Chemical Ecology Plant-Plant Interactions

Types of Interactions:

- can be positive or negative, intra-specific or inter-species

1. "talking trees" (cooperation via plant-plant defense signals)
2. allelopathy (inhibition of competitors)
3. locating hosts (parasitic vascular plants)

The talking tree hypothesis was the first articulation that herbivore attacked trees could warn other trees

Rapid Changes in Tree Leaf Chemistry Induced by Damage: Evidence for Communication Between Plants

Abstract. *Potted poplar ramets showed increased concentrations and rates of synthesis of phenolic compounds within 52 hours of having 7 percent of their leaf area removed by tearing, as did undamaged plants sharing the same enclosure. Damaged sugar maple seedlings responded in a manner similar to that of the damaged poplars. Nearby undamaged maples had increased levels of phenolics and hydrolyzable and condensed tannin within 36 hours, but exhibited no change in rates of synthesis. An airborne cue originating in damaged tissues may stimulate biochemical changes in neighboring plants that could influence the feeding and growth of phytophagous insects.*

Attacks by herbivores on plants may reduce the quality of the plant tissues for subsequent feeding (*1*, *2*). It has not been known whether such changes occur quickly enough to reduce ongoing defoliation. We report here that poplar (*Populus* × *euroamericana*) ramets and sugar maple (*Acer saccharum* Marsh) seedlings exhibit elevated concentrations of phenols and increased protein binding of phenolic compounds in leaf extracts within 75 hours of being mechanically damaged. Synthesis of these compounds apparently increases in response to damage. Recently, Rhoades (*3*) presented bioassay results suggesting that a factor released by damaged trees stimulates changes in the leaf quality of undamaged neighbors. We also report chemical evidence of such communication between trees: leaves of undamaged individuals in the same enclosure as damaged plants exhibit similar chemical changes.

In two separate experiments 45 1.5-month-old poplar ramets and 45 4-month-old sugar maple seedlings grown under controlled conditions (*4*) were placed in two gas-tight Plexiglas enclosures (*5*) inside a growth chamber. One enclosure housed 15 true control plants, while the other housed 15 experimental and 15 "communication control" plants. Two leaves on each experimental plant were damaged (*6*), while the leaves of both control groups were untouched. At the time of damage, $^{14}CO_2$ was introduced into both enclosures and then scrubbed from the air (*7*) before the first of three sampling intervals (*8*). At each interval five plants from each group were removed from the chamber for analyses of four chemical leaf traits known to influence insect feeding and to be affected by herbivore damage in other tree species (*1*, *2*). Four leaves from each seedling (*9*) were extracted and analyzed for total phenolics, hydrolyzable and condensed tannins, and tanning activity (*10*). Carbon-14 was assayed in leaf extracts and in phenolics precipitated by aqueous lead acetate (*11*).

At the first sampling interval all seedlings had elevated chemical measures, probably because of metabolic stimulation by elevated CO_2 (*12*). Hence the effect of damage must be considered

Populus hybrid and sugar maple

- *could not be repeated*

The first 'real' discovery of volatiles that have effects on other plants was the discovery of methyl jasmonate

Proc. Natl. Acad. Sci. USA
Vol. 87, pp. 7713–7716, October 1990
Botany

Interplant communication: Airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves

(jasmonic acid/pathogen/wound-inducible genes/localized/systemic defense responses)

EDWARD E. FARMER AND CLARENCE A. RYAN

Institute of Biological Chemistry, Washington State University, Pullman, WA 99164-6340

Contributed by Clarence A. Ryan, July 13, 1990

ABSTRACT **Inducible defensive responses in plants are known to be activated locally and systemically by signaling molecules that are produced at sites of pathogen or insect attacks, but only one chemical signal, ethylene, is known to travel through the atmosphere to activate plant defensive genes. Methyl jasmonate, a common plant secondary compound, when applied to surfaces of tomato plants, induces the synthesis of defensive proteinase inhibitor proteins in the treated plants and in nearby plants as well. The presence of methyl jasmonate in the atmosphere of chambers containing**

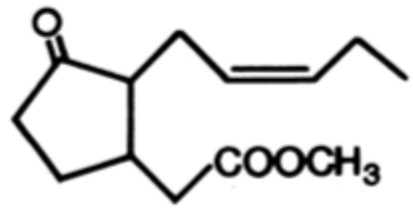


FIG. 1. Structure of methyl jasmonate.

Table 2. Induction of proteinase inhibitors I and II in leaves of tomato plants incubated in the presence of leafy branches of the sagebrush *A. tridentata* ssp. *tridentata*

	Proteinase inhibitor			
	I		II	
Plants	μg/g of tissue	*n*	μg/g of tissue	*n*
Experiment 1				
Incubated with *A. tridentata*	54.5 ± 8.7	4	ND	
Control	0	4	ND	
Experiment 2				
Incubated with *A. tridentata*	71.0 ± 16.1	10	50.6 ± 13.7	12
Control	0	10	0	12

The plants were placed so that no physical contact was possible between the sagebrush leaves and tomato leaves. The chambers (volume, 1250 ml) were sealed, incubated for 2 days under the

Sagebrush– tomato signaling

Farmer and Ryan, PNAS 1990

Synthesis of hexenal and "green leaf" volatiles

(see fatty acids/jasmonic acid lecture)

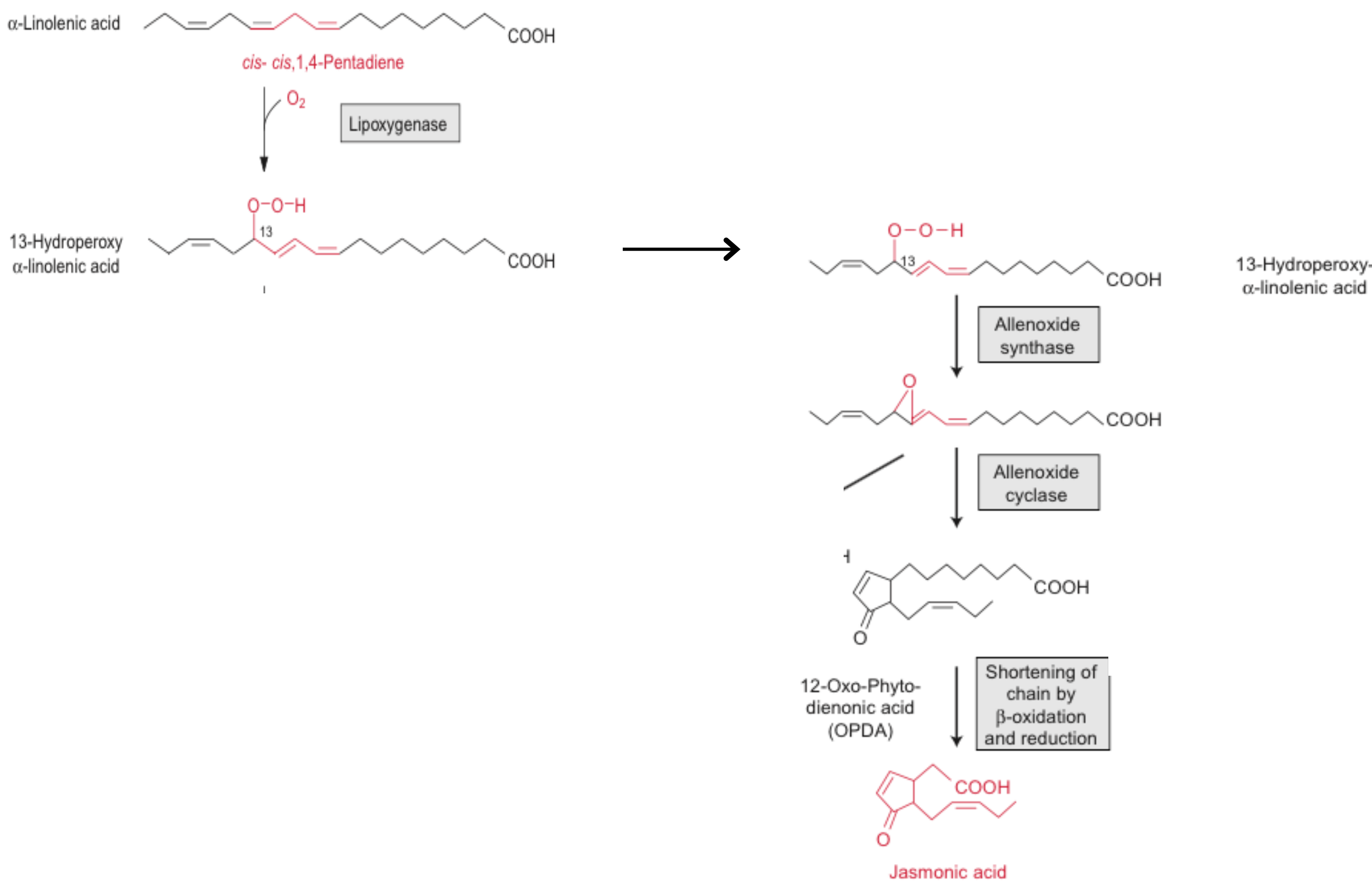


Figure 15.30 An allene oxide synthase and allene oxide cyclase (both belong to the

