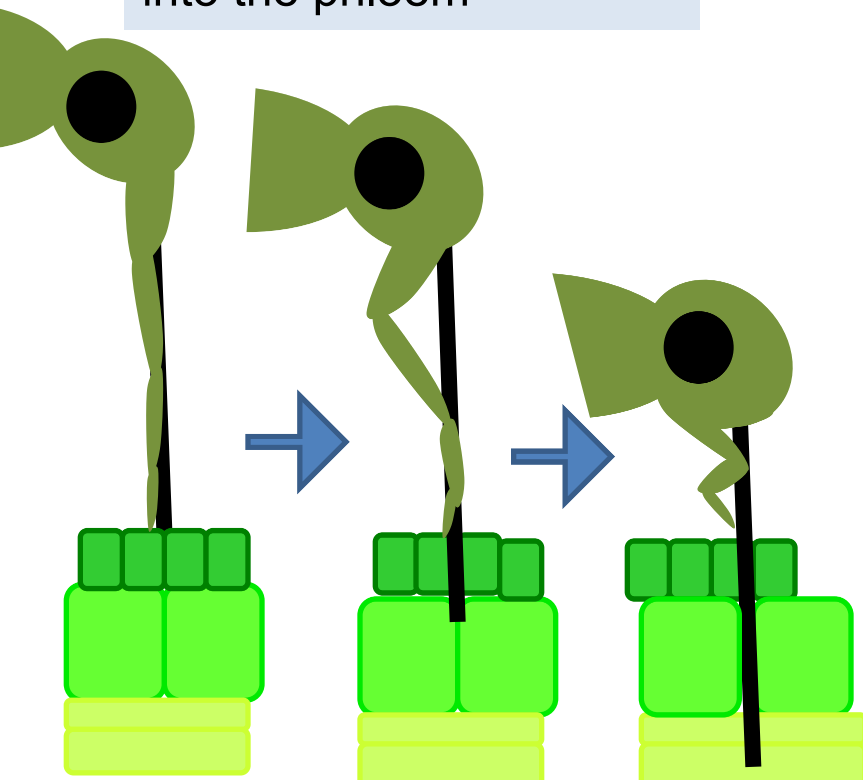


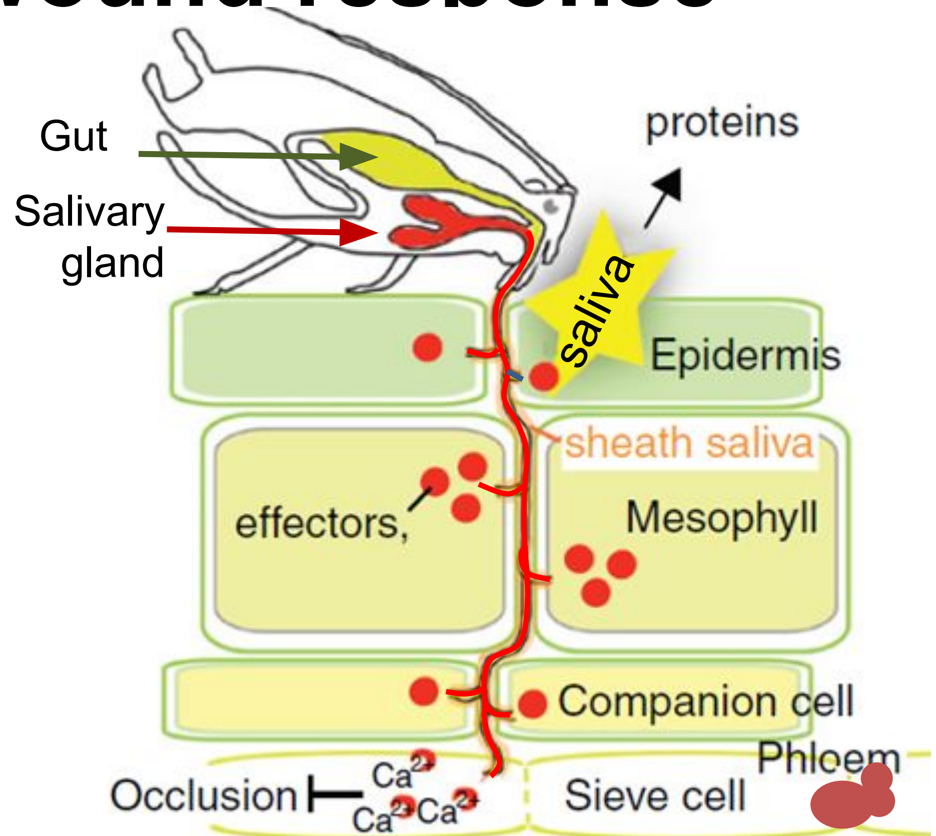
Downy mildew growing on honey dew

Uzest, M., Gargani, D., Drucker, M., Hébrard, E., Garzo, E., Candresse, T., Fereres, A., and Blanc, S. (2007). A protein key to plant virus transmission at the tip of the insect vector stylet. Proceedings of the National Academy of Sciences 104: 17959-17964.

Aphid saliva interferes with the normal phloem-sealing wound response

Aphids insert a thin stylet into the phloem





Normally plants respond to such wounding by plugging the sieve element, but aphids suppress this

Reprinted from Hogenhout, S.A., and Bos, J.I.B. (2011) Effector proteins that modulate plant–insect interactions. Curr. Opin. Plant Biol. 14: 422-428 with permission from Elsevier.

The green pea aphid genome has been sequenced

Aphids can reproduce clonally as well as sexually. Shown here is a female giving birth to live female clones

Acyrthosiphon pisum

The International Aphid Genomics Consortium 2010 Genome Sequence of the Pea Aphid *Acyrthosiphon pisum*. PLoS Biol 8(2): e1000313.

Plants and herbivores - summary

Constitutive defenses like poisonous or sticky trichomes deter most herbivores

- Synthesis of anti-nutritives and toxins
- Wound healing

- Herbivory elicits the induction of additional defense responses
- Some herbivores have evolved counter-measures to deal with plant defenses

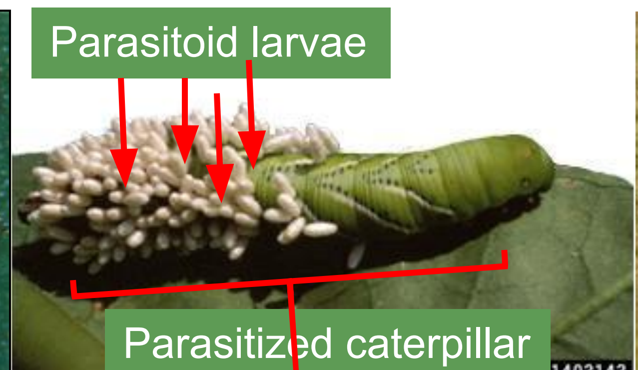
Scott BauerScott Bauer, USDA Agricultural Research Service, Bugwood.org; Mike Speed, University of Liverpool

Alliance #1 – Plants and Carnivores or Parasitoids

Assassin bug

Hyposoter ebeninus attacking a *Pieris rapae* larva

Spider mite and predatory mite (and their eggs)



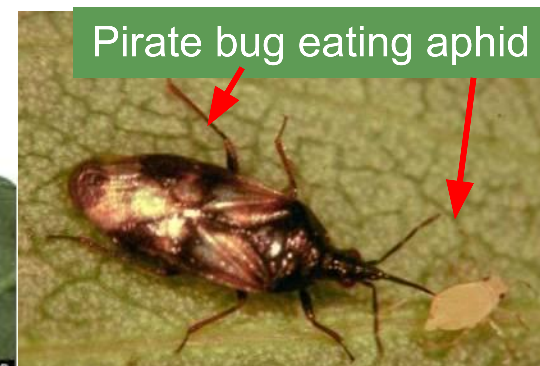
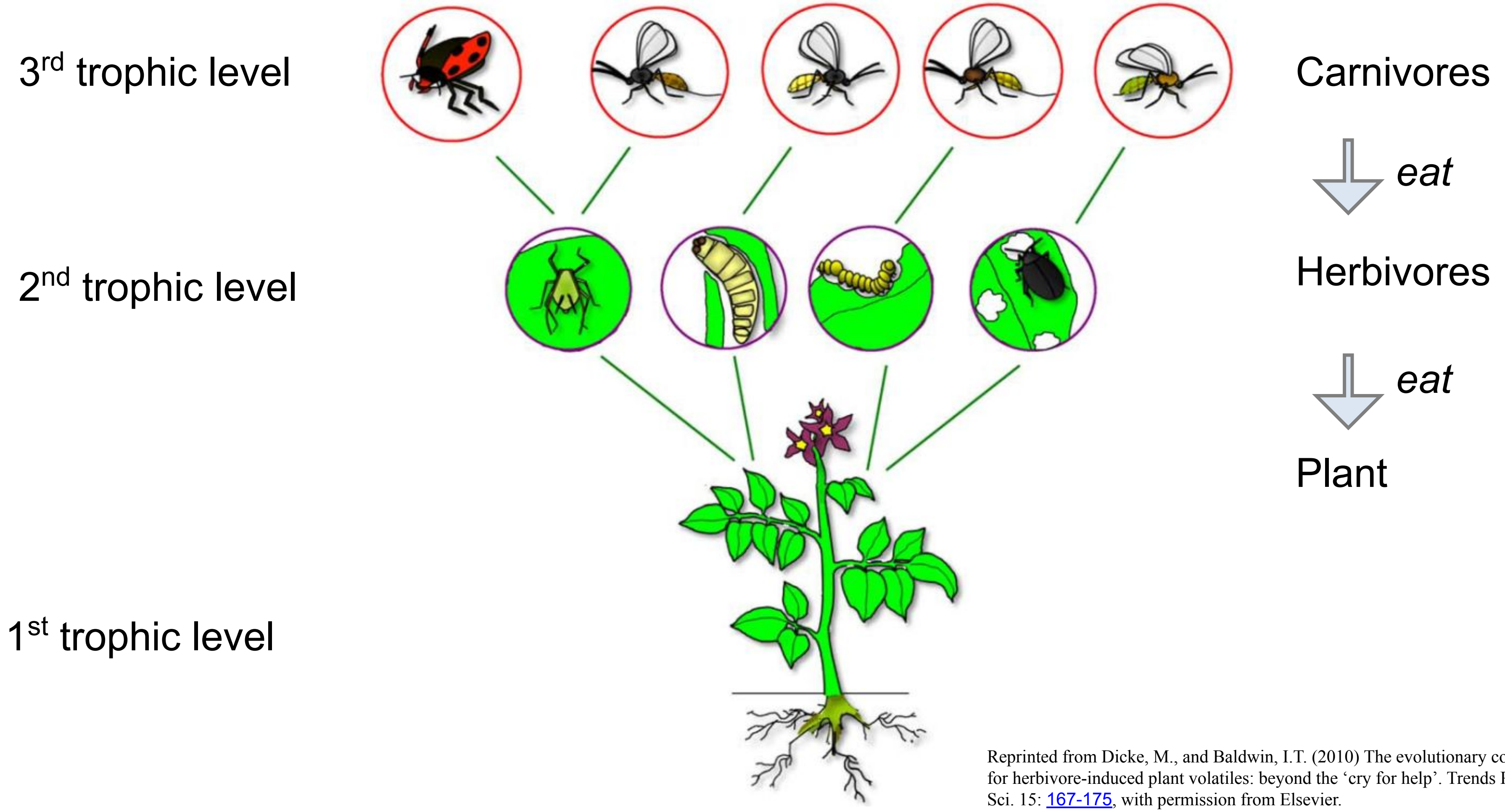


Photo: T. Bukovinszky / www.bugsinthepicture.comwww.bugsinthepicture.com; Thailand IPM; R.J. Reynolds Tobacco Company Slide SetR.J. Reynolds Tobacco Company Slide Set , Bradley HigbeeR.J. Reynolds Tobacco Company Slide Set , Bradley Higbee, Paramount Farming; Bugworld.org; Scott Bauer, USDA

Plants betray herbivores to their natural enemies via volatile signals

Photo credit: Ted Turlings

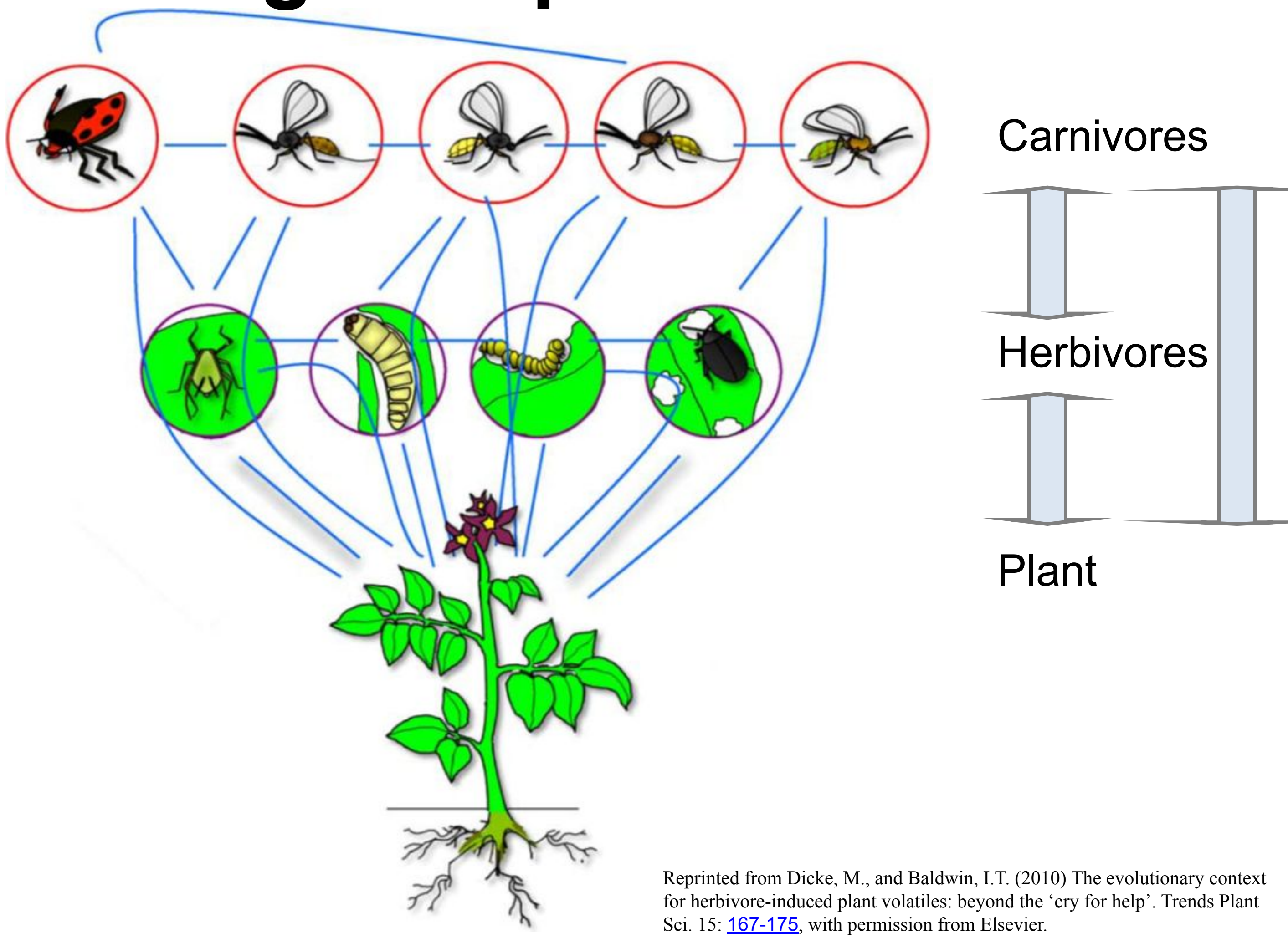
Tritrophic interactions involve three food levels



Reprinted from Dicke, M., and Baldwin, I.T. (2010) The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. Trends Plant Sci. 15: 167-175, with permission from Elsevier.

Chemical information moves between and amongst trophic levels

Herbivore-induced plant volatiles can attract or repel carnivores and other herbivores. Other plants may also perceive this information

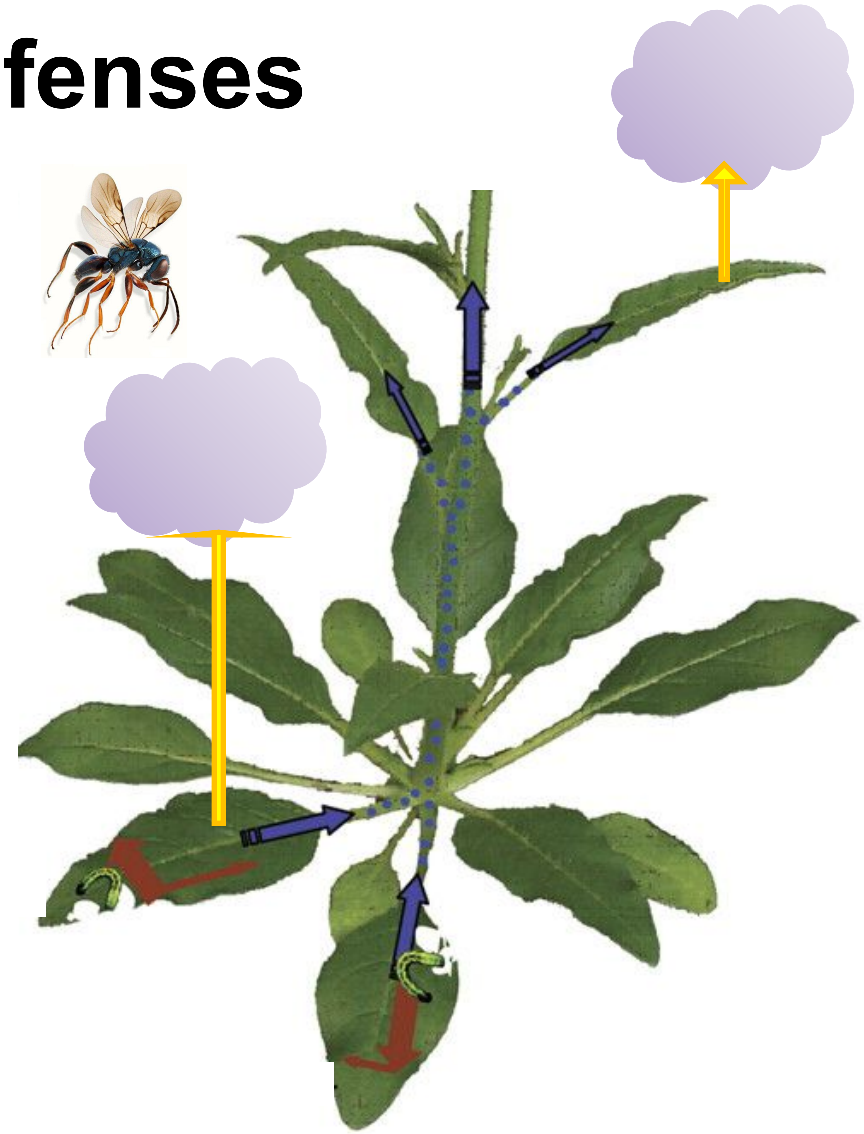


Reprinted from Dicke, M., and Baldwin, I.T. (2010) The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. Trends Plant Sci. 15: [167-175](), with permission from Elsevier.