Heldt Fig 5.30

Synthesis of hexenal and "green leaf" volatiles

(see fatty acids/jasmonic acid lecture)

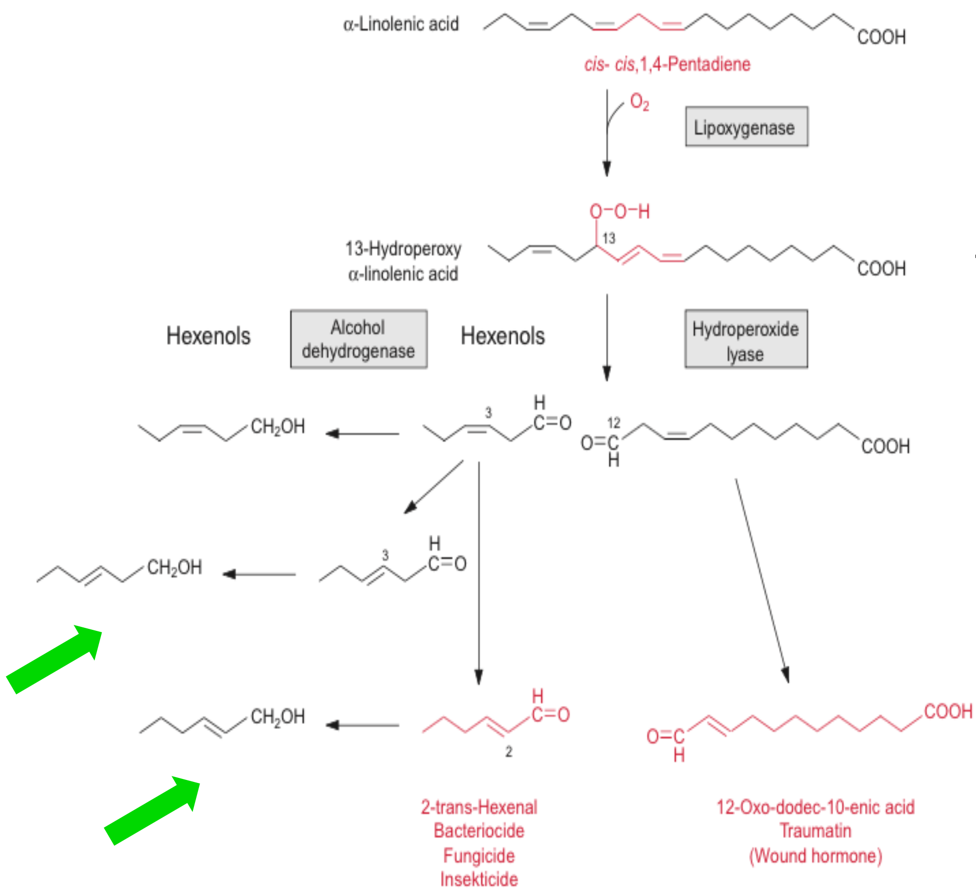


Figure 15.29 By reaction with O_2, lipoxygenase catalyzes the introduction of a

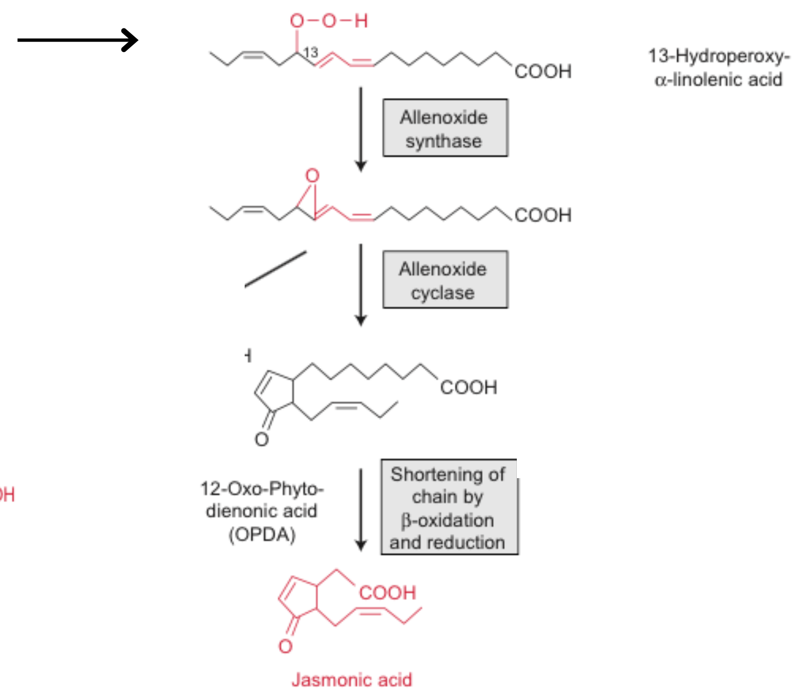
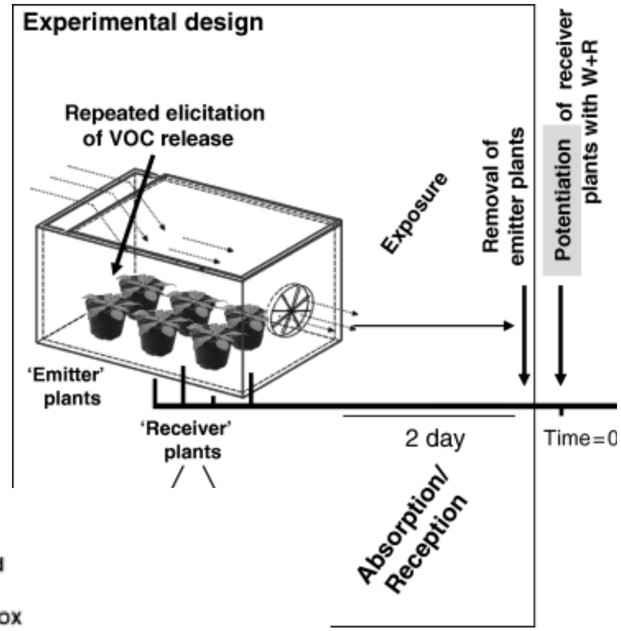
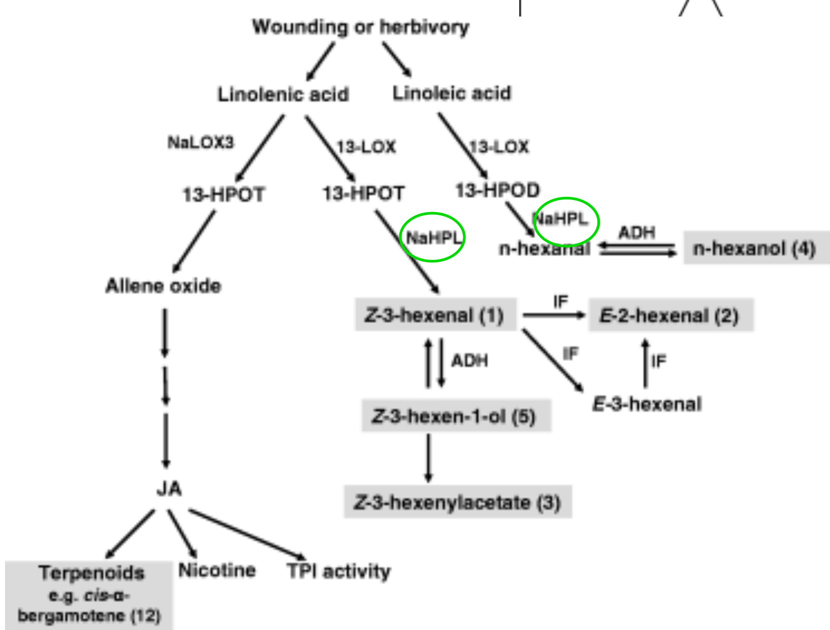


Figure 15.30 An allene oxide synthase and allene oxide cyclase (both belong to the