Volatiles contribute to induced indirect defenses

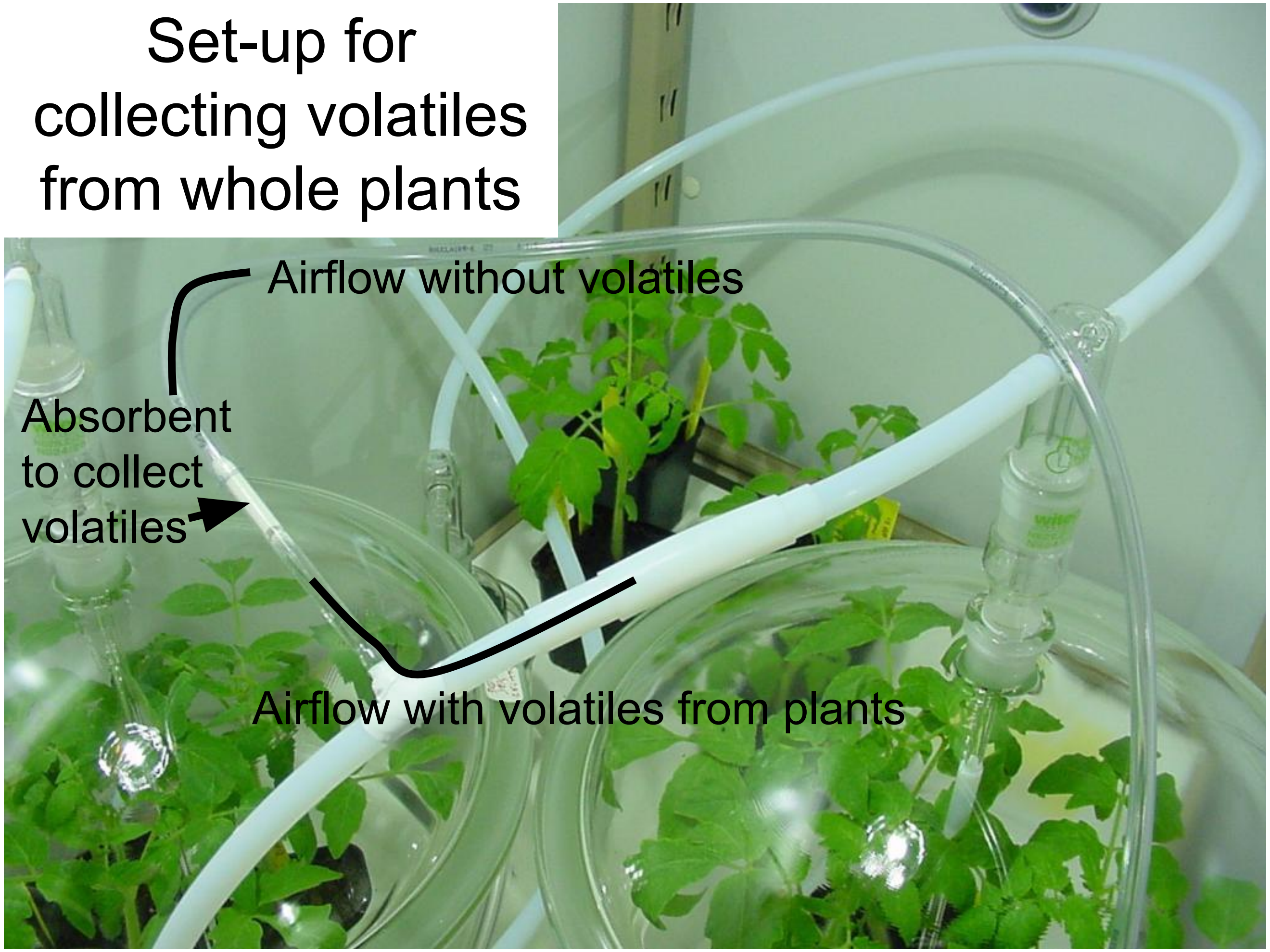
Most natural enemies of arthropods use a combination of visual and olfactory cues to track down their prey or host

When plants facilitate such prey-finding by natural enemies, for example via the release of herbivore-induced odors, we call this *induced indirect defense*



Induced organic volatiles contribute to indirect defense responses

Set-up for collecting volatiles from whole plants



Plants produce many volatile compounds – some of these are **herbivore-induced plant volatiles** that contribute to the establishment of indirect defenses.

The arbitrary air volume surrounding a plant we call the plant's "head space".

Photo: Merijn R. Kant

Induced volatiles: qualifying and quantifying plant volatiles

Gas chromatography mass spectrometry (GC-MS)

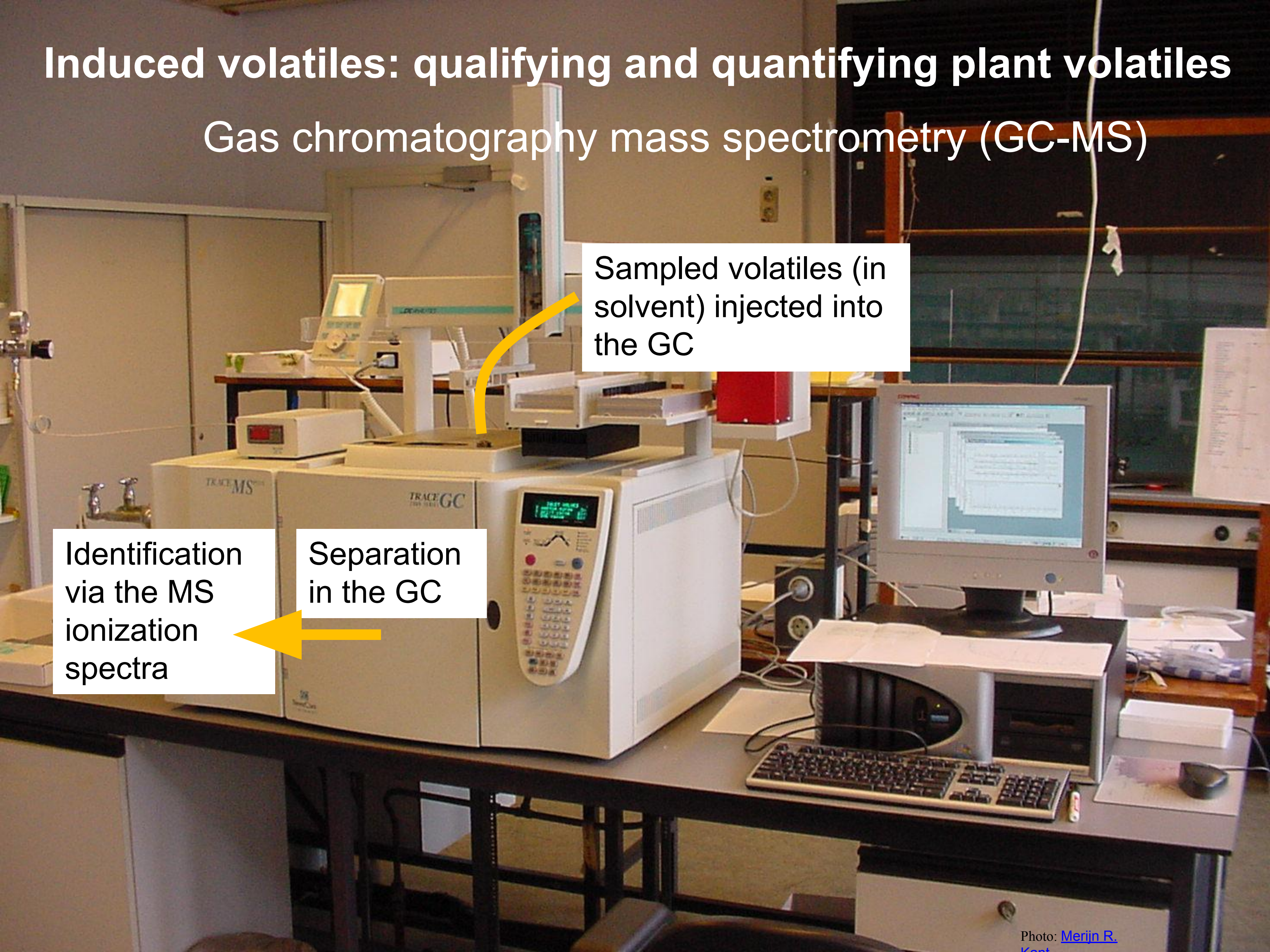
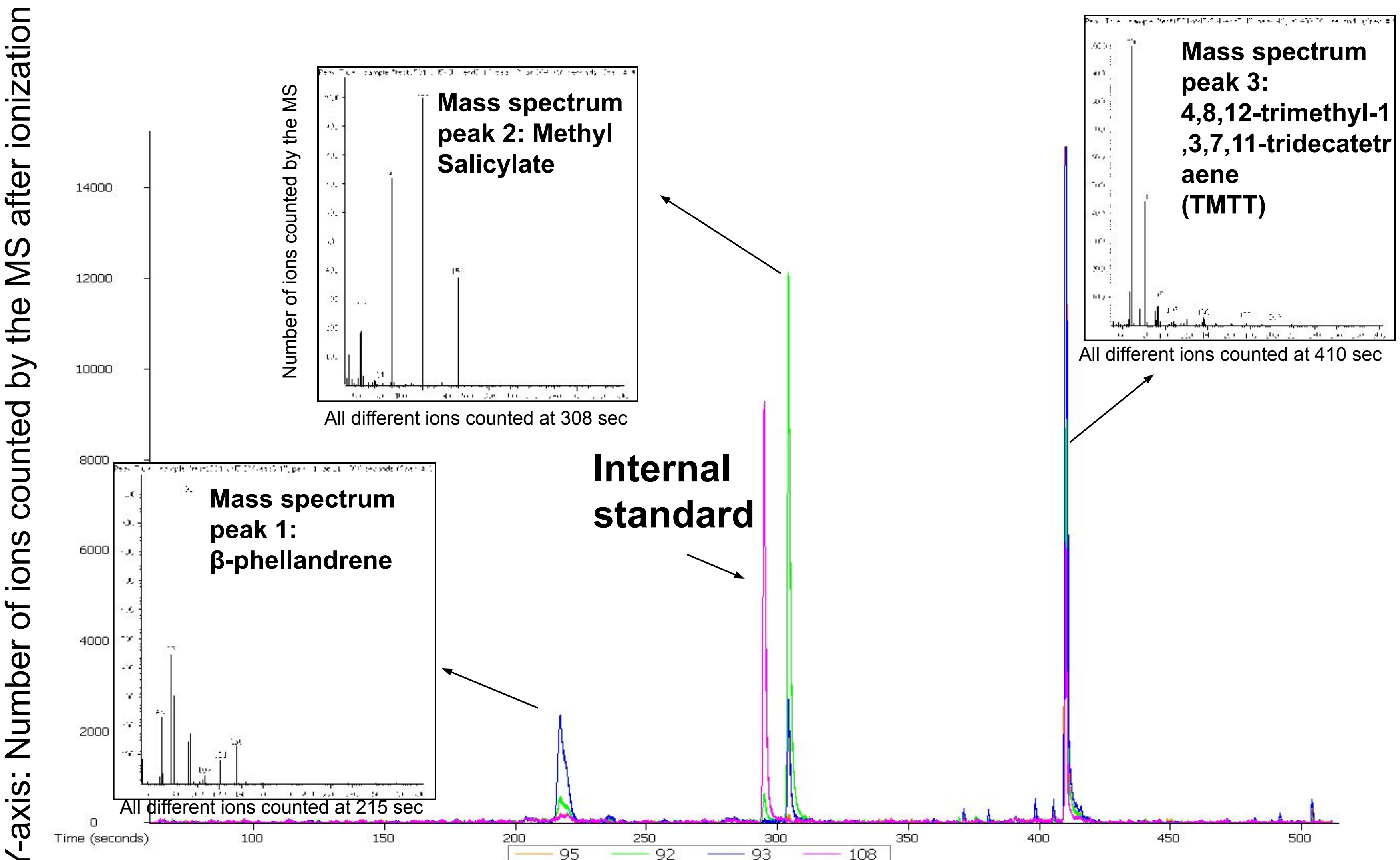


Photo: Merijn R.

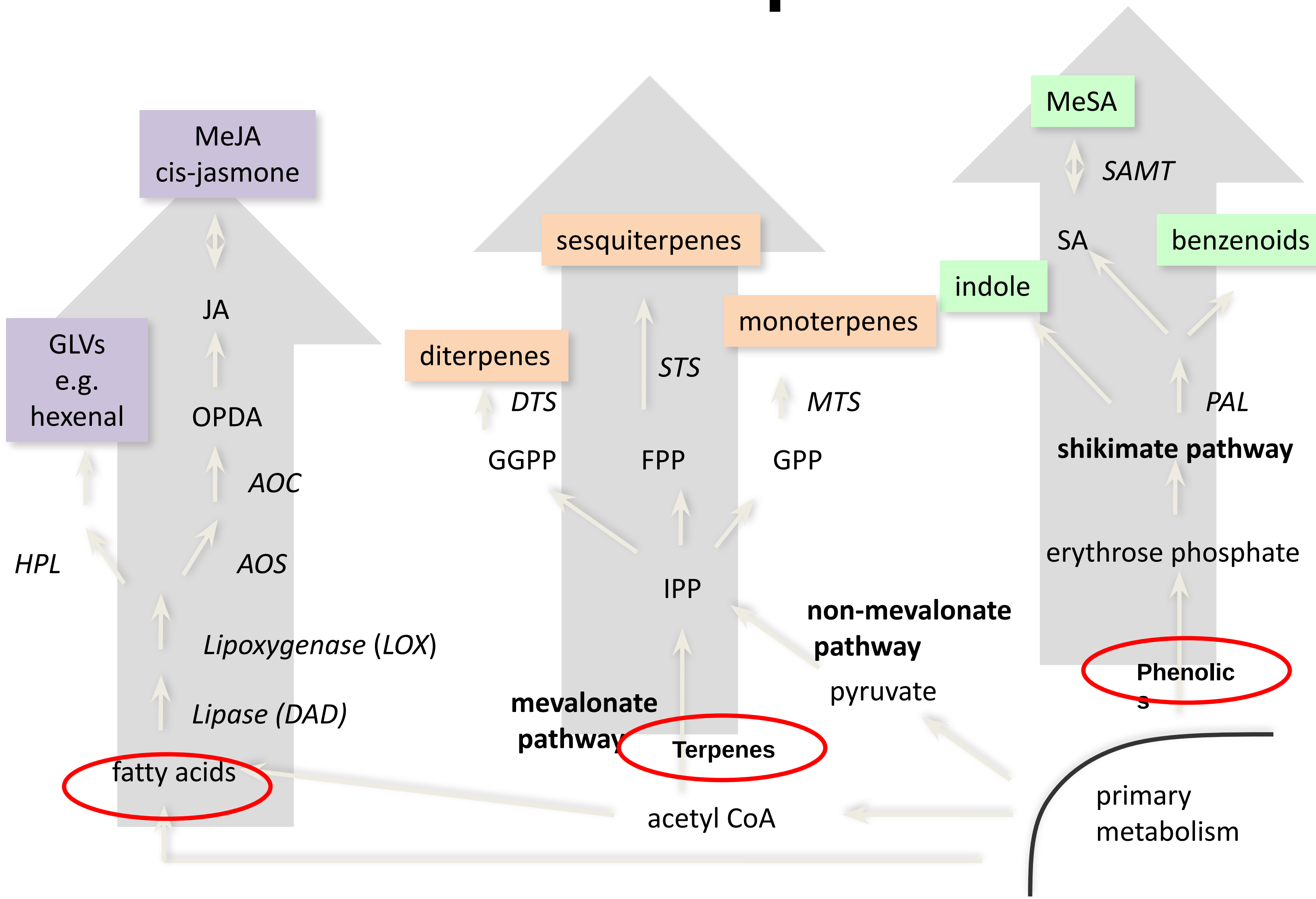
Infested plant head-space chromatogram



X-axis: Time it took each molecule to reach the end of the GC

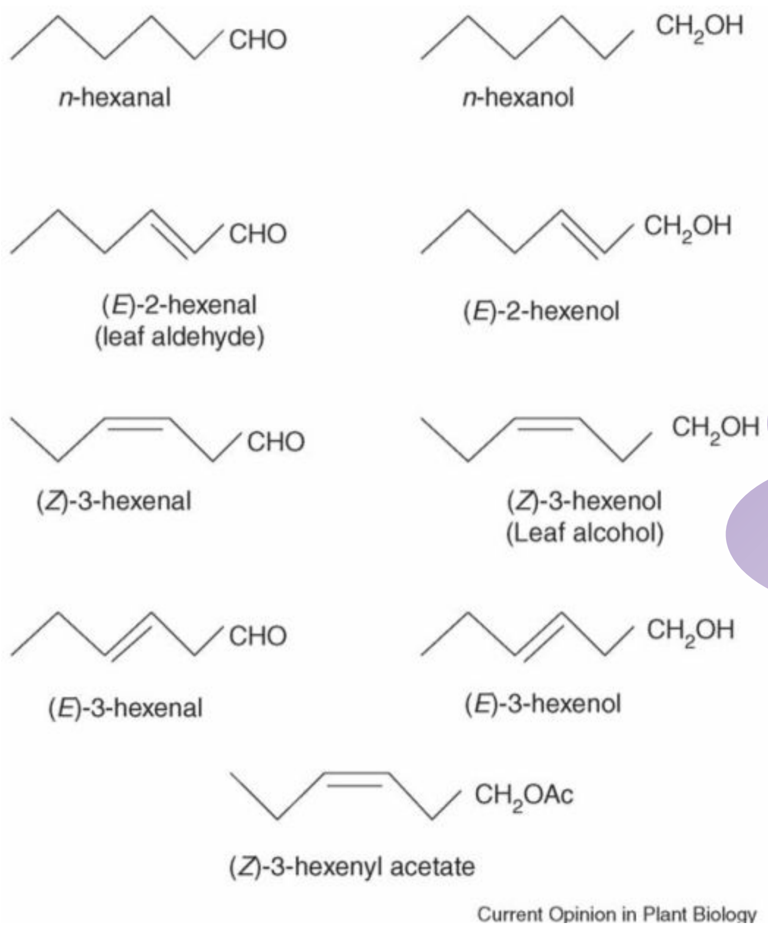
Image: [Merijn R. Kant]

Herbivore-induced plant volatiles

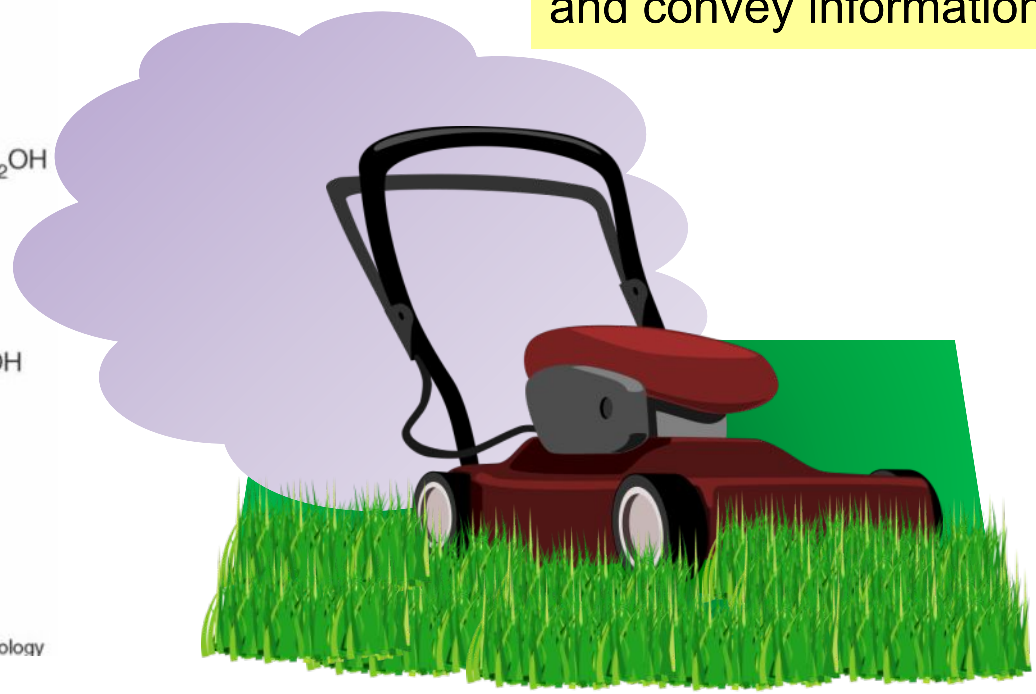


Kant, M.R., Bleeker, P.M., Van Wijk, M., Schuurink., R.C., Haring, M.A. (2009). Plant volatiles in defence. Adv. Bot. Res. 51: 613-666.

Green leaf volatiles are rapidly released from wounded tissue

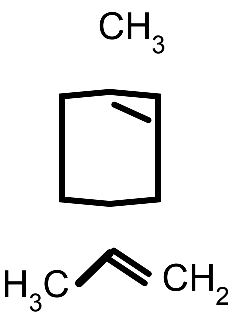


Green leaf volatiles (GLV) are released from wounded tissues (they are the “cut grass” smell) and convey information.

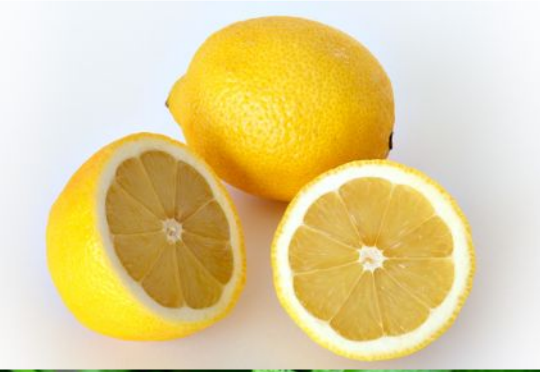


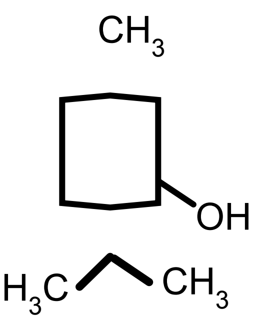
Reprinted from Matsui, K. (2006). Green leaf volatiles: hydroperoxide lyase pathway of oxylipin metabolism. Curr. Opin. Plant Biol. 9: 274-280, with permission from Elsevier.

Terpenoids are common plant compounds: when induced they often attract predatory arthropods



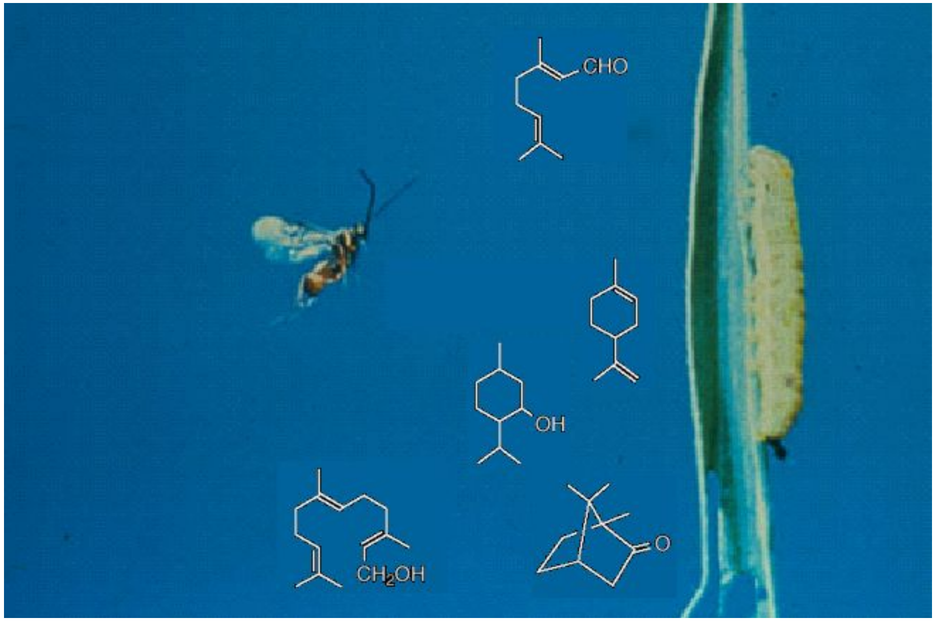
limonene





menthol

Constitutive terpenes



Herbivore induced terpenes

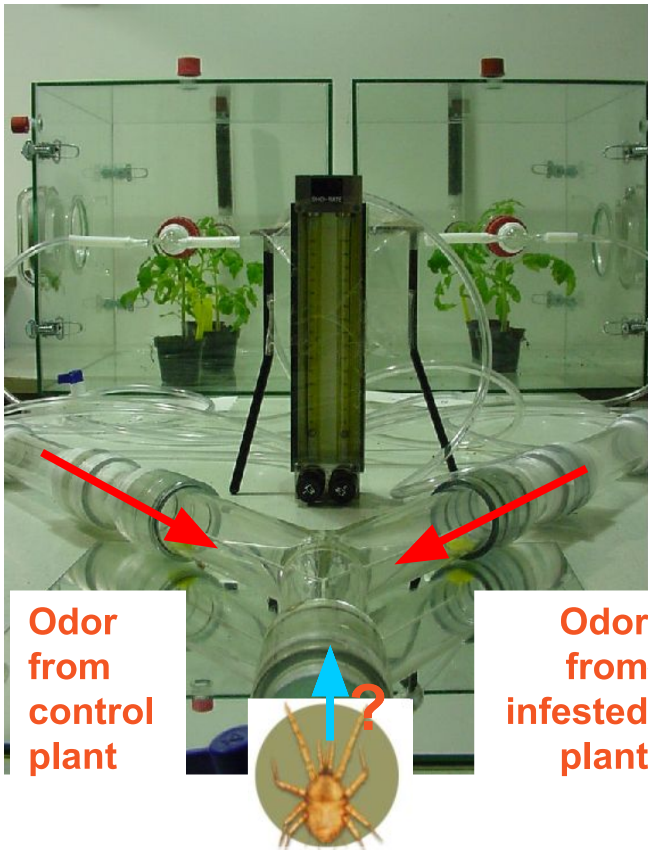
Photo credit: [Ted Turlings]()

Spider mite populations grow rapidly and destroy plants: their blind natural enemy uses plant odors to find them

Tetranychus urticae attacked by its natural enemy, the predatory mite *Phytoseiulus persimilis*

Photo credits: Bill Bumgarner

Quantifying volatile effects on arthropod foraging behaviour – the olfactometer



Hungry predator that has to choose

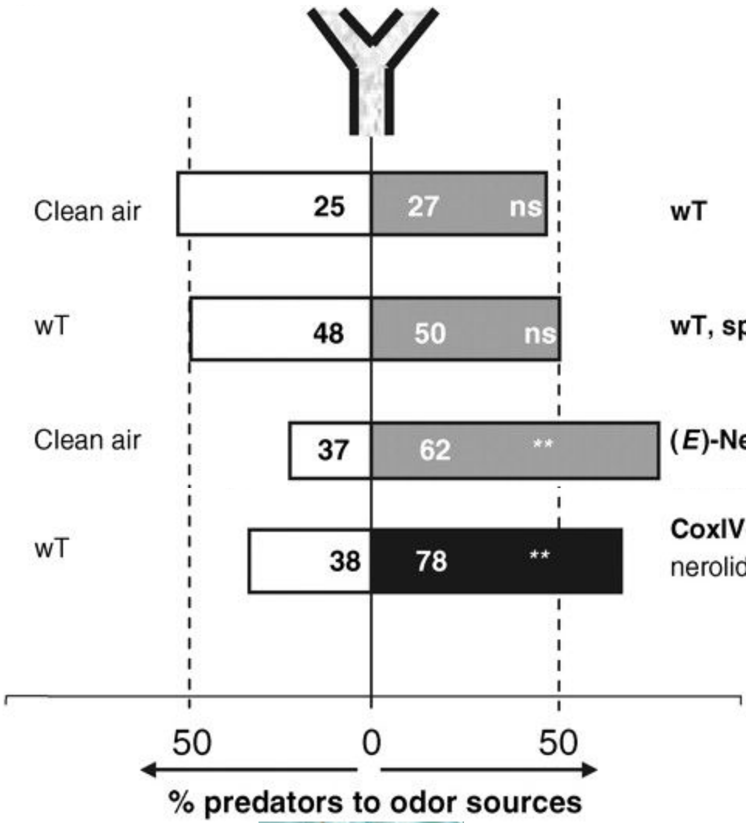
As an example, predatory mites chose volatiles collected from leaves invested with herbivorous mites 3x as often as from control leaves

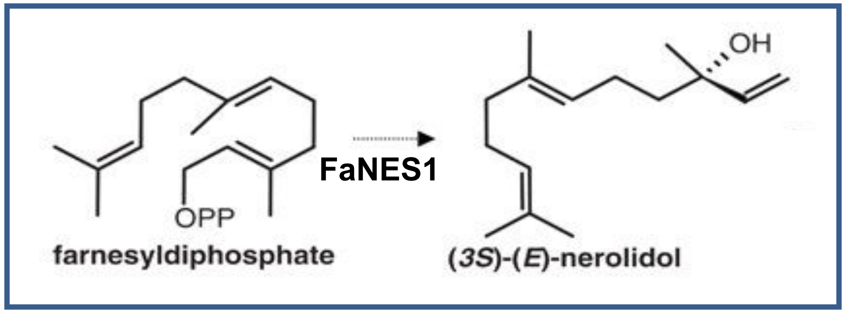
Using a Y-shaped tube, the arthropod is given a choice between two volatile samples, and the frequency that each is chosen is determined

Phytoseiulus persimilis is blind and uses odors to find plants with *T. urticae*

Dicke, M., van Loon, J.J.A. and Soler, R. (2009). Chemical complexity of volatiles from plants induced by multiple attack. Nat Chem Biol. 5: 317-324Dicke, M., van Loon, J.J.A. and Soler, R. (2009). Chemical complexity of volatiles from plants induced by multiple attack. Nat Chem Biol. 5: 317-324; Shimoda, T. and Dicke, M. (2000). Attraction of a predator to chemical information related to nonprey: when can it be adaptive? Behavioral Ecology. 11: 606-613, by permission of Oxford University Press; Photo credit : Merijn R. Kant.

Plants can be engineered to produce predator-attracting volatiles





Predatory mites were attracted to plants producing the terpenoid nerolidol, even in the absence of herbivores

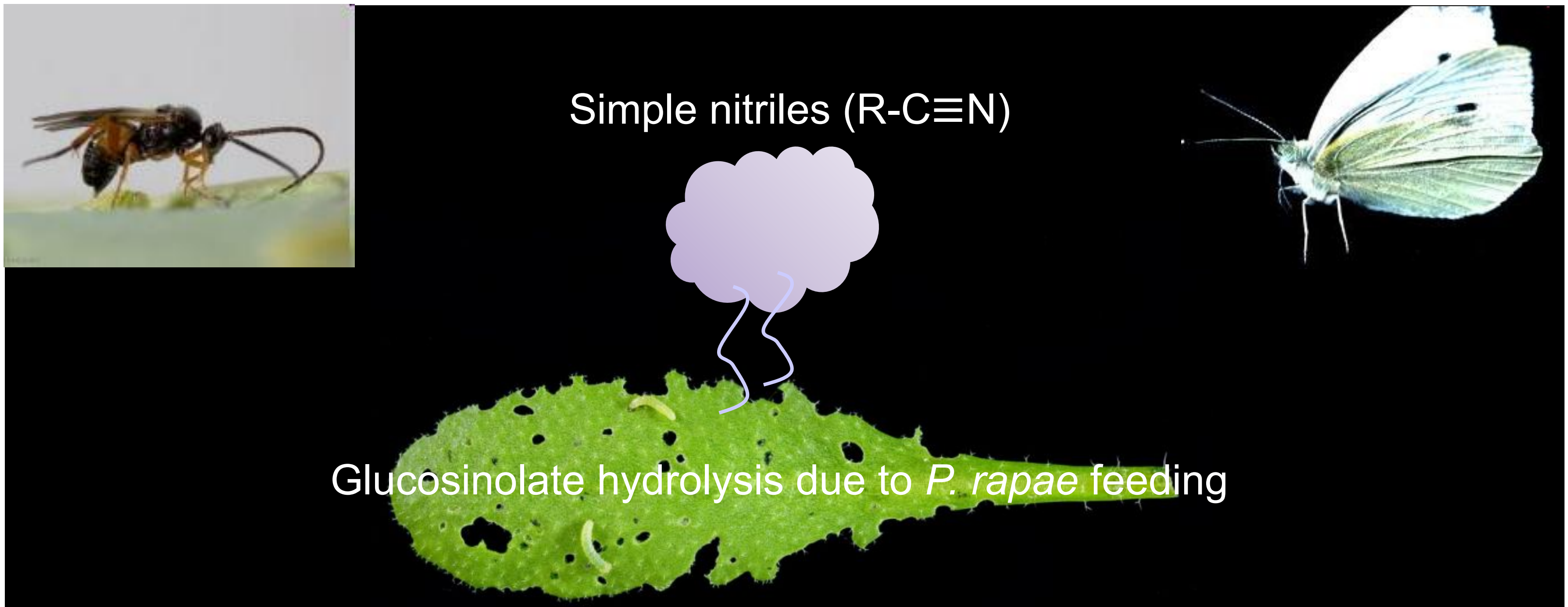
From Kappers, I.F., Aharoni, A., van Herpen, T.W.J.M., Luckerhoff, L.L.P., Dicke, M. and Bouwmeester, H.J. (2005). Genetic engineering of terpenoid metabolism attracts bodyguards to Arabidopsis. Science. 309: [2070-2072](), reprinted with permission from AAAS.

Herbivore-induced plant volatiles can also attract parasitoid arthropods

Parasitoid wasps lay their eggs in other arthropods. When the larvae hatch they eat the host……

Photo: [T. Bukovinszky](#) / www.bugsinthepicture.com

Glucosinolate hydrolysis results in plant volatiles that attract parasitoids

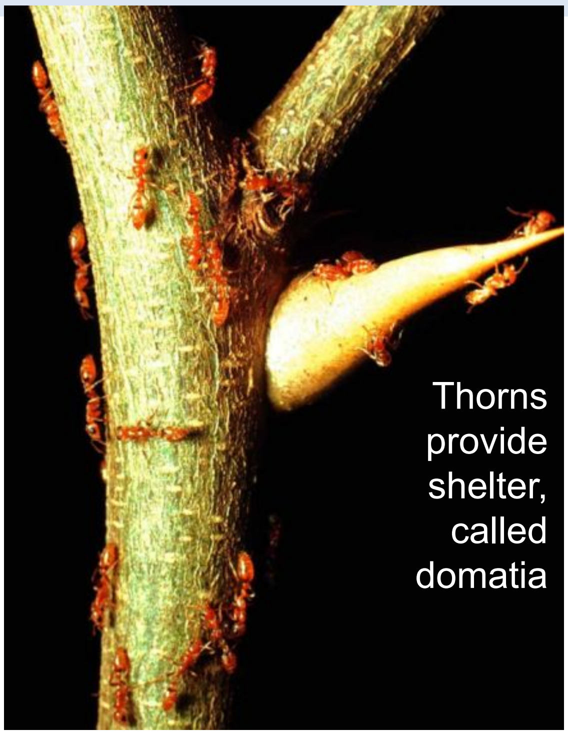


The parasitic wasp *Cotesia rubecula* is attracted to plants that produce nitriles while *Pieris rapae* butterflies avoid ovipositing on these plants when it can choose. The *P. rapae* larvae however do not mind these nitriles.

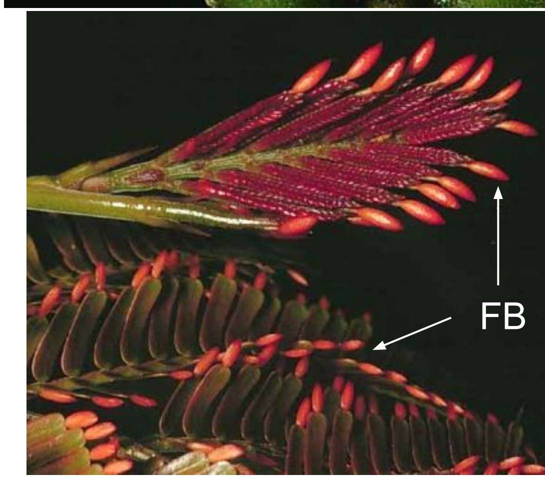
Photo credit: Hans van Pelt

Some plants form longer-term alliances with resident "bodyguards"

Acacias provide ants with shelter and food from extrafloral nectaries (EFN) and food bodies (FB), also known as Beltian bodies



Ants protect acacias from other plants and other arthropods.