Heldt Fig 5.30

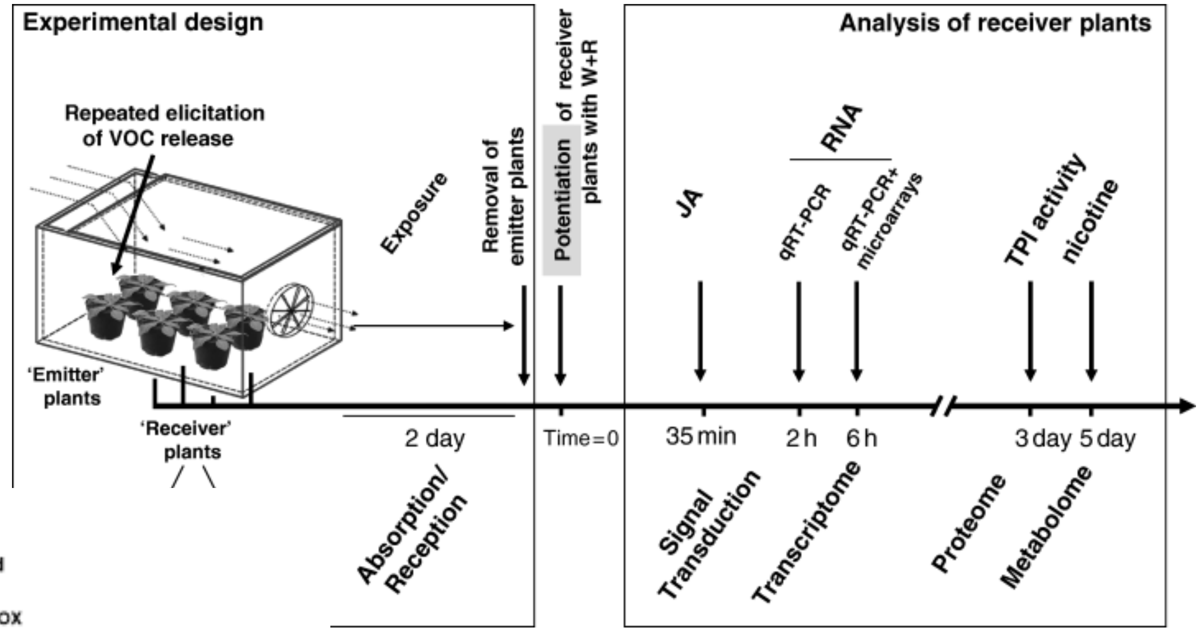
Green leaf volatiles induced by wounding (hydroperoxide lyase-dependent) induce transcriptional changes but **no detectable defense** proteins or nicotine

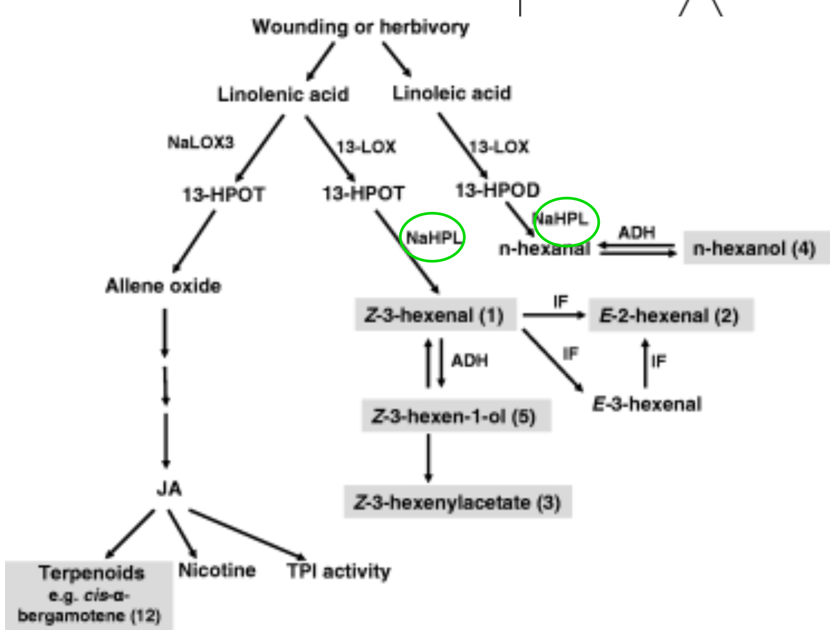




Paschold et al (2006) Plant Journal 45; 275-291

Green leaf volatiles induced by wounding (hydroperoxide lyase-dependent) induce transcriptional changes but **no detectable defense** proteins or nicotine





Plants are listening, but ignoring the message

Paschold et al (2006) Pl Journal 45; 275-291

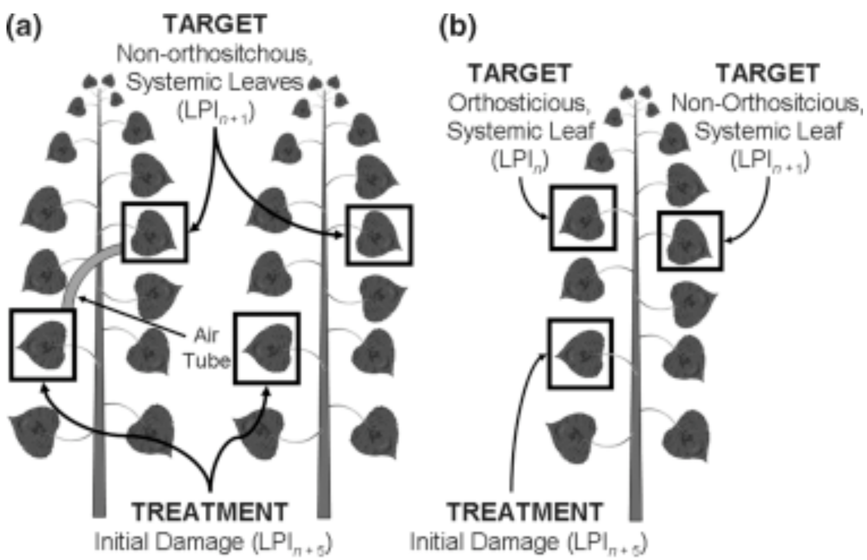
i) intra-specific **defense signals**: *Nicotiana attenuata* with suppressed green leaf volatile synthesis (GLVs)

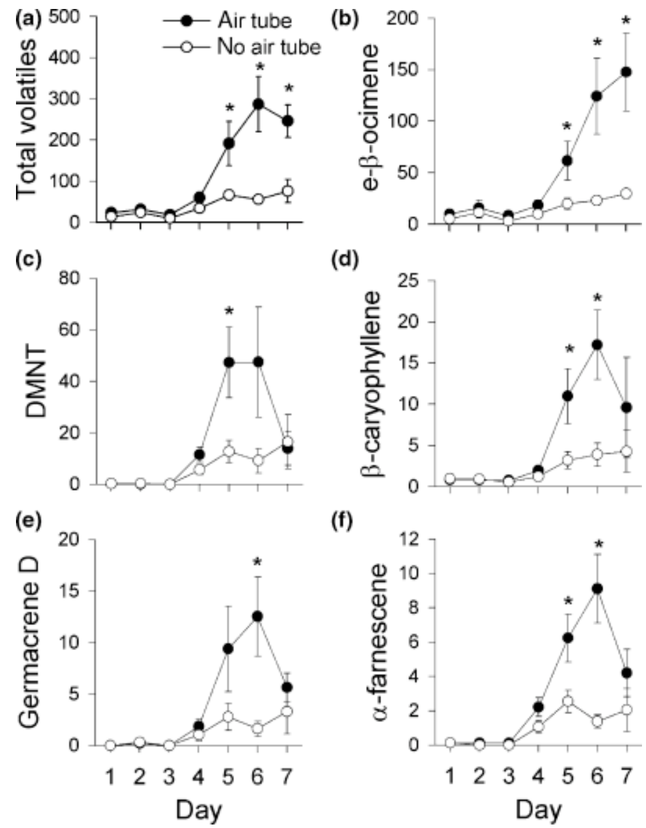
- RNAi-suppression of ***hydroperoxide lyase*** leads to plants that cannot make GLVs

- by subtraction, Paschold et al,. (2006) determined that 30-40 genes are induced (but not proteins) or nicotine

  ("plants are listening, but ignoring the message")

ii) intra-plant signaling: *Populus* GLVs from one leaf can prime defenses in distal leaf via air flow