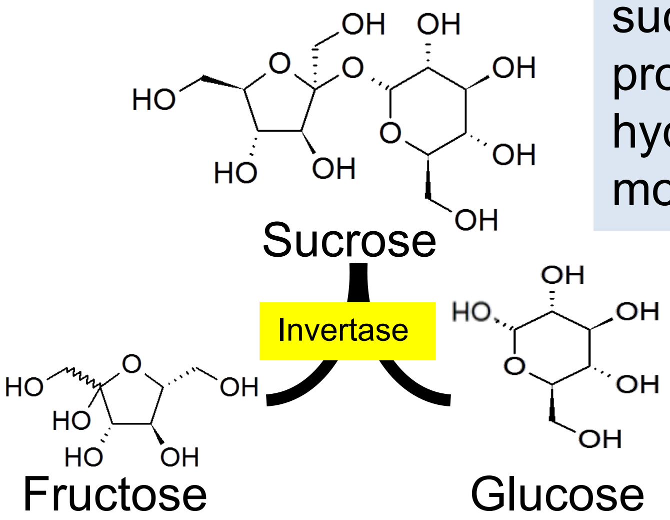


Photos courtesy of Dan Janzen, University of Pennsylvania

Myrmecophyte nectar is optimized for its ant partner

There are > 100 ant-mutualist plants called myrmecophytes

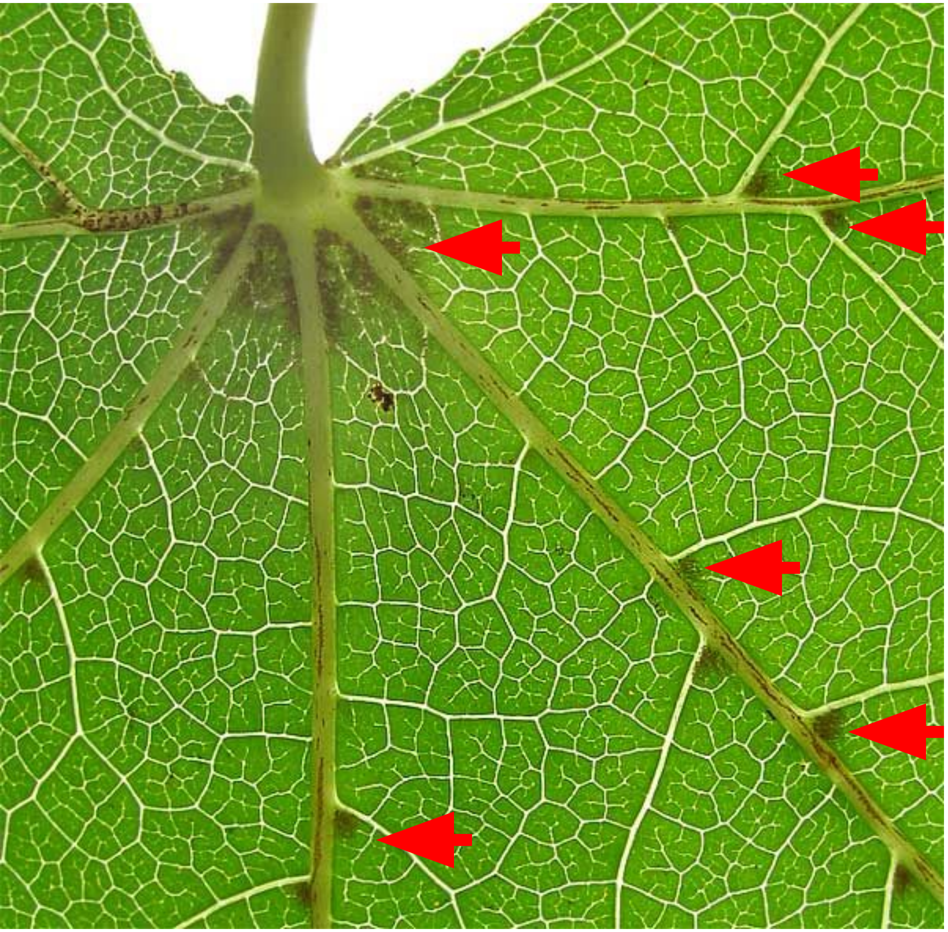
Most nectar contains sucrose and most ants produce invertase that hydrolyzes sucrose to monosaccharides



The *Pseudomyrmex* ants that live on acacia do not produce invertase, and the nectar of myrmecophytes contains fructose and glucose but not sucrose

Heil, M., Rattke, J., and Boland, W. (2005). Postsecretory Hydrolysis of Nectar Sucrose and Specialization in Ant/Plant Mutualism. Science 308: 560-563.

Other plants have other kinds of domatia that shelter predatory arthropods



Domatia can be simple or elaborate, but by providing a dwelling for predatory arthropods plants can protect themselves from herbivory

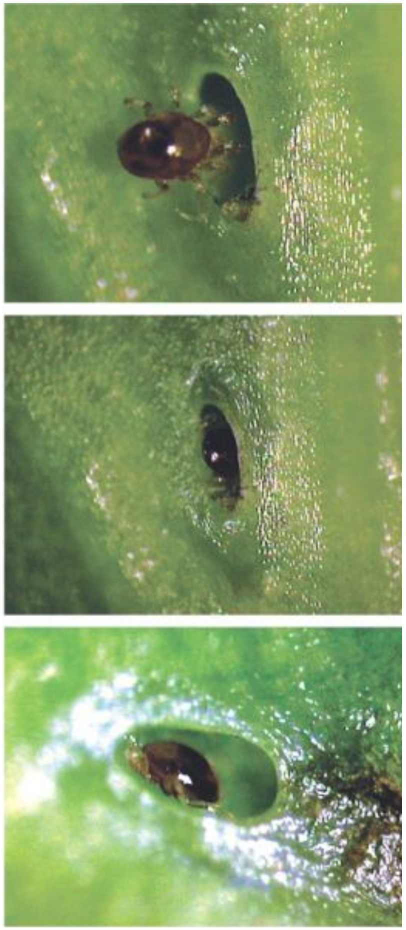
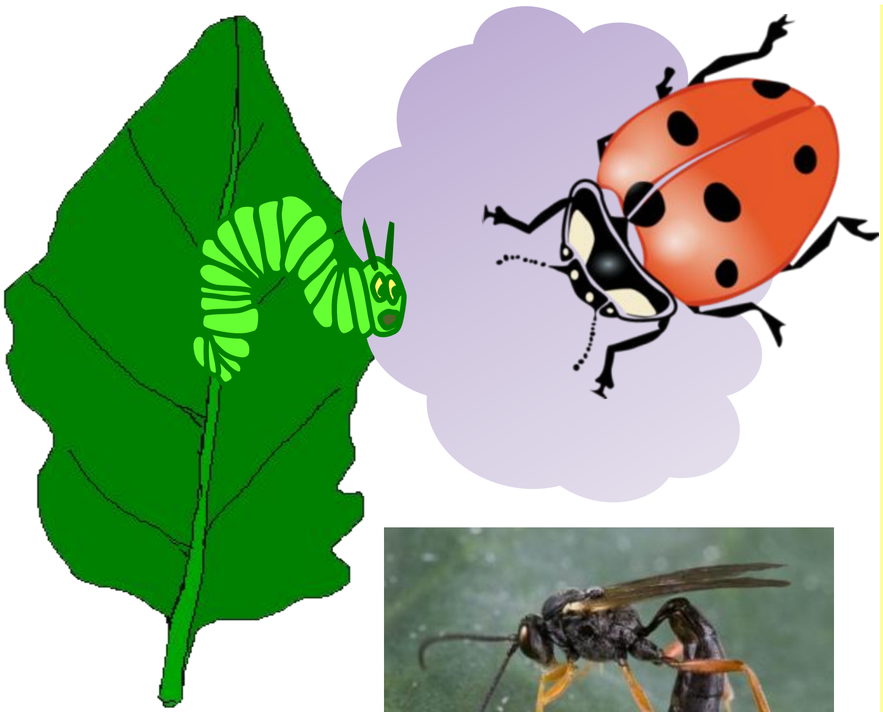


Photo courtesy Jim Conrad: Matos, C.H.C., Pallini, A., Chaves, F.F. and Galbiati, C. (2004). Do coffee domatia benefit the predatory mite *Iphiseiodes zuluagai* Denmark & Muma (Acari: Phytoseiidae)? Neotropical Entomology. 33: 57-63.

Plant alliances with other arthropods against herbivores



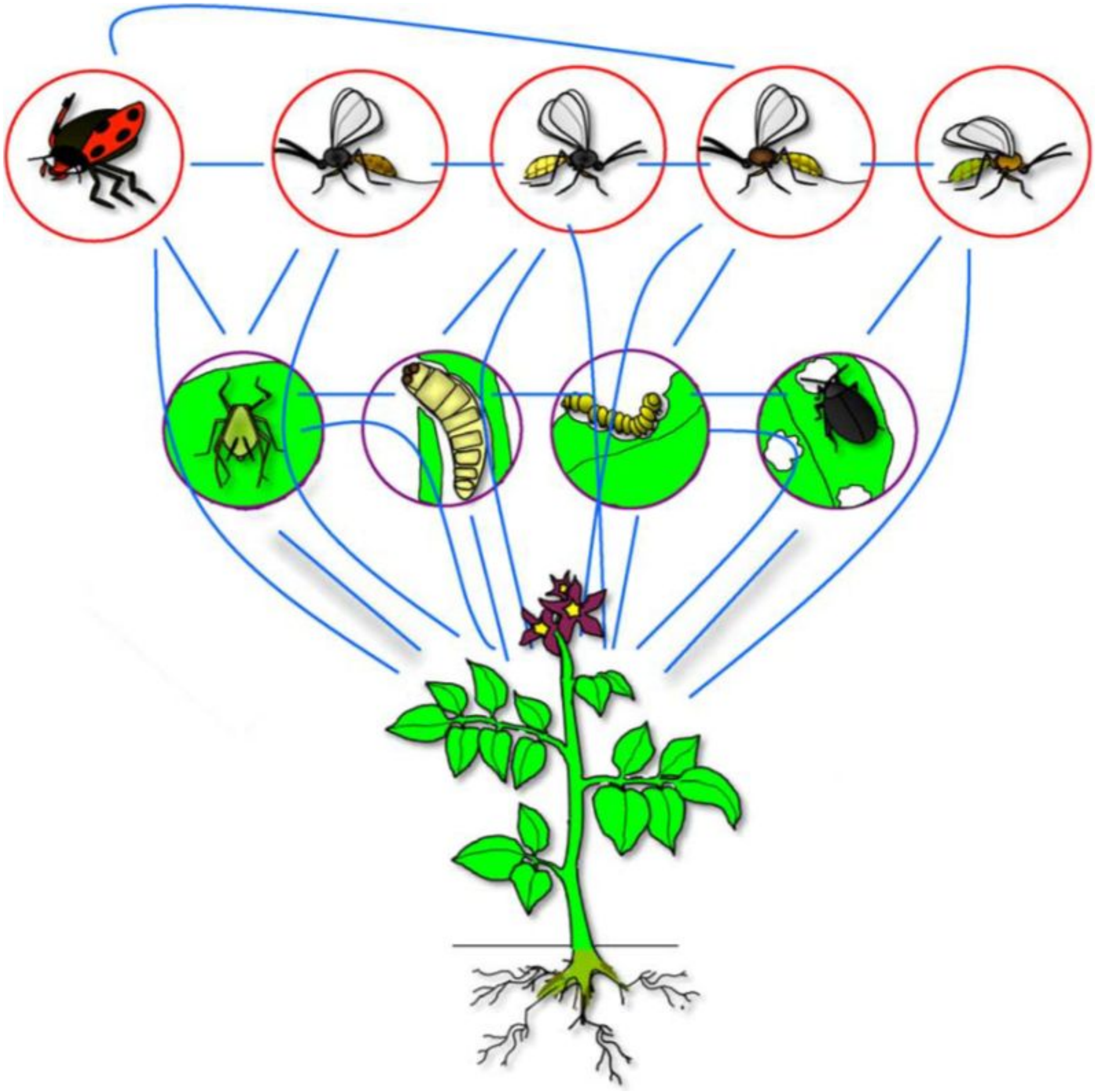
Plant volatiles operate as *direct* defenses when they are toxic or when they repel herbivores

The *indirect* defense mechanism of plants involves:

- the attraction of predatory and parasitoid arthropods via induced plant volatiles
- arrestment and longer-term associations with these beneficial organisms via alternative food and shelter

Photo: T. Bukovinszky / www.bugsinthepicture.com

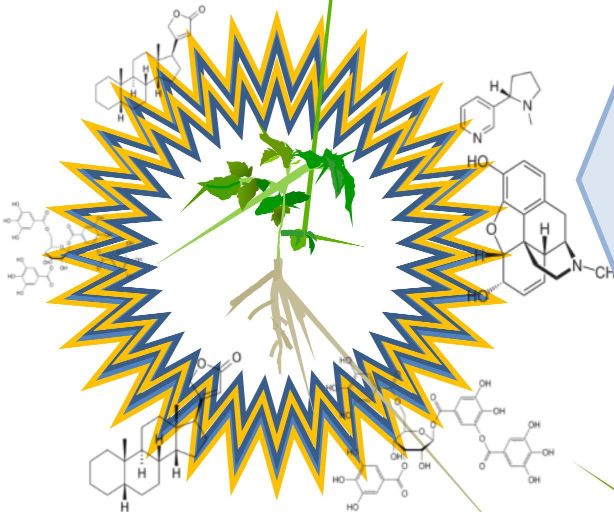
Summary



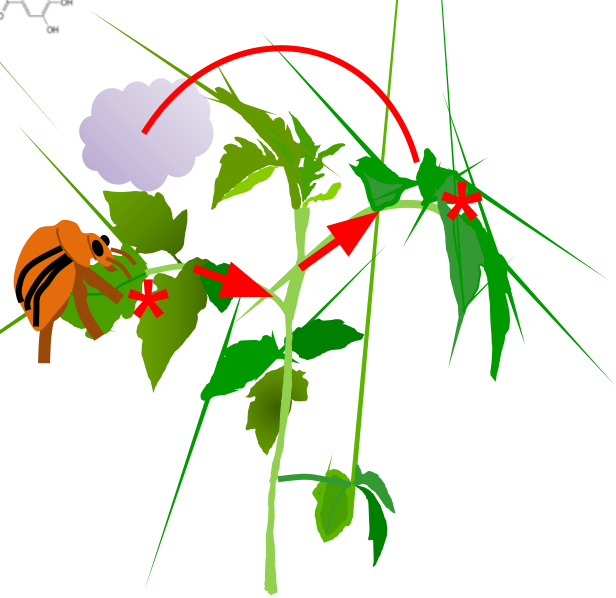
Many of the compounds that contribute to plant direct and indirect defenses have been identified, opening up the possibility to engineer plants with enhanced defenses

Reprinted from Dicke, M., and Baldwin, I.T. (2010) The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. Trends Plant Sci. 15: 167-175, with permission from Elsevier.

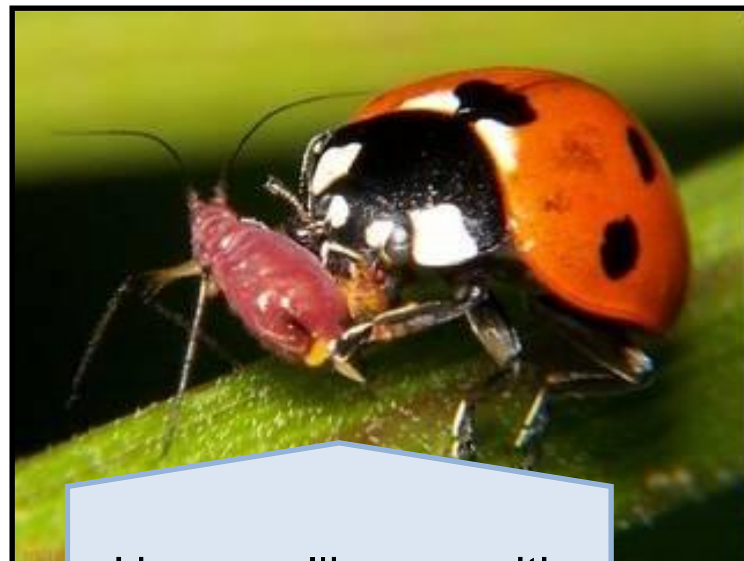
Towards herbivore-resistant crops



Defense compounds are often toxic to humans as well and can cost the plant quite some energy to produce. Hence many such defenses were lost, deliberately or not, during breeding, making crops vulnerable to pests



Enhancing plants' inducible defenses may make them more herbivore-resistant

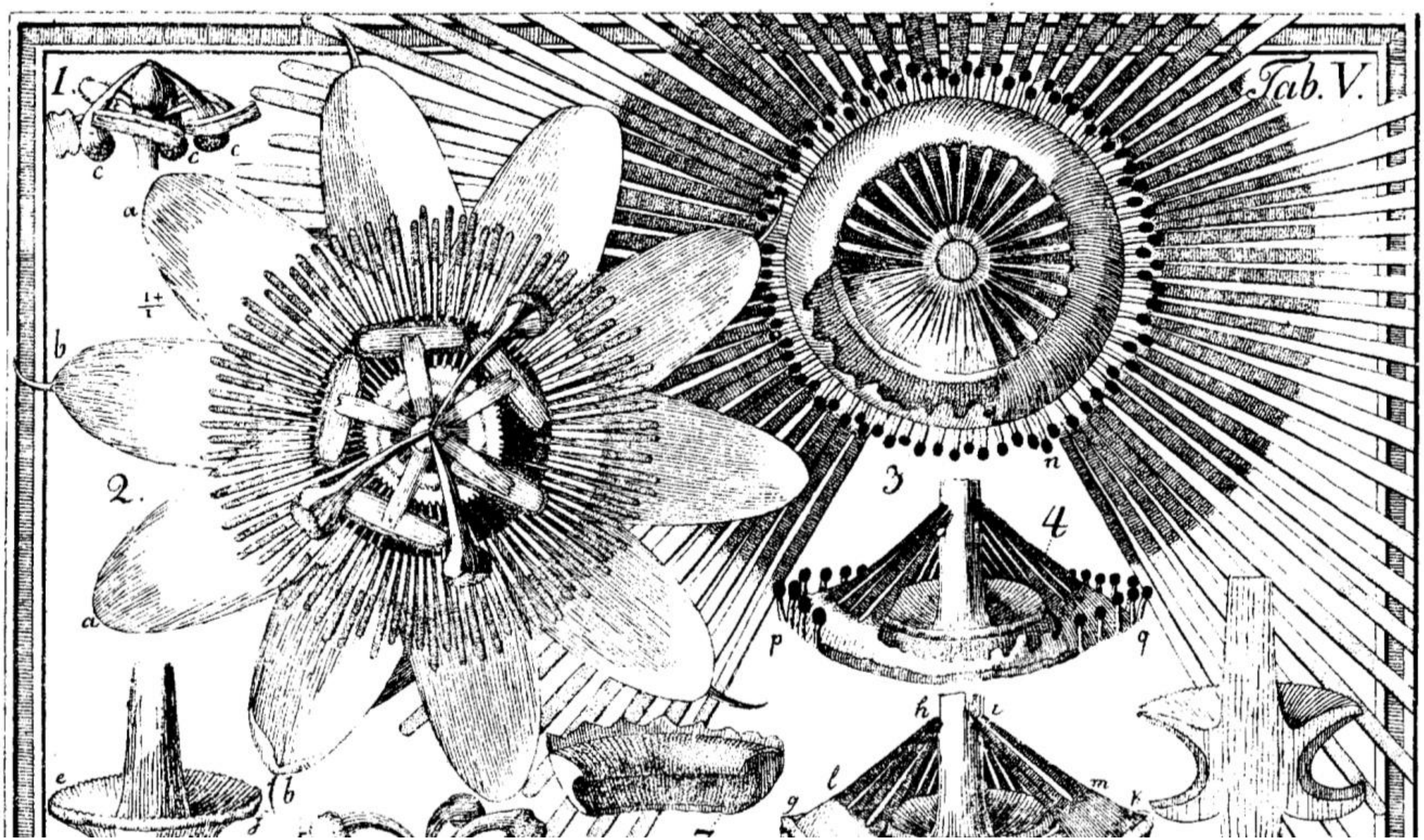


Human alliances with herbivore-predators can enhance food production

Many plants distribute their pollen via mobile arthropods

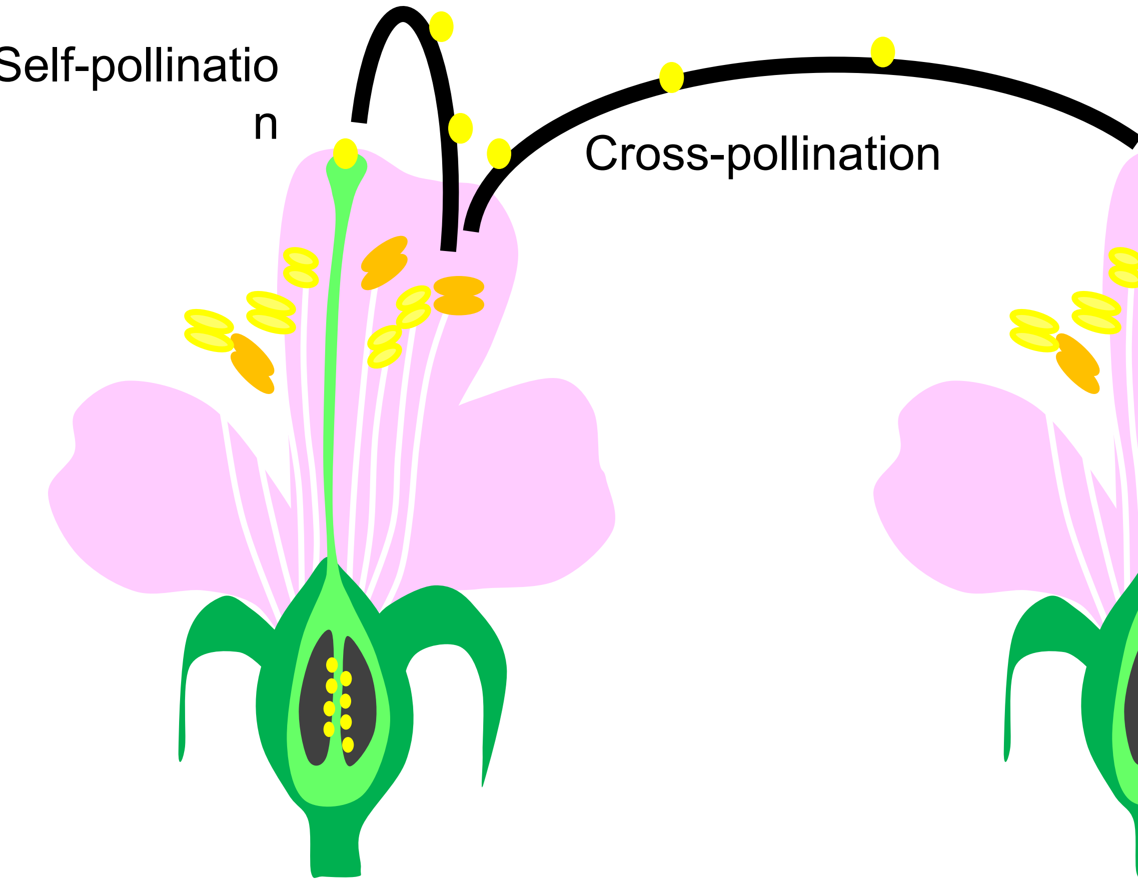
Image source: [Market wallpapers]

Alliance #2 – Plants and Pollinators



Christian Konrad Sprengel (1793) "*Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen*"

Pollination is the transfer of pollen from the anther to the stigma

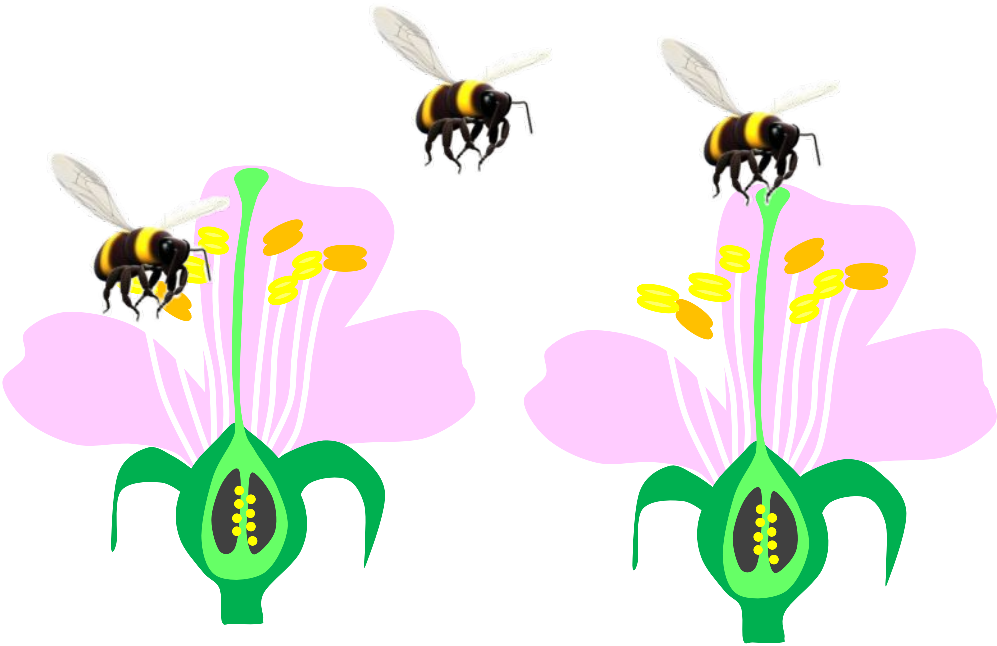


The pollen contains the sperm which travels through the pistil to fertilize the egg

Only a small number of plants regularly self-pollinate; most require cross-pollination

Pollination by arthropods is mutually beneficial

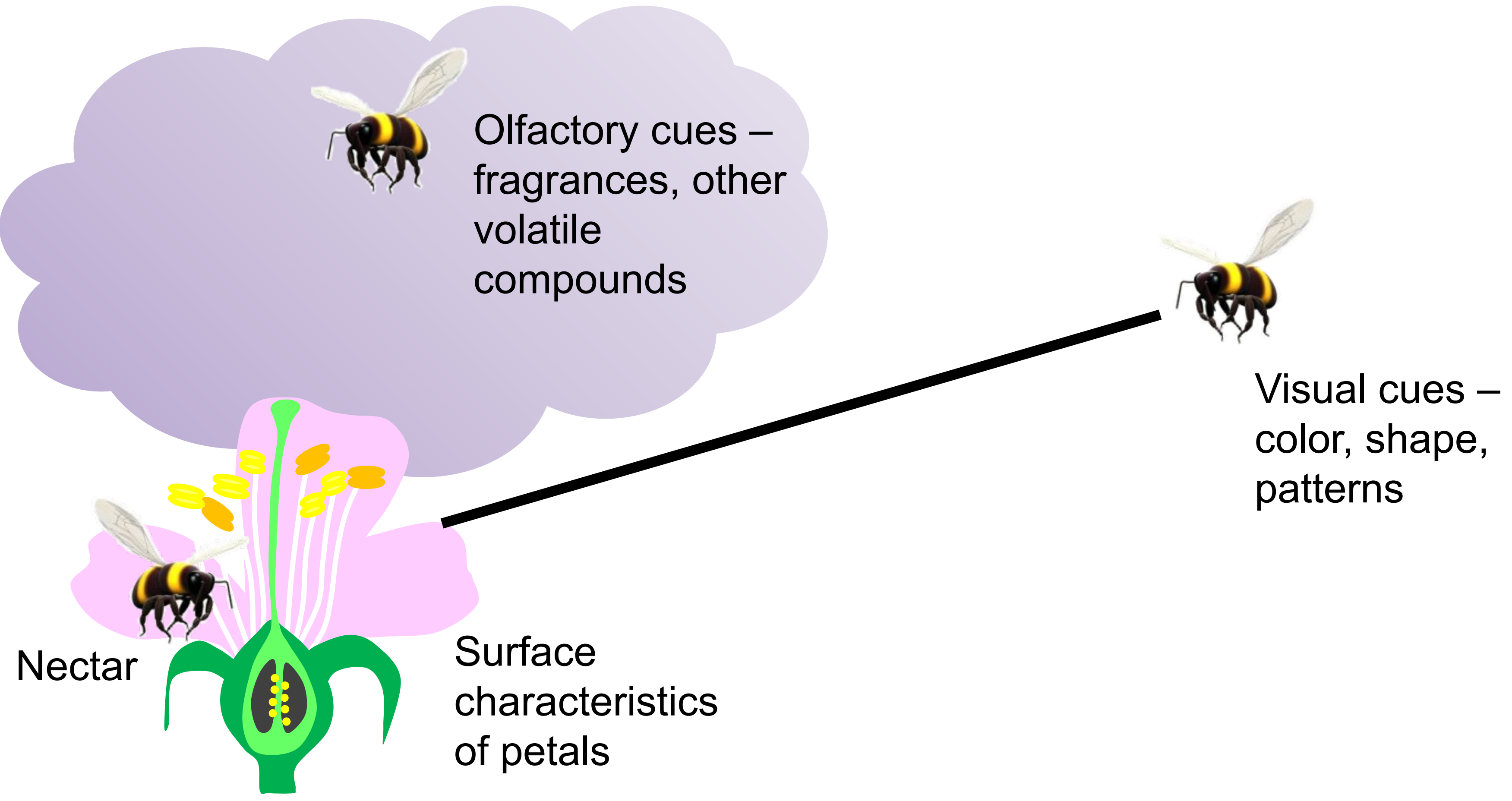
Pollinators are rewarded by eating nectar or protein-rich pollen



Approximately 84% of commercial crops depend on pollinators, mostly insects and mostly **honeybees**

Photo courtesy of Jeff Pettis, ARS.

What attracts pollinators?



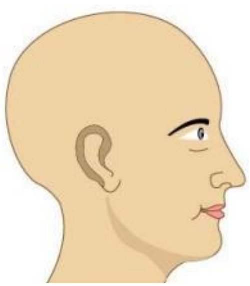
Flowers and pollinators evolved physiological compatibilities

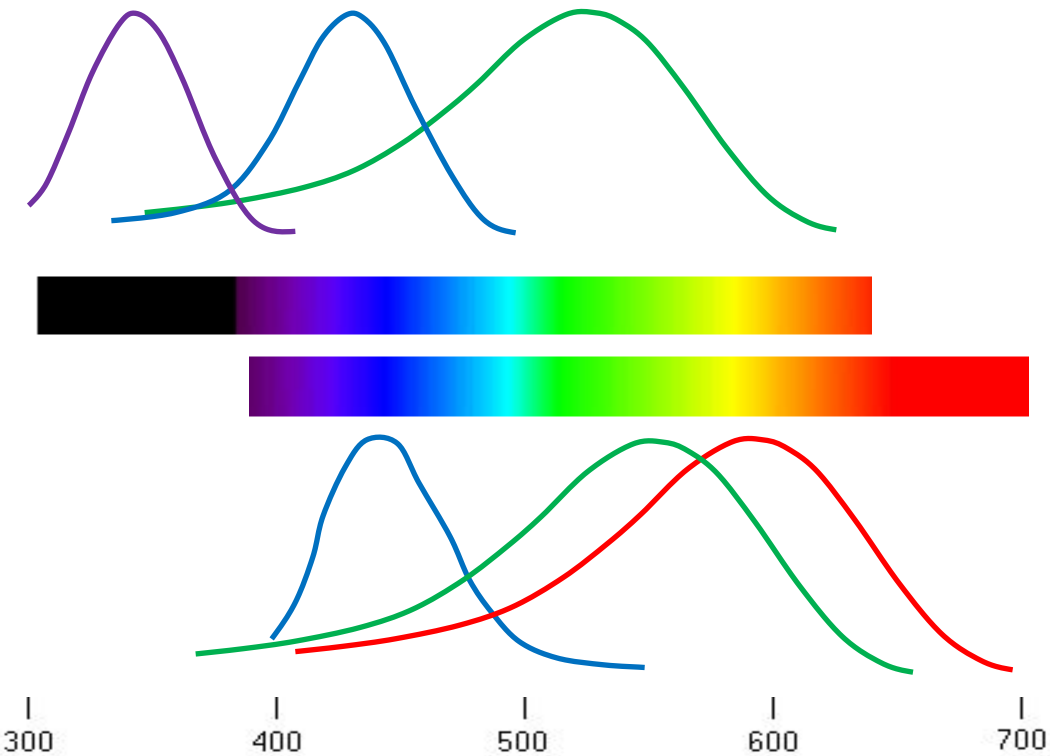
Photos by Jack DykingaPhotos by Jack Dykinga; Rob Flynn, USDA-ARSPhotos by Jack Dykinga; Rob Flynn, USDA-ARS; Hans Hillewaert

Bee vision color spectrum is shifted as compared to human

Bee photoreceptors are most sensitive to **UV**, **blue** and **green**

Human photoreceptors are most sensitive to **blue**, **green** and **red**



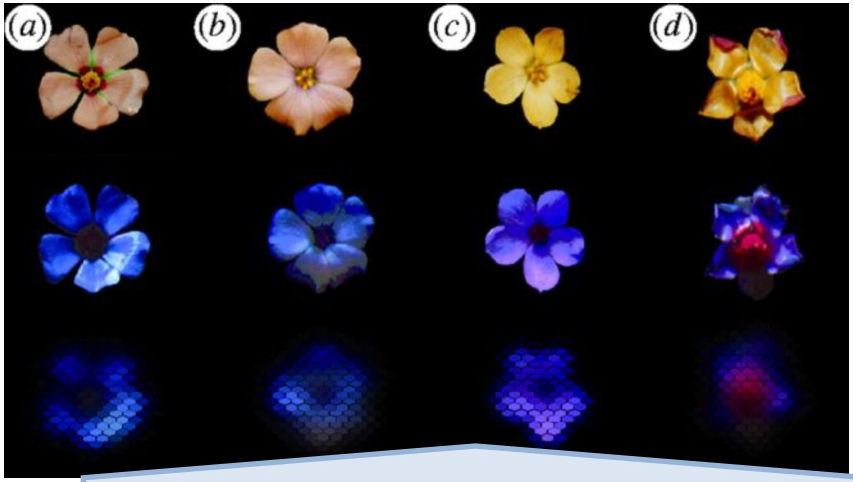


Bee spectral sensitivity adapted from Arnold, S., Savolainen, V. and Chittka, L. (2009). Flower colours along an alpine altitude gradient, seen through the eyes of fly and bee pollinators. Arthropod-Plant Interactions. 3: 27-43.

Flower pigments also reflect or absorb UV-light which is visible to bees

Visible light

Simulated bee color vision



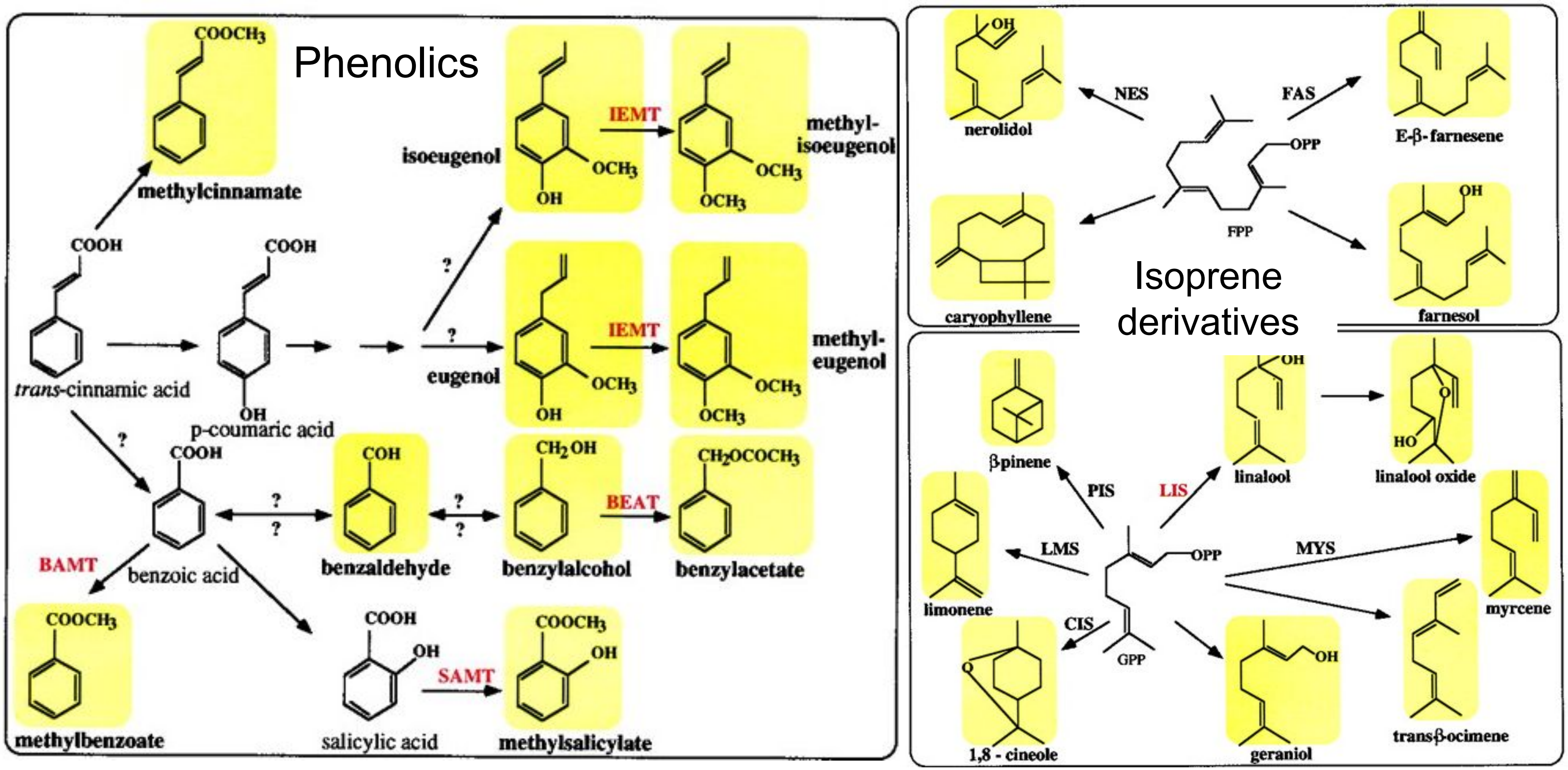
Bees also have lower spatial resolution than humans, which is represented in the third row

Images (c) Dr Klaus Schmitt, Weinheim, www.uvir.eu; Benitez-Vieyra, S., de Ibarra, N.H., Wertlen, A.M. and Cocucci, A.A. (2007). How to look like a mallow: evidence of floral mimicry between Turneraceae and Malvaceae. Proc. Roy. Soc. B. 274: 2239-2248.