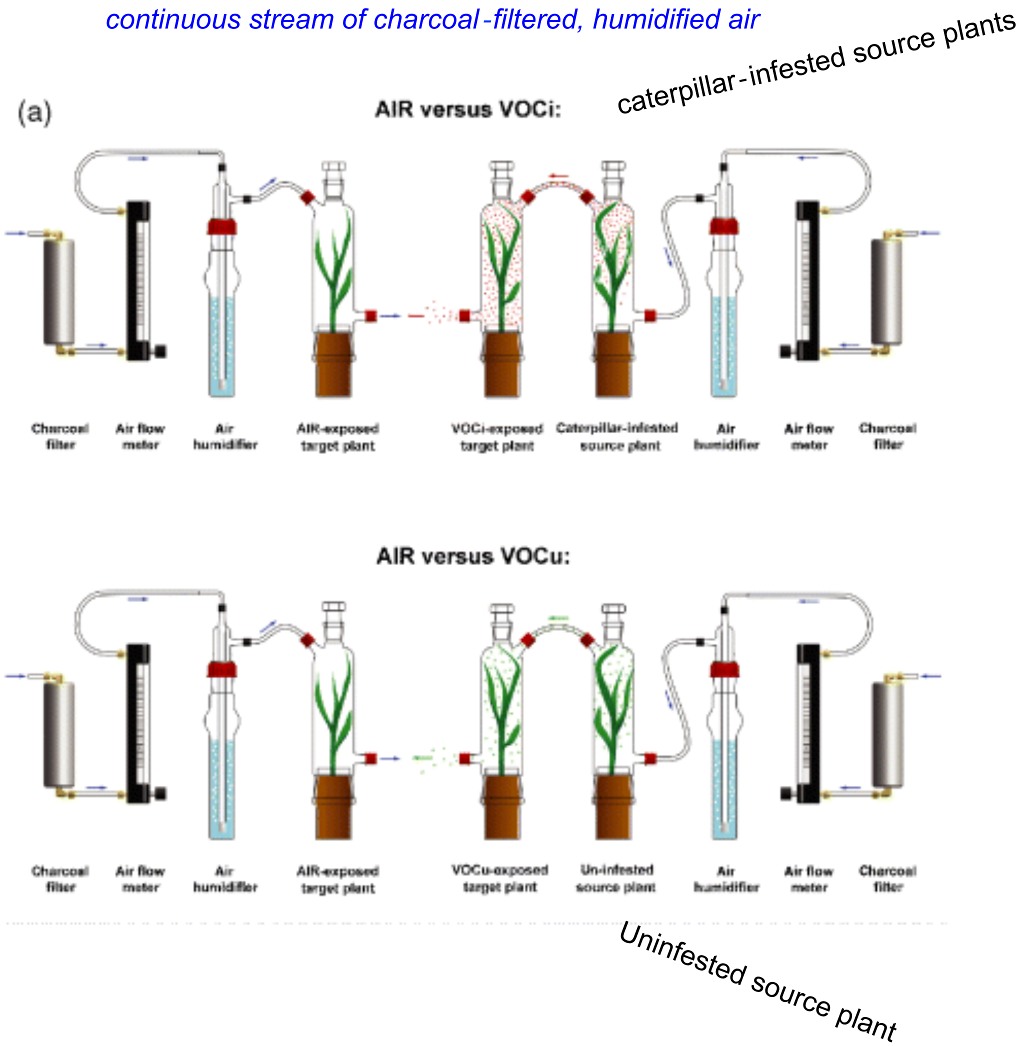




Frost et al, Ecol Lett 2007

iii) plant-plant signaling in maize: priming by airborne signals boosts caterpillar resistance in maize

continuous stream of charcoal-filtered, humidified air

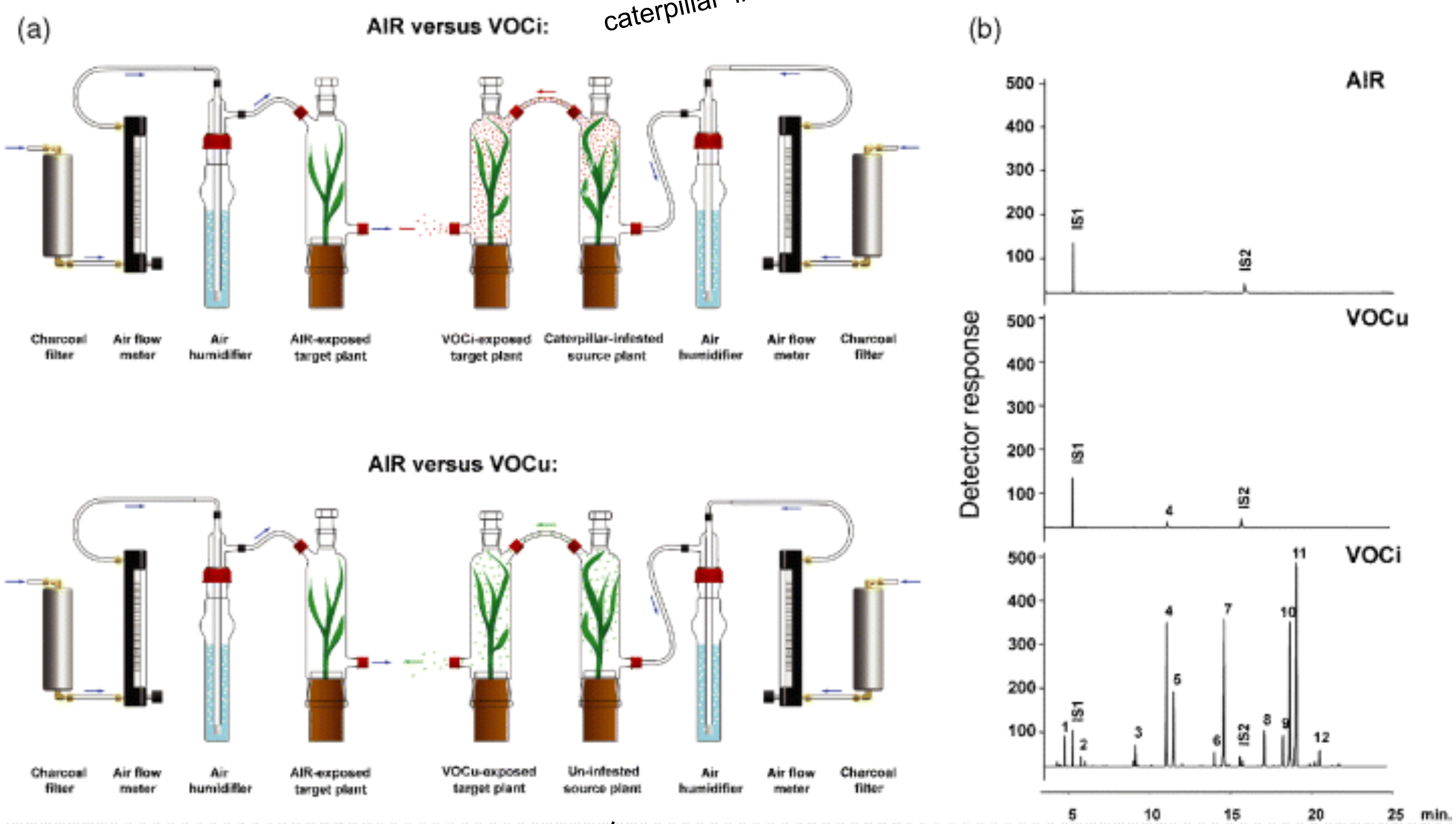


The Plant Journal 49: 16-26 (2006)

iii) plant-plant signaling in maize: priming by airborne signals boosts caterpillar resistance in maize

continuous stream of charcoal-filtered, humidified air

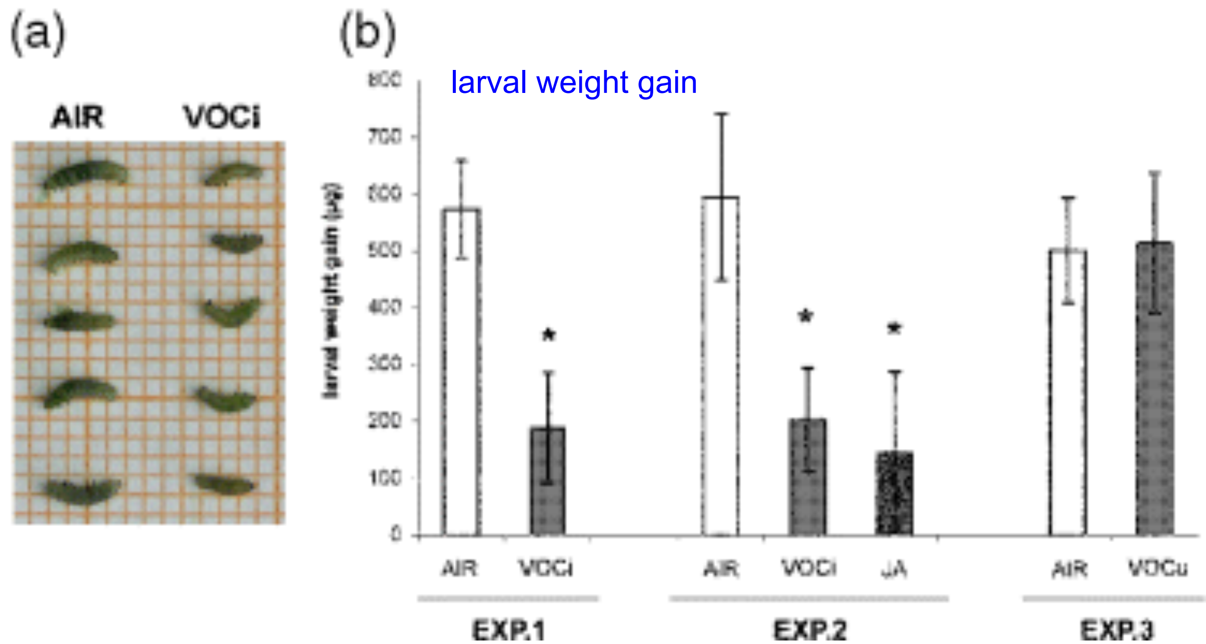
caterpillar-infested source plants



Uninfested source plant

The Plant Journal 49: 16-26 (2006)

iii) plant-plant signaling in maize: priming by airborne signals boosts caterpillar resistance in maize



- is this relevant in the field?

The Plant Journal 49: 16-26 (2006)

iii) plant-plant signaling in maize (via priming)

- damage by caterpillar damage -> releases volatiles (sesquiterpenoids: ß-farnesene, caryophyllene)
- sophisticated set-up for air flow between maize plants
- wound-induced plants emit different volatiles than uninduced plants.
- both direct and indirect defenses
- herbivore growth is reduced if plants are volatile-induced previously, substantiating the priming effect.

Can plant-plant communication take place via shared mycorrhizae?

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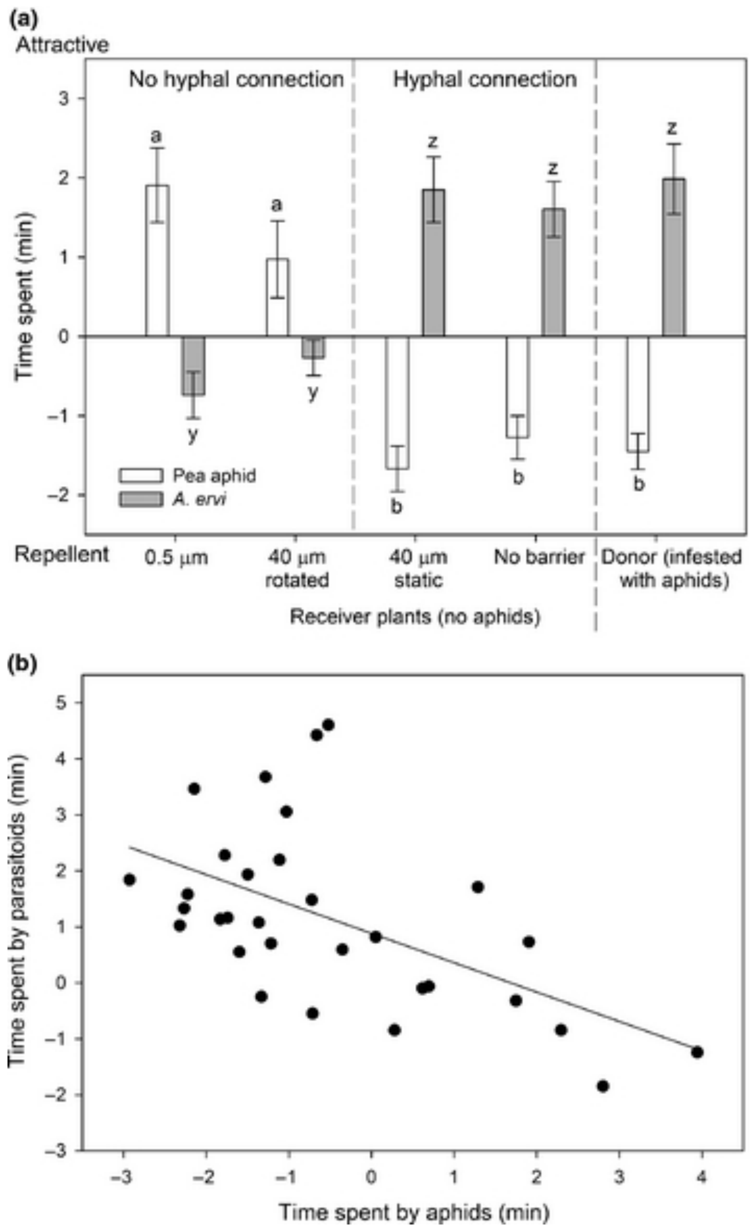

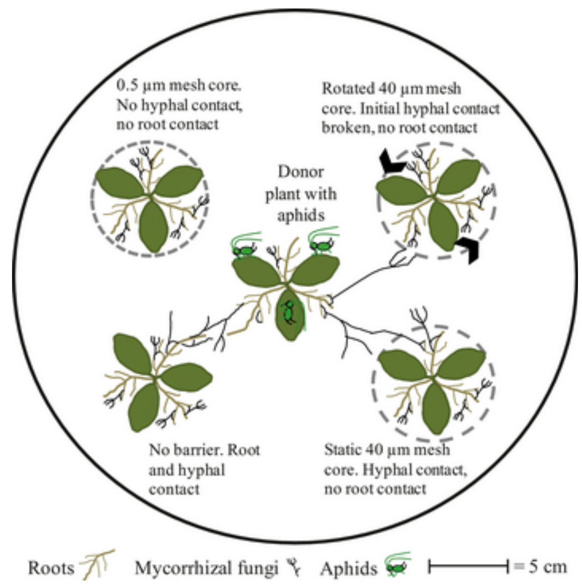

Ecology Letters 16: 835 (
Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack

Can plant-plant communication take place via shared mycorrhizae?

SCIENTIFIC REPORTS

OPEN

Hijacking common mycorrhizal networks for herbivore-induced defence signal transfer between tomato plants

SUBJECT AREAS:
HERBIVORY
FOOD WEBS
ARBUSCULAR MYCORRHIZA

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RESEARCH ARTICLE

Interplant Communication of Tomato Plants through Underground Common Mycorrhizal Networks

Yuan Yuan Song, Ren Sen Zeng, Jian Feng Xu, Jun Li, Xiang Shen, Woldemariam Gebrehiwot Yihdego

Published: October 13, 2010 • https://doi.org/10.1371/journal.pone.0013324

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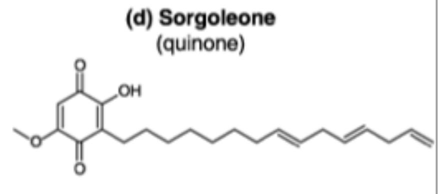
<u>Allelopathy</u>: *the suppression of growth of neighbouring plants by the release of phytotoxic compounds into the environment*

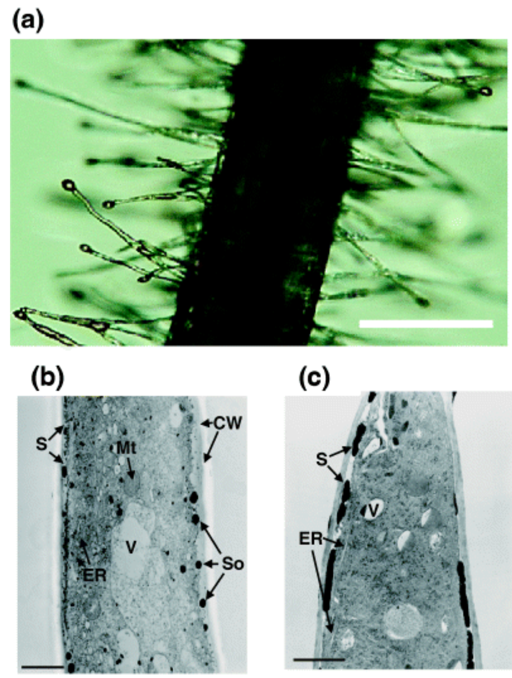
Sorghum and ***sorgoleone***

- sorghum is a tropical cereal crop (like millet)
- also contains cyanogenic glycosides, and tannins
- sorgeolone is a quinone, actively **secreted** from root hairs
- inhibits H+/ATPase in roots of other species
- 10 µM inhibits competitor seed germination, and up to 10-100 µM is found in soil

Allelopathy: *the suppression of growth of neighbouring plants by the release of phytotoxic compounds into the environment*