Flowers vary in their aroma, and aroma production is developmentally regulated

Guterman, I., et al. (2002). Rose scent: Genomics approach to discovering novel floral fragrance- related genes. Plant Cell. 14: [2325-2338](2325-2338).

Many fragrance elements are conserved but the blend is unique

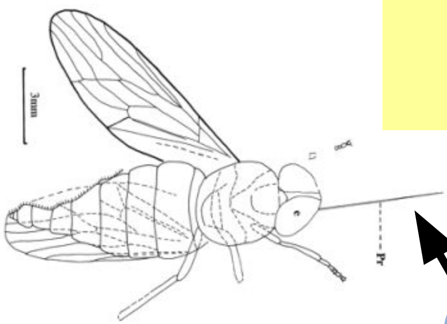


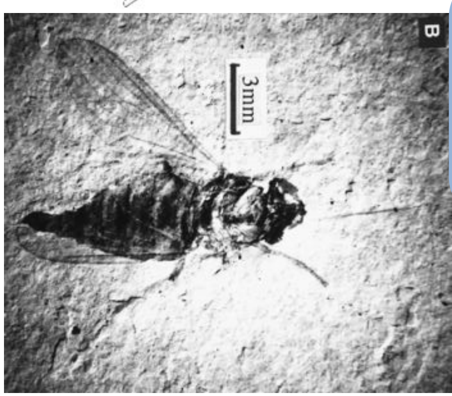
Compounds in yellow are volatile, enzymes in red are expressed in flowers

Dudareva, N. and Pichersky, E. (2000). Biochemical and molecular genetic aspects of floral scents. Plant Physiology. 122: 627-634.

Floral nectar is an attractor and sweet reward for pollinators

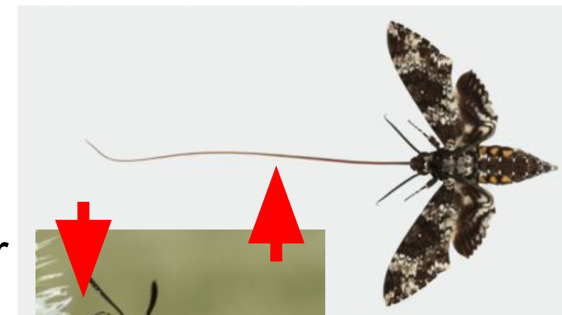
Nectar was an early innovation of flowers and is an important contributor to the success of angiosperms





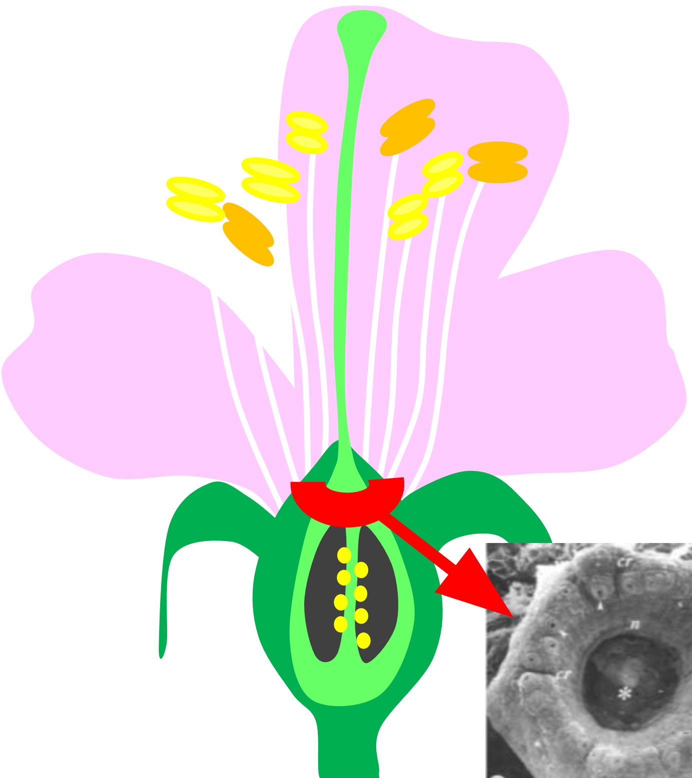
150 million year old insect with nectar-feeding mouthparts

Many pollinators have tongues or other mouthparts specialized for nectar sipping

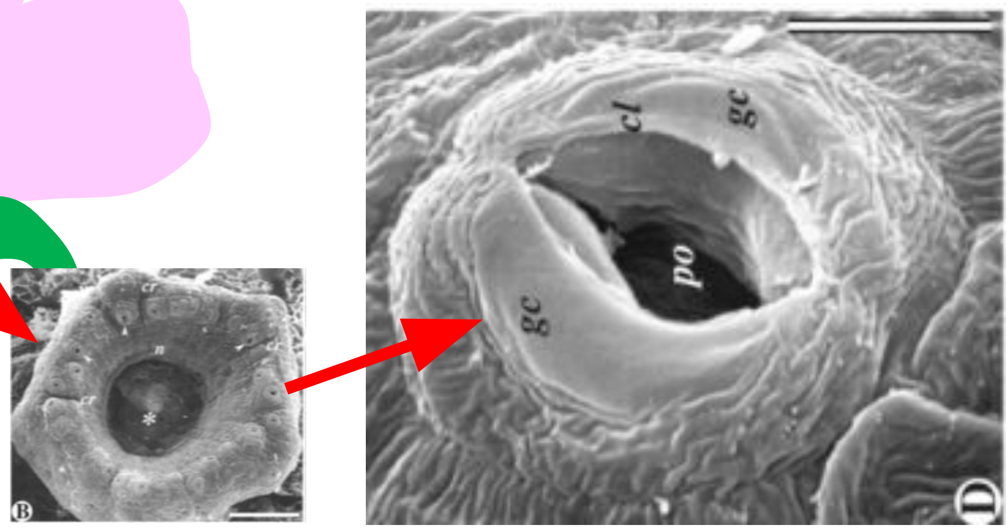


Ren, D. (1998). Flower-associated brachycera flies as fossil evidence for jurassic angiosperm origins. Science 280: 85-88., reprinted with permission from AAAS; Image by artist Joseph ScheerRen, D. (1998). Flower-associated brachycera flies as fossil evidence for jurassic angiosperm origins. Science 280: 85-88., reprinted with permission from AAAS; Image by artist Joseph Scheer. David Cappaert, Michigan State University, Bugwood.org

Nectaries are structurally and positionally diverse



Nectaries can be found at the base of the ovary, filament or petal, often as a ring of tissue. Nectar can be secreted through trichomes, epidermal cells or non-functioning guard cells



Wist, T.J., and Davis, A.R. (2006). Floral Nectar Production and Nectary Anatomy and Ultrastructure of Echinacea purpurea (Asteraceae). Ann. Botany 97: 177-193Wist, T.J., and Davis, A.R. (2006). Floral Nectar Production and Nectary Anatomy and Ultrastructure of Echinacea purpurea (Asteraceae). Ann. Botany 97: 177-193, by permission of Oxford University Press; Heil, M. (2011). Nectar: generation, regulation and ecological functions. Trends Plant Sci 16: 191-200.

Antirrhinum and bumblebee

Its genetic resources make *Antirrhinum* an excellent experimental organism for studies of plant – pollinator coevolution

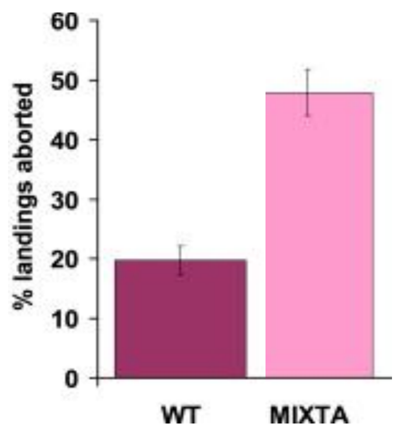
These studies indicate that the shape, color, pattern, scent, and arrangement of flowers on the inflorescence are optimized for pollination by heavy, short-tongued, bumblebees

Rough petals help bees get a grip

Bees need a rough petal surface to grip onto – the smooth cells of the *mixta* mutant cause increased aborted landings as bees slip and slide

Wild-type conical cells

mixta flat cells



Movie S6. Flat Landing 3.

Reprinted from Whitney, H.M., Chittka, L., Bruce, T.J.A., and Glover, B.J. (2009). Conical epidermal cells allow bees to grip flowers and increase foraging efficiency. Curr.Biol. 19: 948-953 with permission from Elsevier.

Which floral cues are most important?

Petunia axillaris

Petunia integrifolia

Petunia exserta

Three closely related petunias are pollinated by moths, bees and hummingbirds

Hoballah, M.E., Gübitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., Dell'Olivo, A., Arnold, M., and Kuhlemeier, C. (2007). Single gene-mediated shift in pollinator attraction in petunia. Plant Cell 19: 779-790Hoballah, M.E., Gübitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., Dell'Olivo, A., Arnold, M., and Kuhlemeier, C. (2007). Single gene-mediated shift in pollinator attraction in petunia. Plant Cell 19: 779-790; Reprinted from Klahre et al., (2011) Pollinator choice in petunia depends on two major genetic loci for floral scent production, Curr. Biol. 21: 730-739 with permission from Elsevier.

Which cues are most important?

Petunia axillaris

Petunia integrifolia

Petunia exserta

Moth	Bee	Hummingbird
White petals	Violet petals	Red petals
Strong fragrance	Little fragrance	Little fragrance
Abundant nectar	Little nectar	Abundant nectar
Long tube	Short tube	Exserted sexual organs

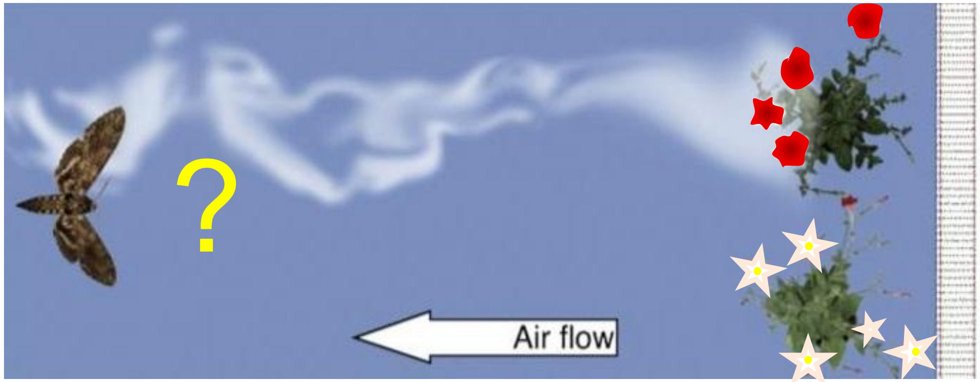
Hoballah, M.E., Gübitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., Dell'Olivo, A., Arnold, M., and Kuhlemeier, C. (2007). Single gene-mediated shift in pollinator attraction in petunia. Plant Cell 19: 779-790Hoballah, M.E., Gübitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., Dell'Olivo, A., Arnold, M., and Kuhlemeier, C. (2007). Single gene-mediated shift in pollinator attraction in petunia. Plant Cell 19: 779-790; Reprinted from Klahre et al., (2011) Pollinator choice in petunia depends on two major genetic loci for floral scent production, Curr. Biol. 21: 730-739 with permission from Elsevier.

Mixing and matching traits in *Petunia*

Petunia axillaris

Petunia integrifolia

Petunia exserta



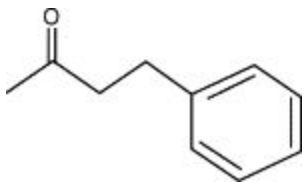
When presented with mixed cues (red scented vs white non-scented), moths get confused and select at random.

Hoballah, M.E., Gübitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., Dell'Olivo, A., Arnold, M., and Kuhlemeier, C. (2007). Single gene-mediated shift in pollinator attraction in petunia. Plant Cell 19: 779-790Hoballah, M.E., Gübitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., Dell'Olivo, A., Arnold, M., and Kuhlemeier, C. (2007). Single gene-mediated shift in pollinator attraction in petunia. Plant Cell 19: 779-790; Reprinted from Klahre et al., (2011) Pollinator choice in petunia depends on two major genetic loci for floral scent production, Curr. Biol. 21: 730-739 with permission from Elsevier.

Plants are picky about which pollinators they choose as allies

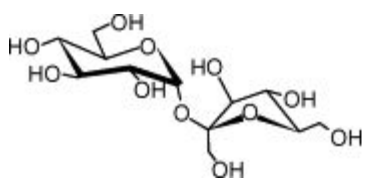
Photo courtesy of David CappaertPhoto courtesy of David Cappaert, Michigan State University, Bugwood.org; Hoballah, M.E., Gübitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., Dell'Olivo, A., Arnold, M., and Kuhlemeier, C. (2007). Single gene-mediated shift in pollinator attraction in petunia. Plant Cell 19: 779-790;

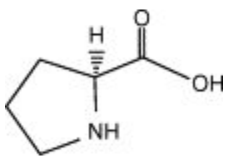
Some flower components are attractive



Benzyl acetone

Pollinators





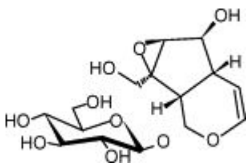
Nutrients – sugars and animo acids

Pollinators

Predators, parasitoids

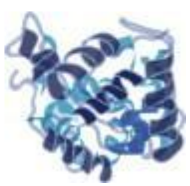
Redrawn from Heil, M. (2011). Nectar: generation, regulation and ecological functions. Trends Plant Sci 16: 191-200 with permission from Elsevier.

Some flower components e.g. from nectar are “repellent”



Catalpol

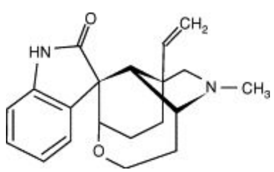
Nectar robbers



Nectarins

H_2O_2

Microorganisms (i.e. yeast)



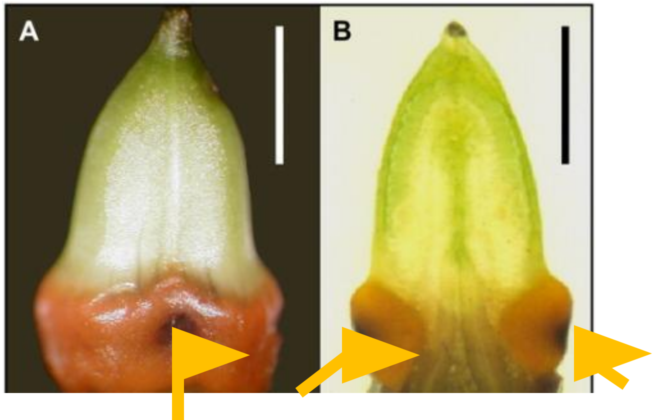
Gelsemine

Nicotine

Nectar robbers

Pollinators

H_2O_2 prevents microbial growth in sugar-rich nectar



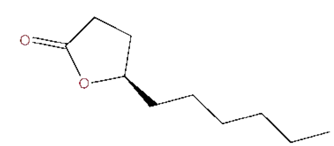
Hydrogen peroxide accumulation at nectary opening

Redrawn from Heil, M. (2011). Nectar: generation, regulation and ecological functions. Trends Plant Sci 16: 191-200Redrawn from Heil, M. (2011). Nectar: generation, regulation and ecological functions. Trends Plant Sci 16: 191-200 with permission from Elsevier; Carter, C., Healy, R., O'Tool, N.M., Naqvi, S.M.S., Ren, G., Park, S., Beattie, G.A., Horner, H.T., and Thornburg, R.W. (2007). Tobacco nectaries express a novel NADPH xxidase implicated in the defense of floral reproductive tissues against microorganisms. Plant Physiology 143: 389-399..

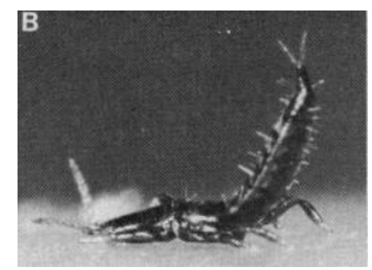
Fragrance can also be deceptive or repellent

Many orchids produce female pheromones and are fertilized by sexual deception

Osmanthus fragrans produces a pollination deterrent that is also a defense compound produced by thrips

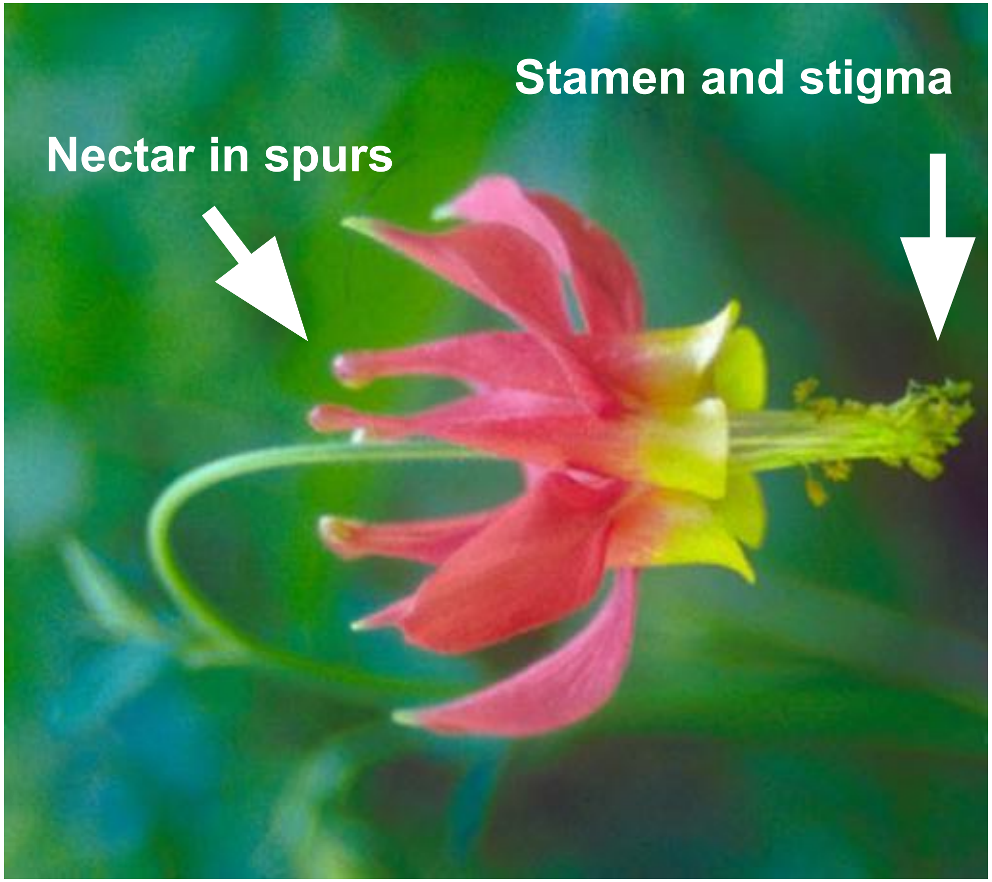


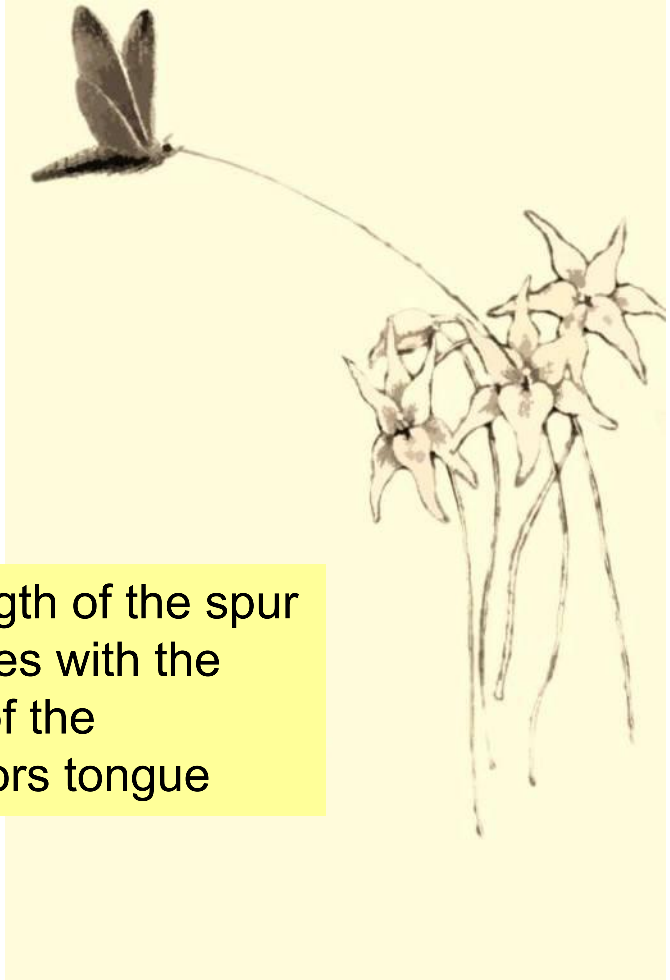
γ-decalactone



Howard, D.F., Blum, M.S., and Fales, H.M. (1983). Defense in thrips: Forbidding fruitiness of a lactone. Science 220: 335-336 with permission from AAAS; Ômura, H., Honda, K., and Hayashi, N. (2000). Floral scent of *Osmanthus fragrans* discourages foraging behavior of cabbage butterfly, *Pieris rapae*. J. Chem. Ecol. 26: 655-666. J. Chem. Ecol. 26: 655-666; Reprinted by permission from Macmillan Publishers Ltd. Ledford, H. (2007) Plant biology: The flower of seduction. Nature 445: 816-817.

Nectar location forces the pollinator to interact with reproductive tissues





The length of the spur correlates with the length of the pollinators tongue

Dave Powell, USDA Forest Service, Bugwood.org

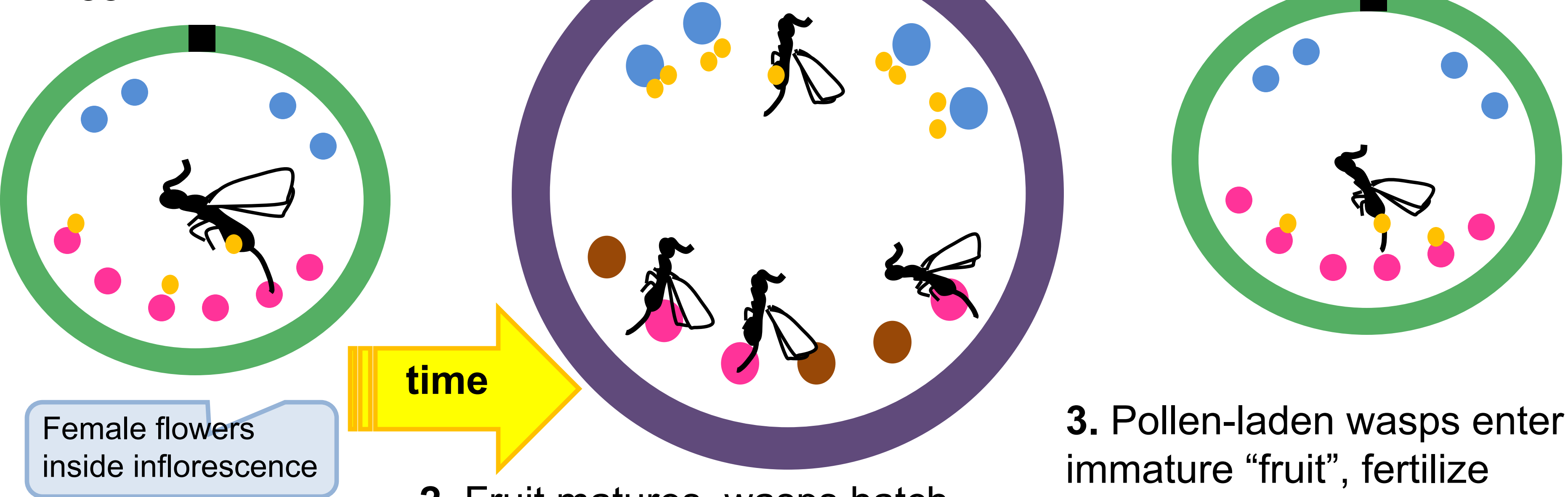
Figs and fig wasps need each other

Figs and fig wasps are mutually interdependent for reproduction. Most figs are pollinated by a single species of wasp

Photo credits: David KarpPhoto credits: David Karp, Forest & Kim Starr, Starr Environmental, Bugwood.org

Figs have an enclosed inflorescence that the pollinator must enter

1. Adult female crawls into immature “fruit” and deposits eggs into female flowers



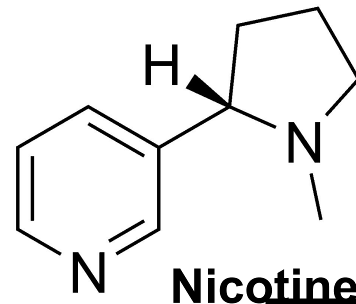
2. Fruit matures, wasps hatch, pick up pollen as leave “fruit” (some flowers make seeds)

3. Pollen-laden wasps enter immature “fruit”, fertilize female flowers and deposit eggs (REPEAT....)

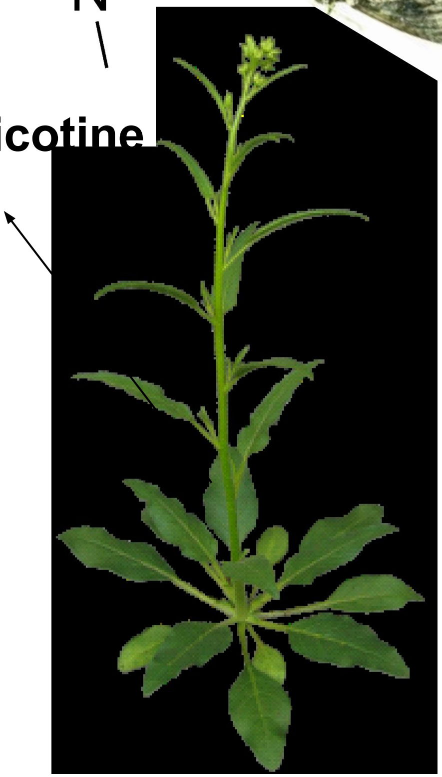
Adapted from Cook, J.M., and Rasplus, J.-Y. (2003). Mutualists with attitude: coevolving fig wasps and figs. Trends Ecol. Evol. 18: 241-248.

Nicotiana attenuata and *Manduca sexta*

Manduca is a specialist herbivore that feeds on *Nicotiana* and can sequester and secrete nicotine. *Manduca* is also the main pollinator of this plant, so it is both a “friend” and “foe”.



Nicotine



Nicotiana attenuta

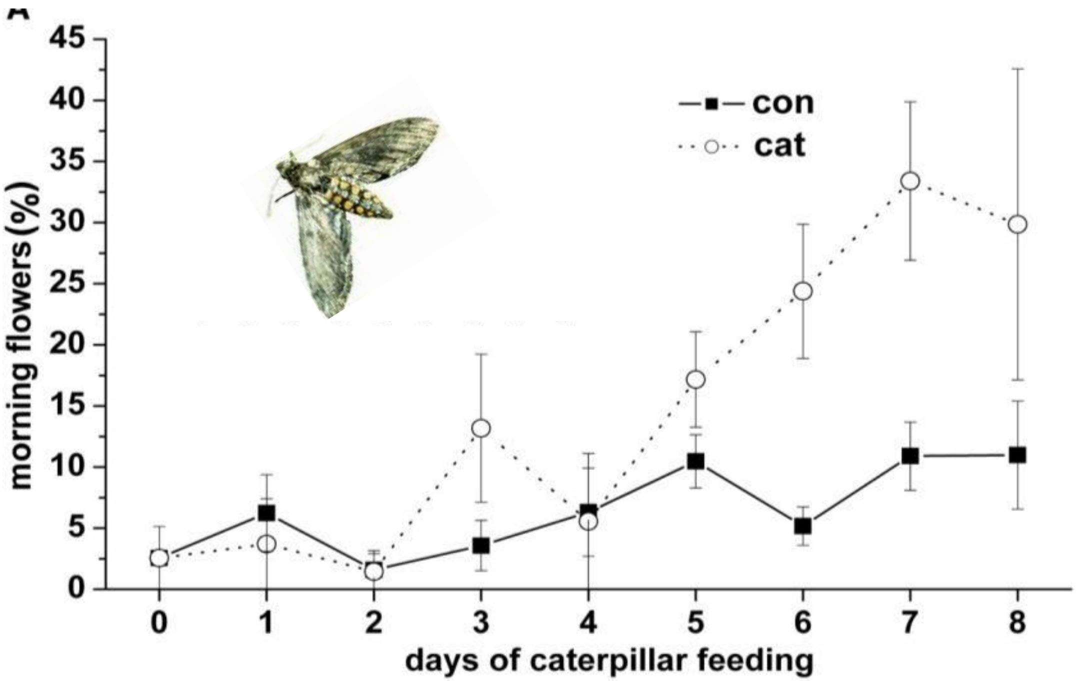
How does the plant balance its two conflicting relationships with *Manduca*??

Manduca sexta

Severe caterpillar herbivory shifts flowers to opening in the morning

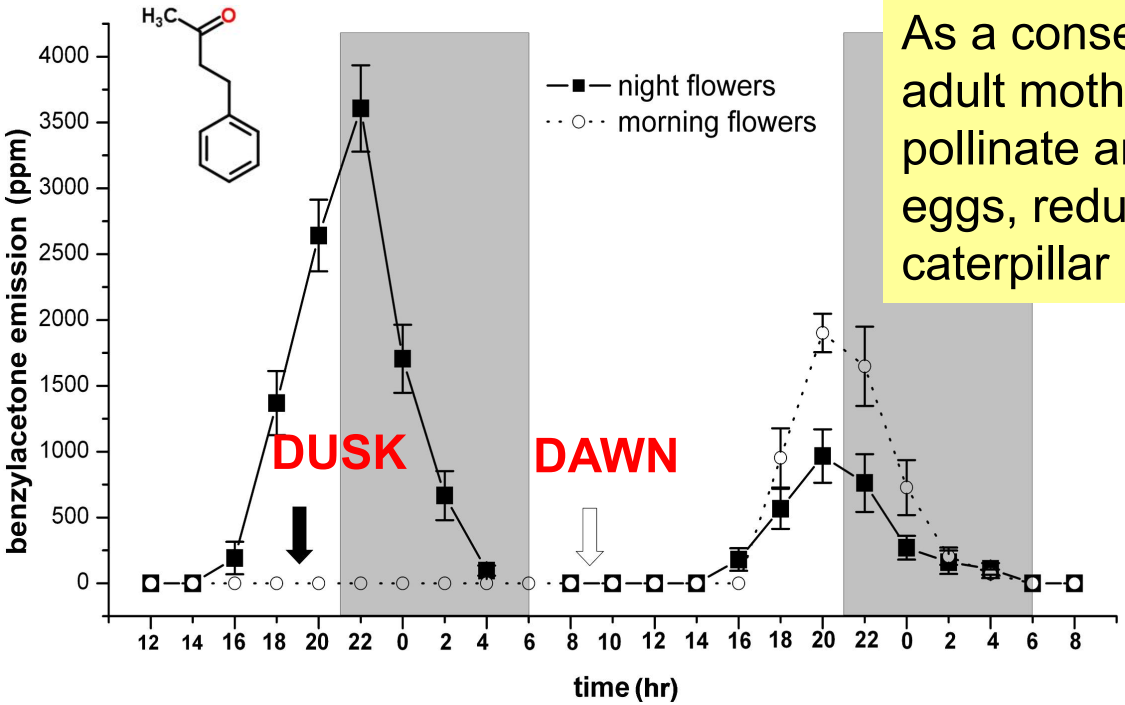
Caterpillar infestation leads to more flowers opening in the morning, when the moths are not active

The adult moths are nocturnal and normally the flowers open at night



Kessler, D., Diezel, C., and Baldwin, I.T. (2010). Changing pollinators as a means of escaping herbivores. Curr. Biol. 20: 237-242, reprinted by permission of Elsevier.

The morning-opening flowers don't attract moths

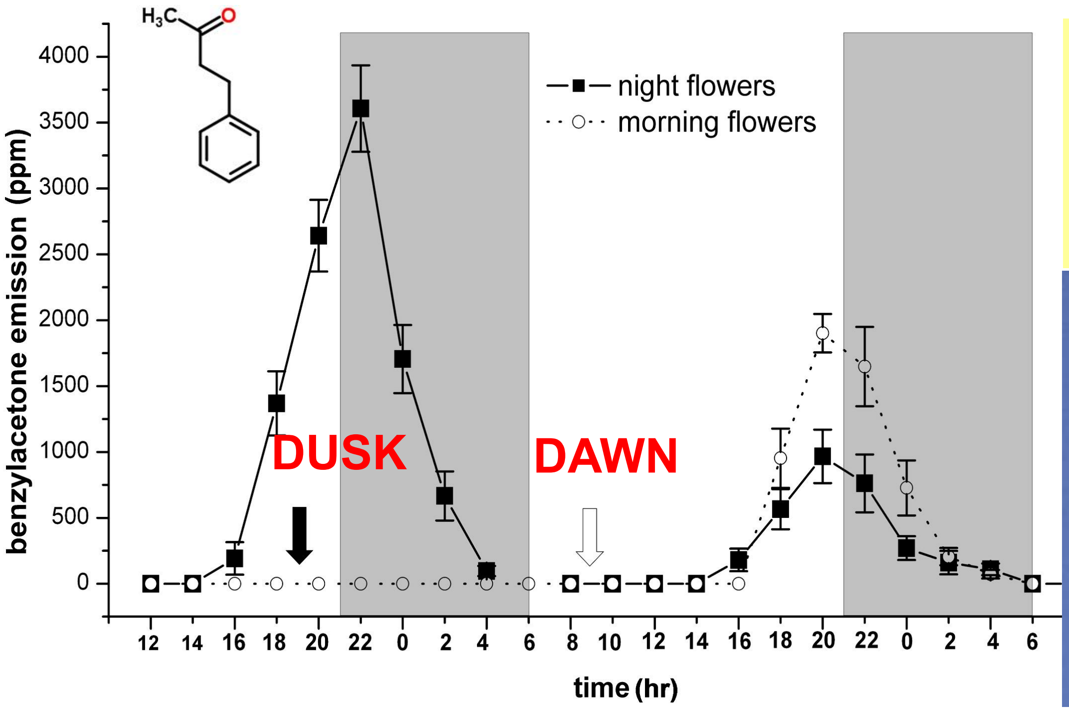


As a consequence, adult moths don't pollinate and don't lay eggs, reducing caterpillar numbers

The moth-attractant *benzyl acetone* (BA) is emitted at night, when open in the morning the flowers are not producing the attractant BA.

Kessler, D., Diezel, C., and Baldwin, I.T. (2010). Changing pollinators as a means of escaping herbivores. Curr. Biol. 20: 237-242, reprinted by permission of Elsevier.

The morning-opening flowers don't attract moths



The plant switches pollinators to escape herbivory!

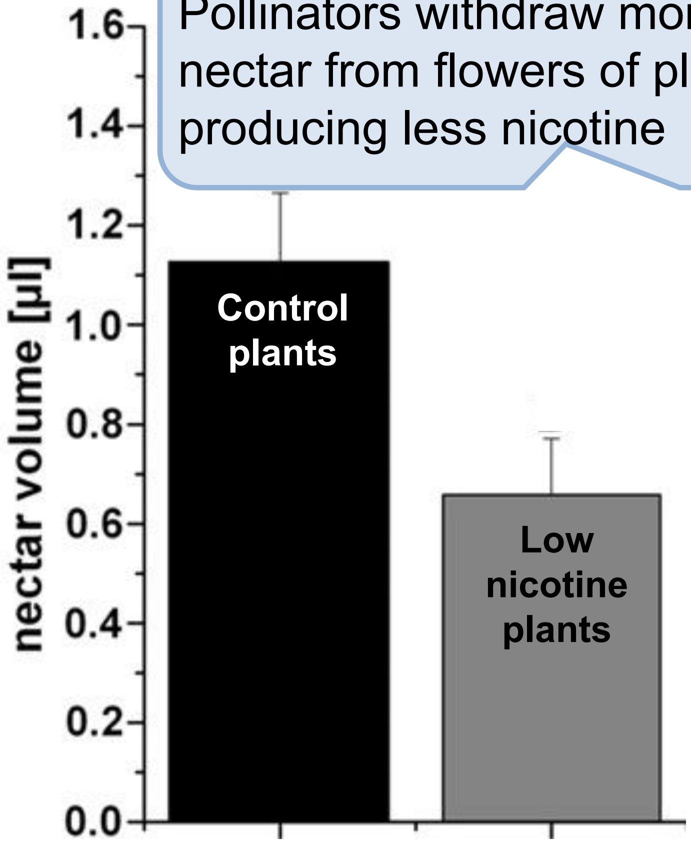
Opportunistic hummingbirds take nectar from and pollinate the morning-open flowers

The moth-attractant *benzyl acetone* (BA) is emitted at night, when open in the morning the flowers are not producing the attractant BA.