Sorghum



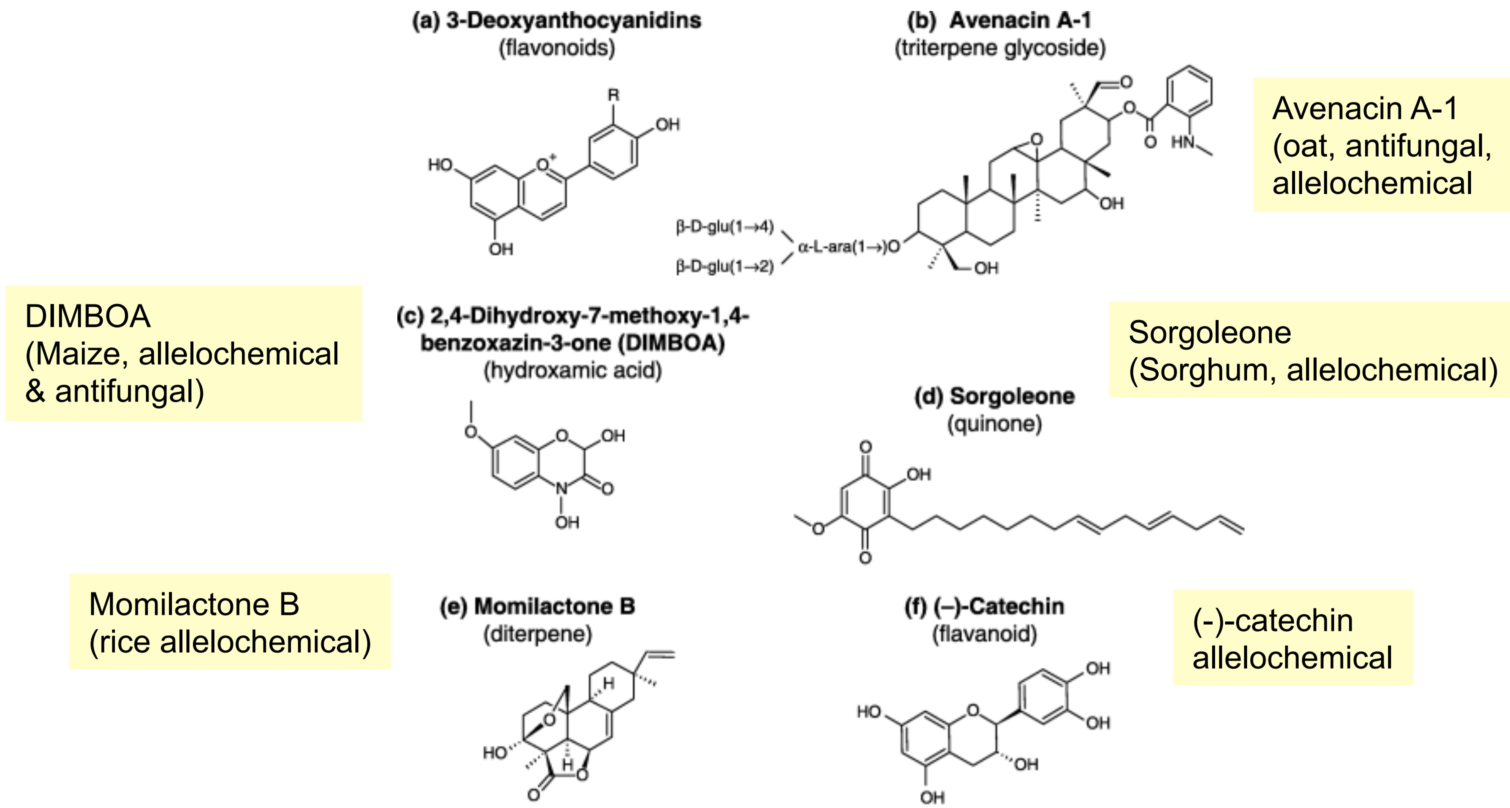


Root hairs containing sorgoleone

Sorghum exudates **sorgoleone** from roots

B. Field et al., New Phytologist 172: 193-207 (2006)

<u>Allelopathy</u>: *the suppression of growth of neighbouring plants by the release of phytotoxic compounds into the environment*



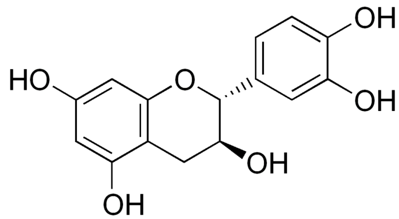
Examples of allelopathic compounds

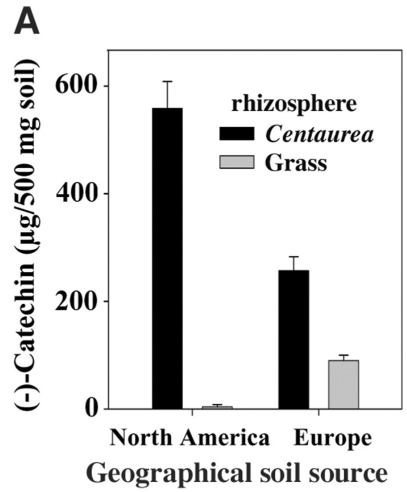
B. Field et al., New Phytologist 172: 193-207 (2006)

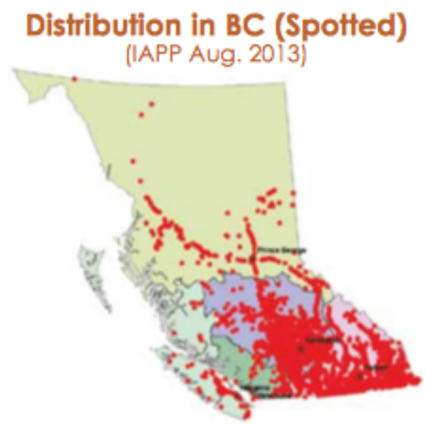
Spotted Knapweed (*Centureae maculosa*) is invasive in rangelands & releases (-)-catechin into soils

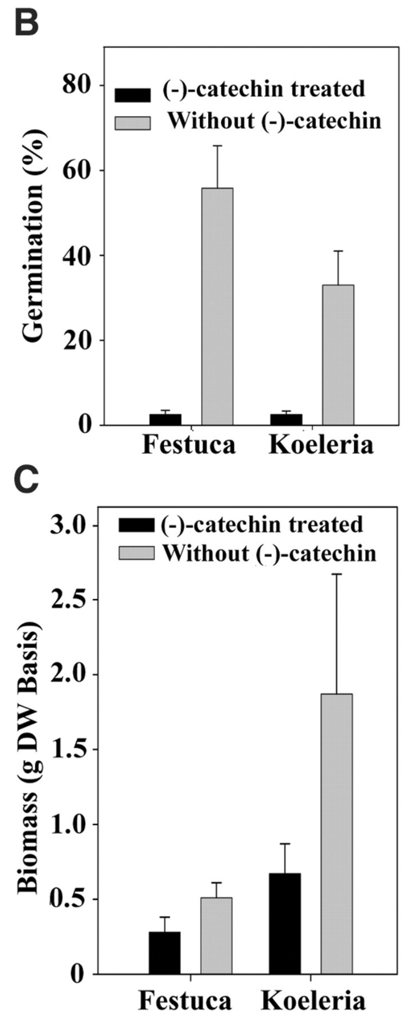
Spotted knapweed
(*Centureae maculosa*
C. biebersteinii)

http://bcinvasives.ca/documents/Knapweed_TIPS_Final_08_06_2014.pdf









H. P. Bais et al., Science 301, 1377 -1380 (2003)

Science AAAS

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Sorghum and ***sorgoleone***

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- also contains cyanogenic glycosides, and tannins
- sorgeolone is a quinone, actively **secreted** from root hairs
- inhibits H+/ATPase in roots of other species
- 10 µM inhibits competitor seed germination, and up to 10-100 µM is found in soil

Spotted knapweed in BC

- invasive weed problem for BC (rangelands, competes with native grasses and forages)
- contains (-)-catechin, but role unclear, .. original experiments / catechin concentrations could not be repeated.
- catechin is flavanol, related to the condensed tannins

Parasitic plants

3. Parasitic Plants and Phytochemical Signals

[Common parasitic plants: *Striga, Orobanche, Cuscuta*]

- obtain nutrients by tapping into vascular system of hosts

note: distinguish parasites from epiphytes, which only use other plants for support)

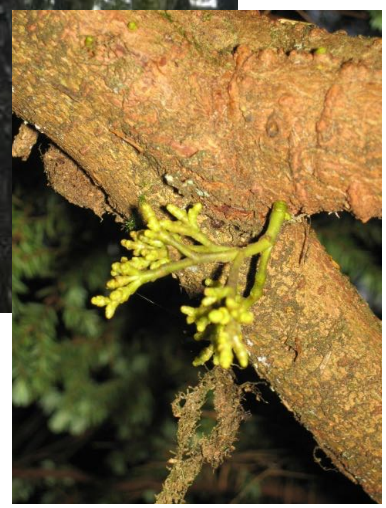
- dwarf mistletoes (*Arceuthium* - witches broom) in BC leads to significant forestry losses
- *Striga* (witchweed) can cause severe crop losses

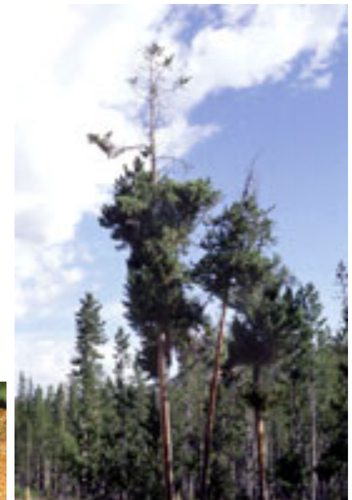
(root parasite on sorghum, rice, millet, maize)

=> How do these parasitic plants locate their hosts?

Parasitic plants

Arceuthobium , dwarf mistletoe
(common parasite on BC conifers)





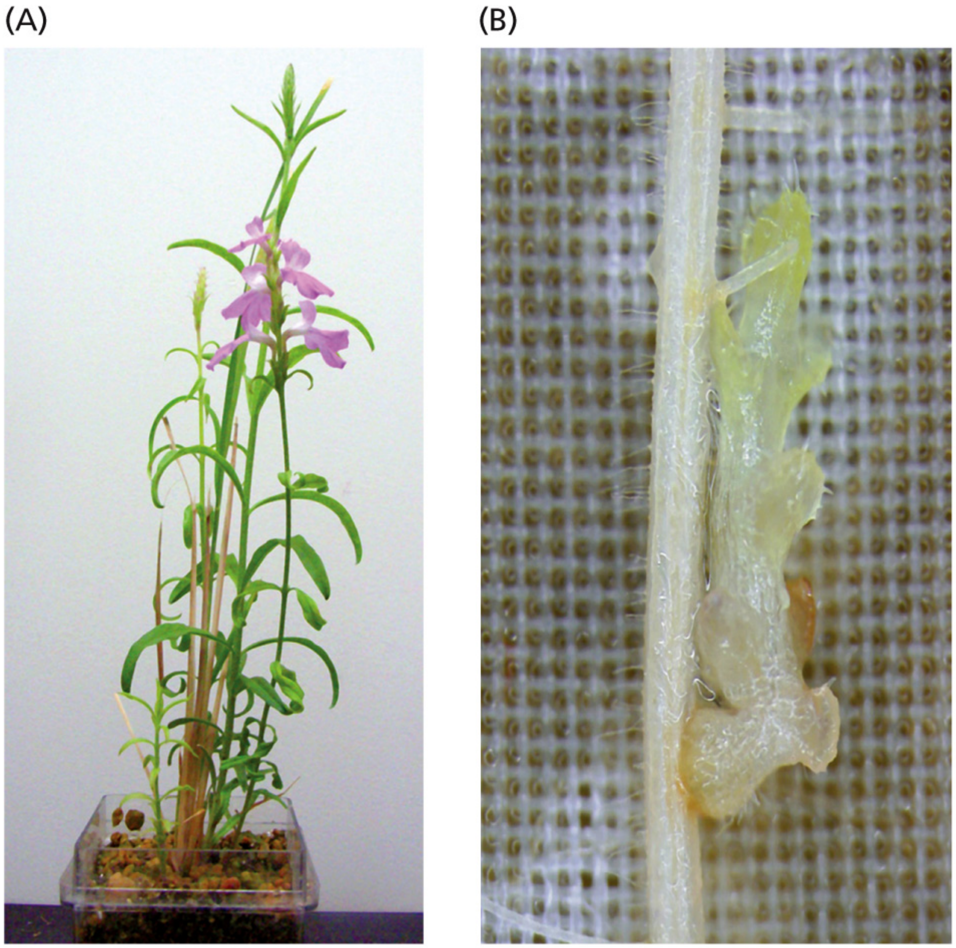
http://www.apsnet.org/

Parasitic plants

Striga asiatica (witchweed) on sorghum (millet)