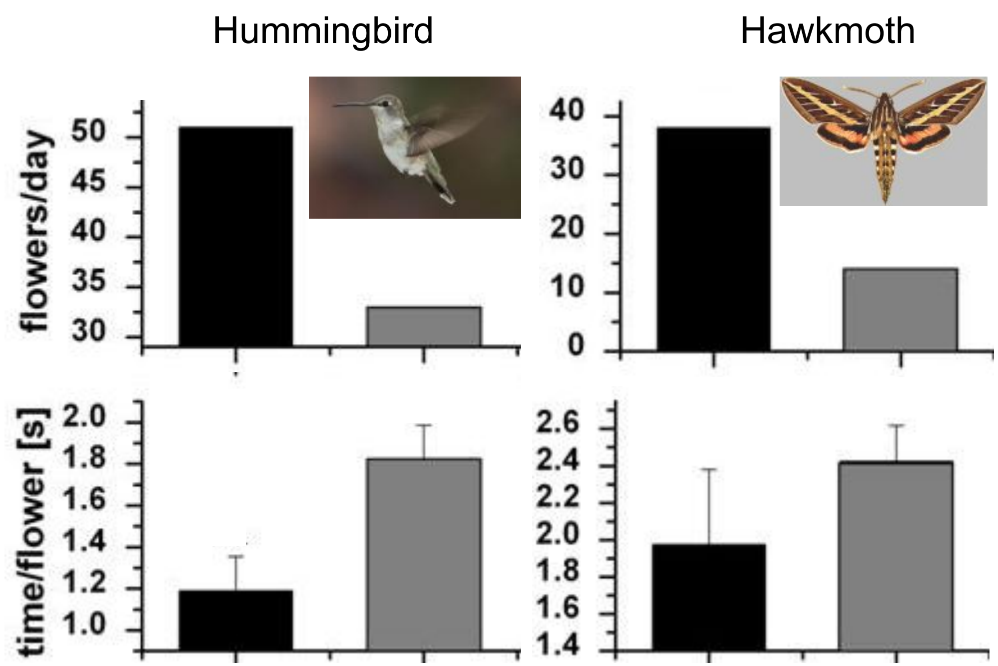
Kessler, D., Diezel, C., and Baldwin, I.T. (2010). Changing pollinators as a means of escaping herbivores. Curr. Biol. 20: 237-242, reprinted by permission of Elsevier.

Nicotine gets plants more pollination service for less nectar production

Pollinators withdraw more nectar from flowers of plants producing less nicotine

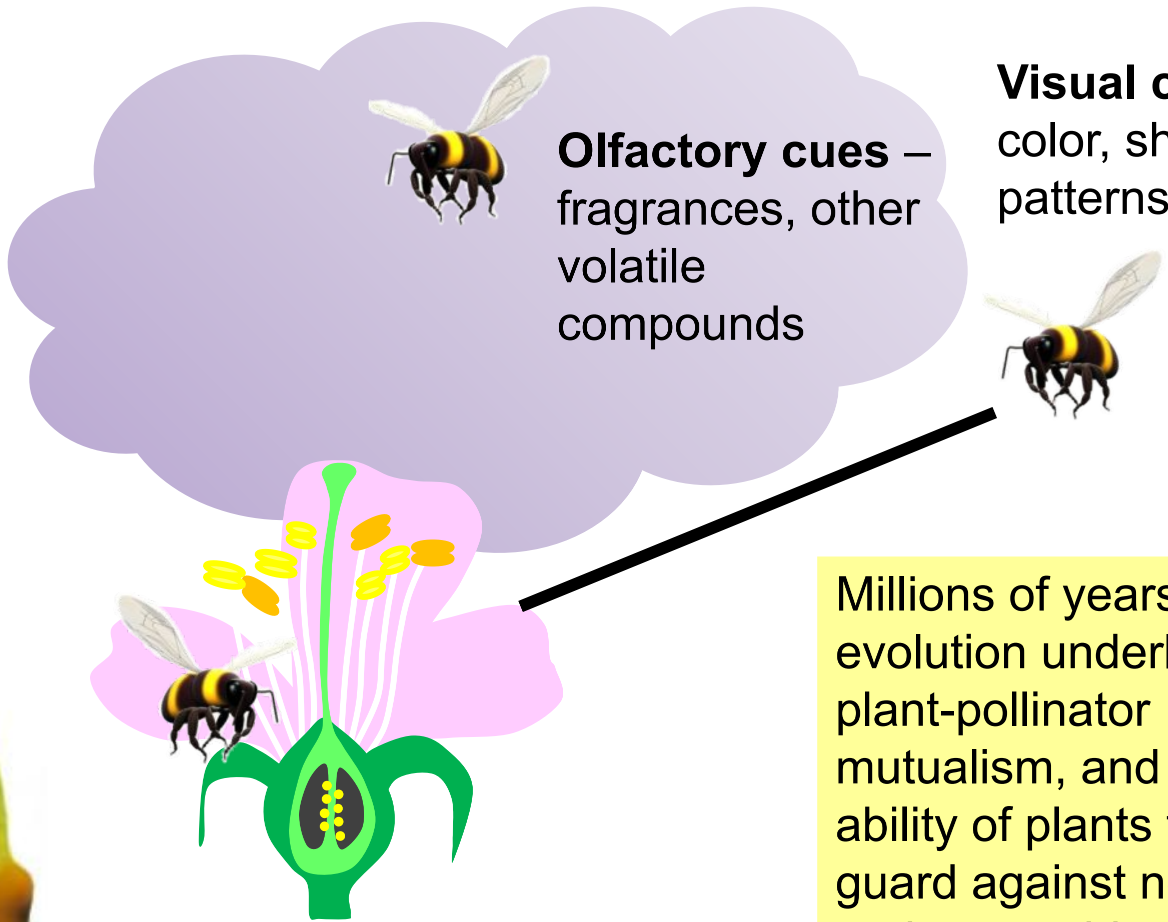


Plants producing nicotine get more and shorter visits from pollinators: shorter because the pollinator can handle only small amounts of nicotine; more since the pollinator needs nectar



Kessler, D., Gase, K. and Baldwin, I.T. (2008). Field experiments with transformed plants reveal the sense of floral scents. Science. 321: 1200-1202 reprinted by permission of AAAS.

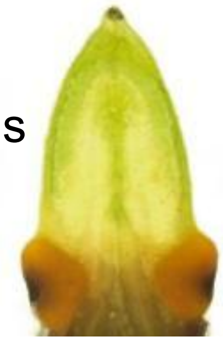
Plants and pollinators - summary



Olfactory cues – fragrances, other volatile compounds

Visual cues – color, shape, patterns

Nectar – food, attractant and repellent compounds, antimicrobials



Millions of years of evolution underlie plant-pollinator mutualism, and the ability of plants to guard against nectar and pollen thieves

Cheaters, Thieves and Deceivers

Thief - One who breaks into a mutualism by not returning a favor

Cheater – A freeloader who abuses the honesty of its own kind

Deceiver – tricks other species into providing services under false pretences

Natural selection maximizes reproductive success and dishonesty can do just that

But do organisms that cheat, steal and deceive succeed on the long run?

Thieves: Nectar robbers take nectar without loading pollen

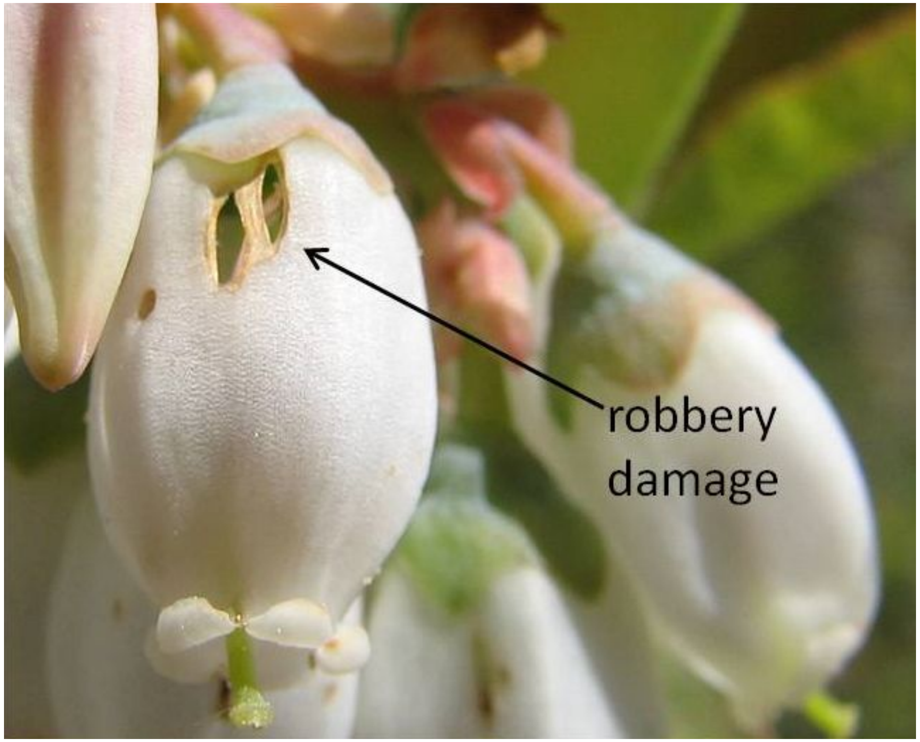
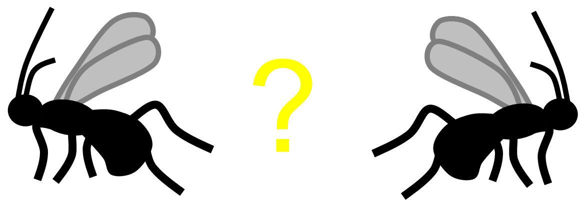


Photo credit: Debbie Roos, North Carolina Agricultural Extension Agent

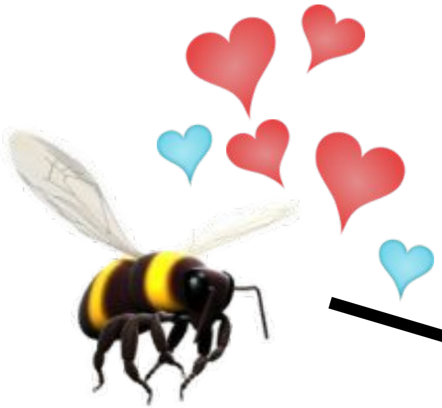
Cheaters: Some cabbages excessively produce volatiles (they *cry wolf*)



Plants that *cry wolf* or produce large amounts of volatiles under low herbivory pressure pressure gain in the short term but undermine the alliance between plant and carnivore……

Shiojiri, K., Ozawa, R., Kugimiya, S., Uefune, M., van Wijk, M., Sabelis, M.W. and Takabayashi, J. (2010). Herbivore-specific, density-dependent induction of plant volatiles: Honest or "Cry wolf" signals? PLoS ONE. 5: e12161.

Deceivers: Why does this flower look like a female bee?



Many orchids have evolved similarity to female arthropods, to entice visits by males. Some also emit the female's chemical attractants. By the time the males realize their mistake, they've already delivered or picked up pollen. **Final score: Plant 1, Pollinator 0**.

Image courtesy Hans Hillewaert

Some plants have moved up to the third tropic level: deceivers?

Carnivorous plants use trap and sticky trichomes to catch their prey

Photo credits: Tom DonaldPhoto credits: Tom Donald; Sturgis McKeeverPhoto credits: Tom Donald; Sturgis McKeever, Georgia Southern University; Rebekah D. Wallace, University of Georgia, Bugwood.org

Leaf cutter bee: Friend or Foe?

Leaf cutter bees are efficient pollinators but also damage plants: *friendly foes*?

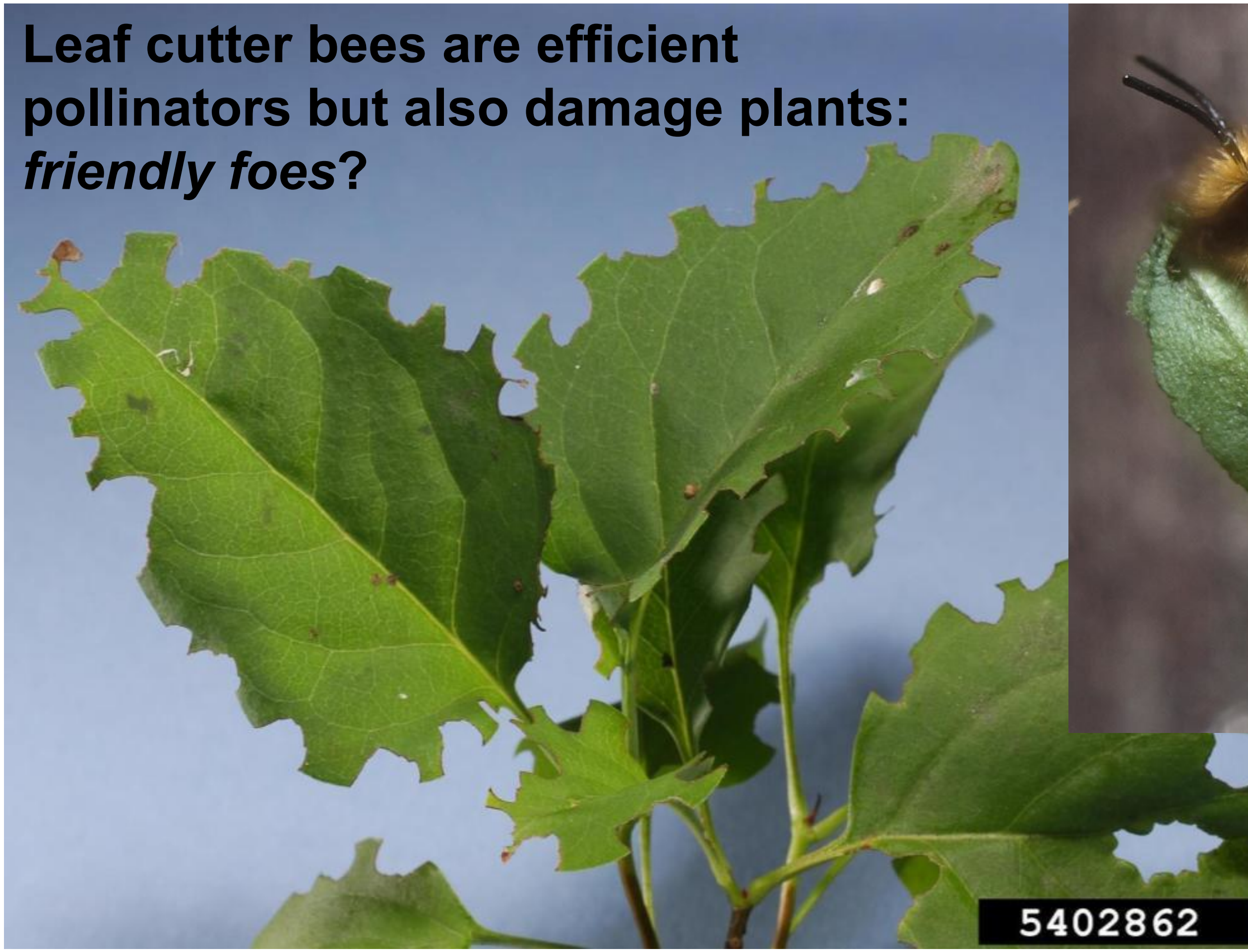
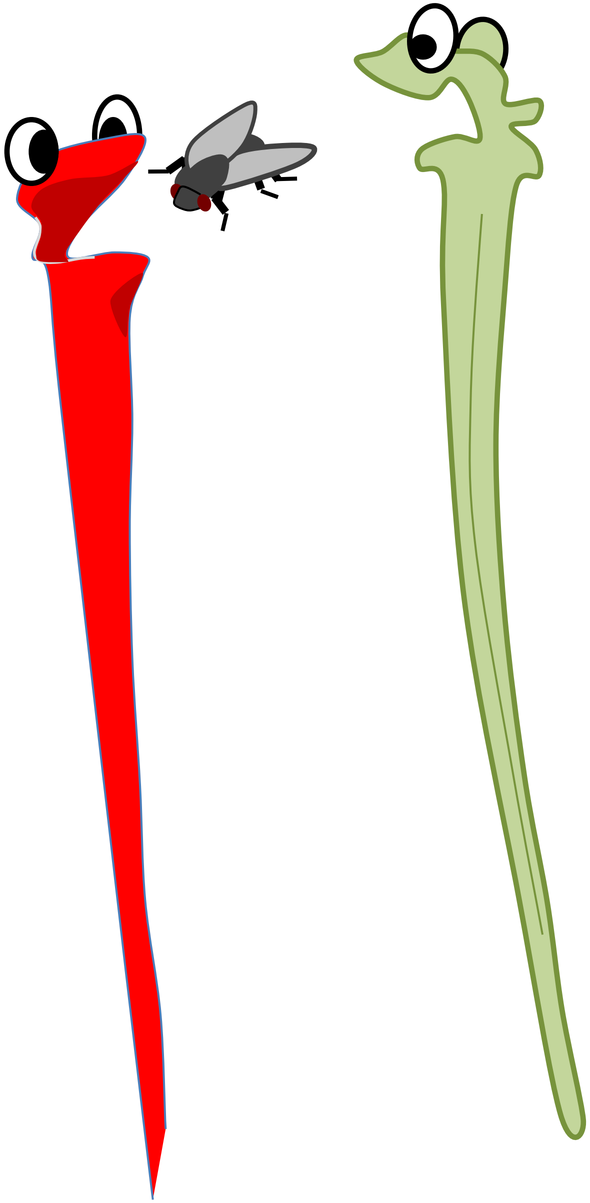


Photo courtesy [Joseph Berger]Photo courtesy Joseph Berger, Bugwood.org; [Jim Bennett]

- Alliances are tenuous
- Organisms act in their own self-interest and are the product of selection for maximal fitness
- When species use each other, opportunities arise for stealing, cheating and / or deception

- As honesty becomes rarer, the advantage of dishonesty decreases
- Many arthropods can learn; this will select against dishonesty in plants
- Cheating and deception may emerge and disappear through time



Ongoing questions and studies

- How do herbivores suppress and evade plant defenses?
- How can we control herbivore damage to crop plants, including the ongoing problems of locusts in Australia and phylloxera aphid infestations of wine grapes, in a sustainable manner?
- How can we protect pollinators and natural enemies of herbivores as we battle herbivores?
- What are the long-term and tri-trophic effects of plant varieties that produce false alarm signals?