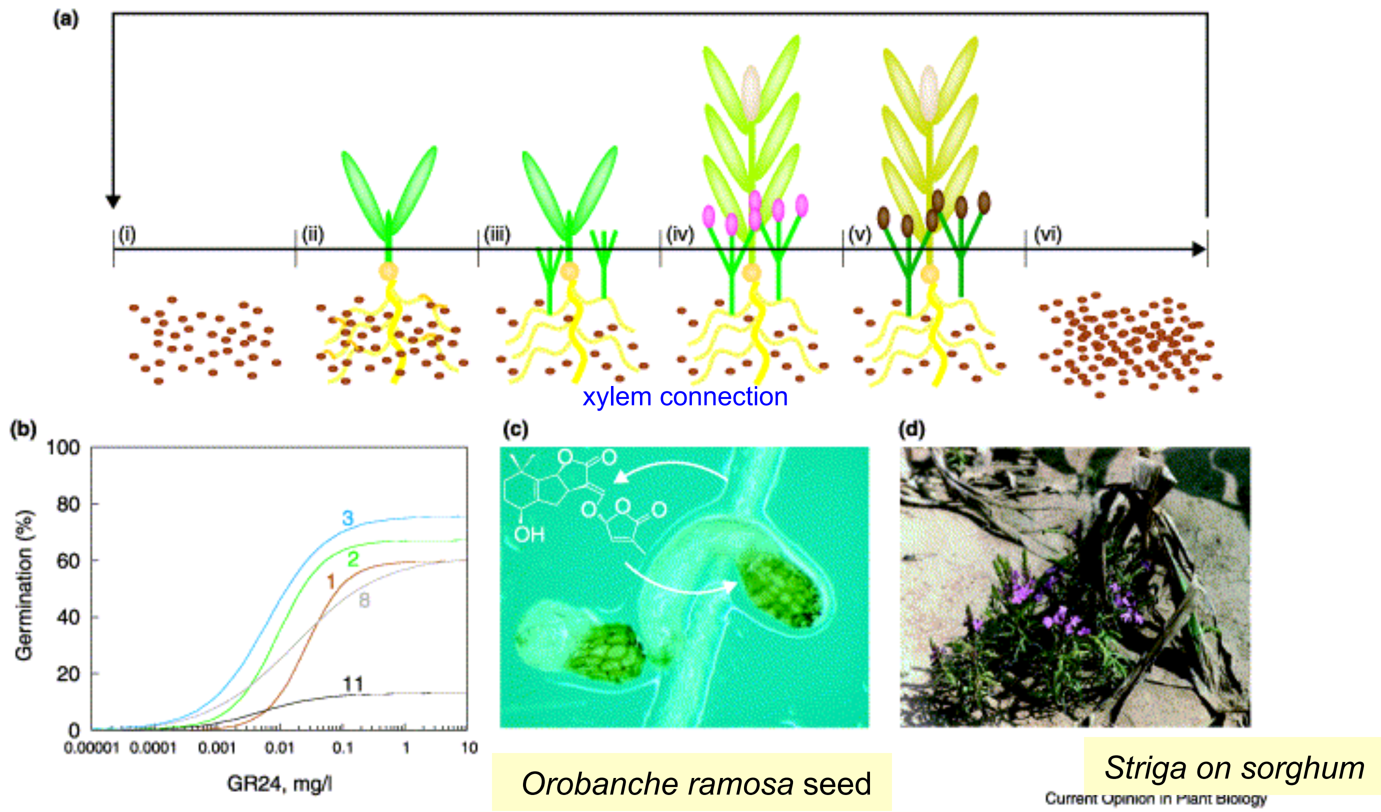
*A **striga** (Polish: strzyga) is a woman transformed into a monster by a curse. She is filled with hatred towards all living beings, devouring them without a second thought*

Figure 15.15 Rice plants colonized by root parasitic plants



PLANT PHYSIOLOGY AND DEVELOPMENT 6e, **Figure 15.15**

Germination of seeds of parasitic plants (*Striga*) requires plant stimulants



Bouwmeester et al. Curr Opin Plant Biol 6 358-364

Germination of seeds of parasitic plants (Striga, Orobanche) requires stimulants, found in various root exudates

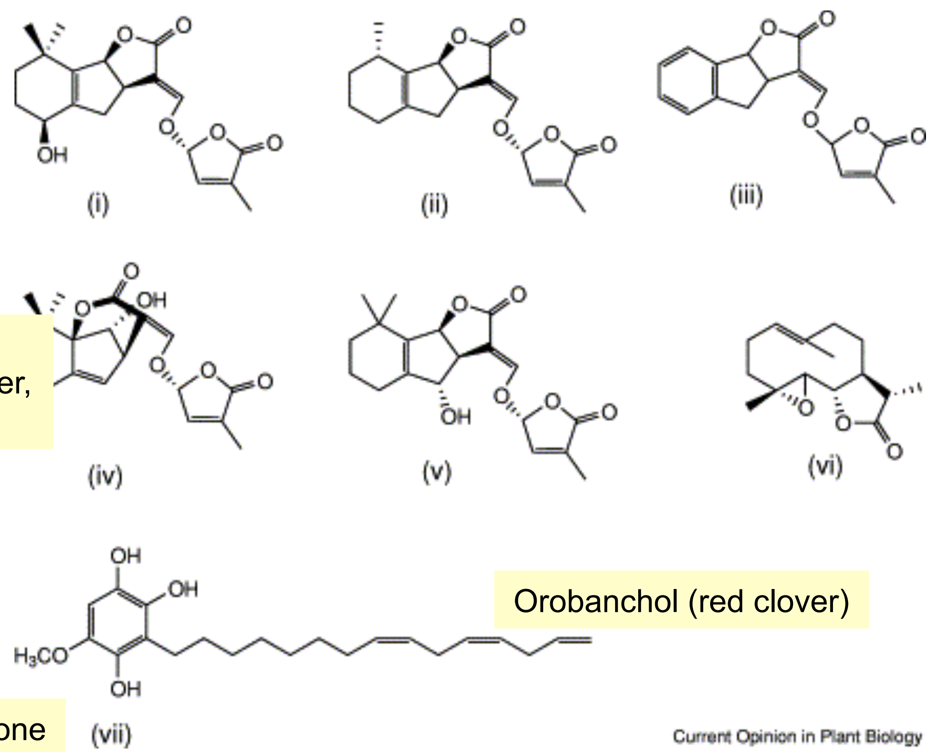
(+)–Strigol (Sorghum, maize)

Sorgolactone (Sorghum)

Alectrol (red clover, cowpea)

Orobanchol (red clover)

Dihydrosorgoleone (Sorghum)

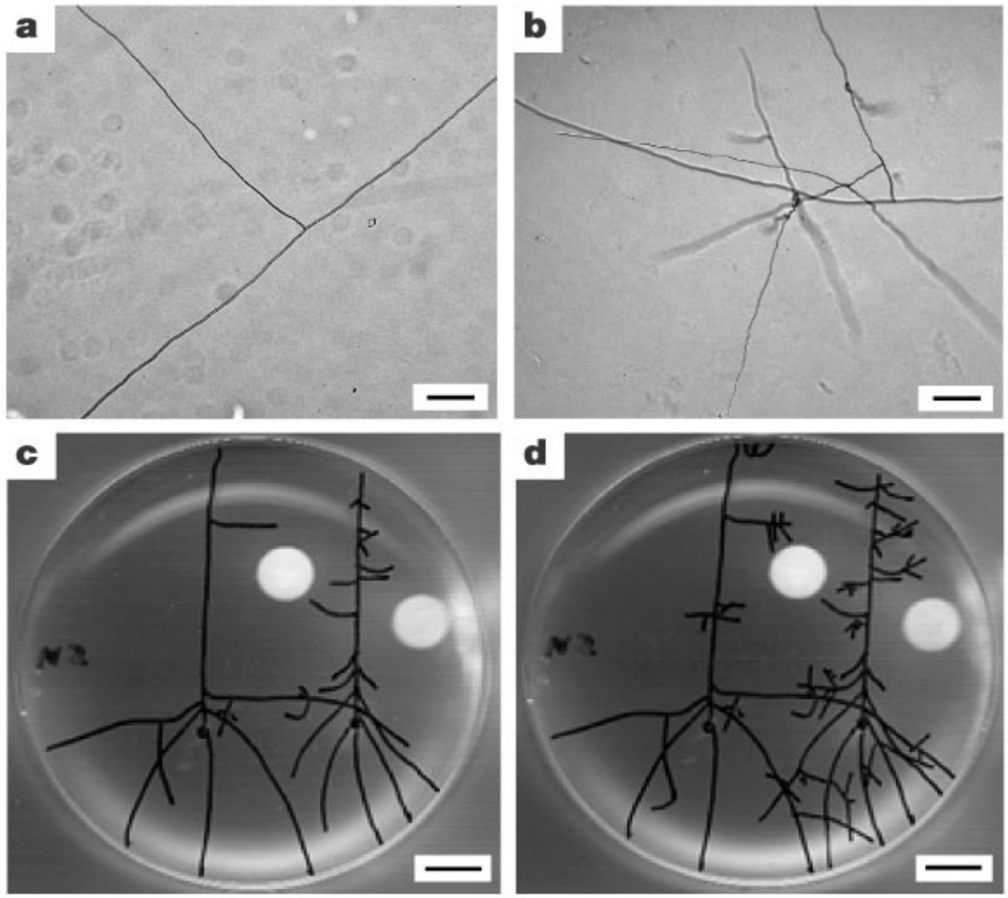


Why do plants make such germination stimulants??

Bouwmeester et al. Curr Opin Plant Biol 6 358-364

Hyphal branching assay for *Gigaspora margarita* (arbuscular mycorrhizal fungus)

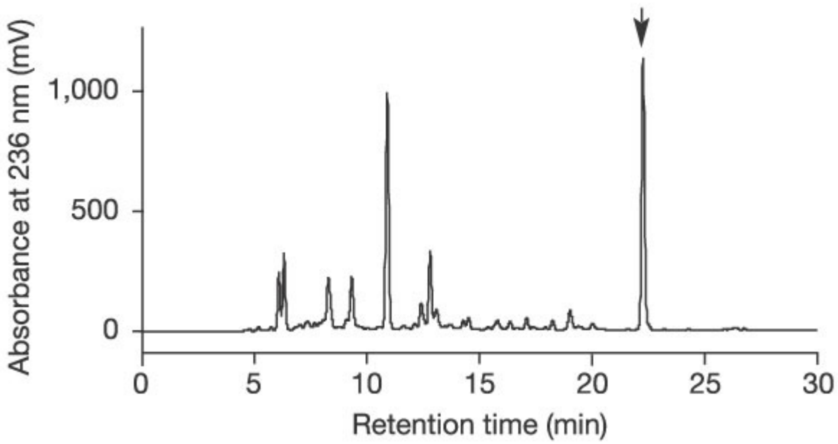
controls



ethyl acetate extracts (15 microg per disk)

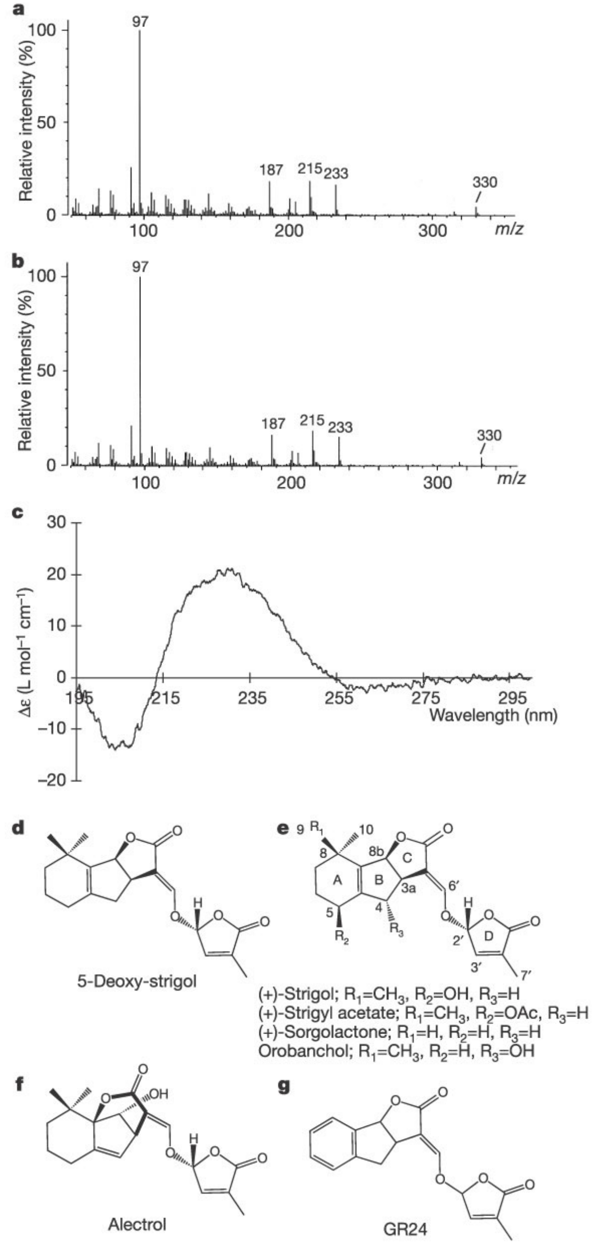
Akiyama et al, Nature 2005

Identification of hyphal branching factor from *Lotus japonicus* roots



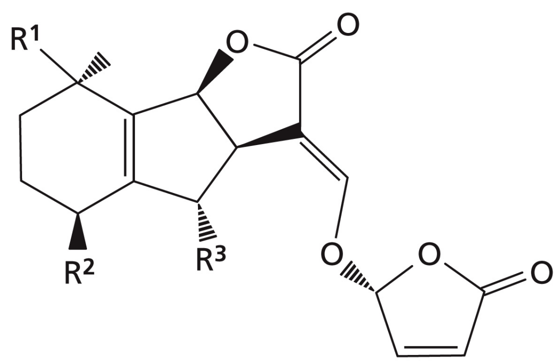
5-deoxy strigol

Alectrol



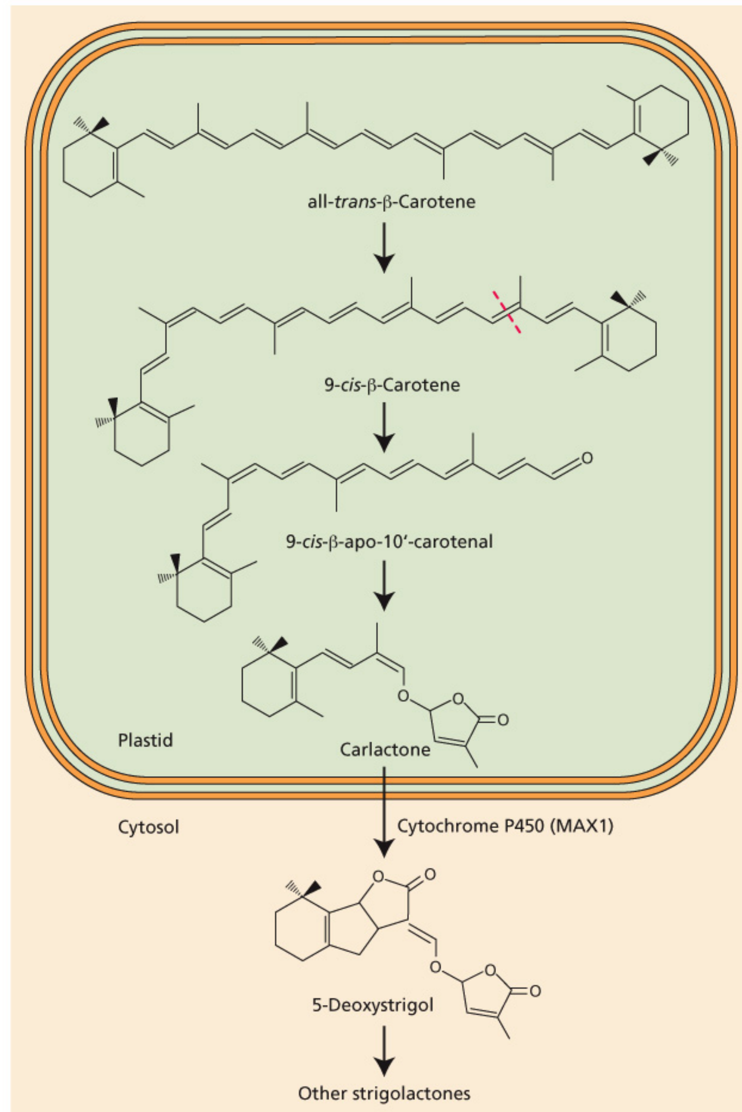
Strictolactones are now know as root-generated regulators of shoot branching - phytohormones (**inhibit** branching)

(H) **Strigolactone**



PLANT PHYSIOLOGY AND DEVELOPMENT 6e, Figure 15.8 (Part 8)

Figure 15.8 Synthesis of strigolactones

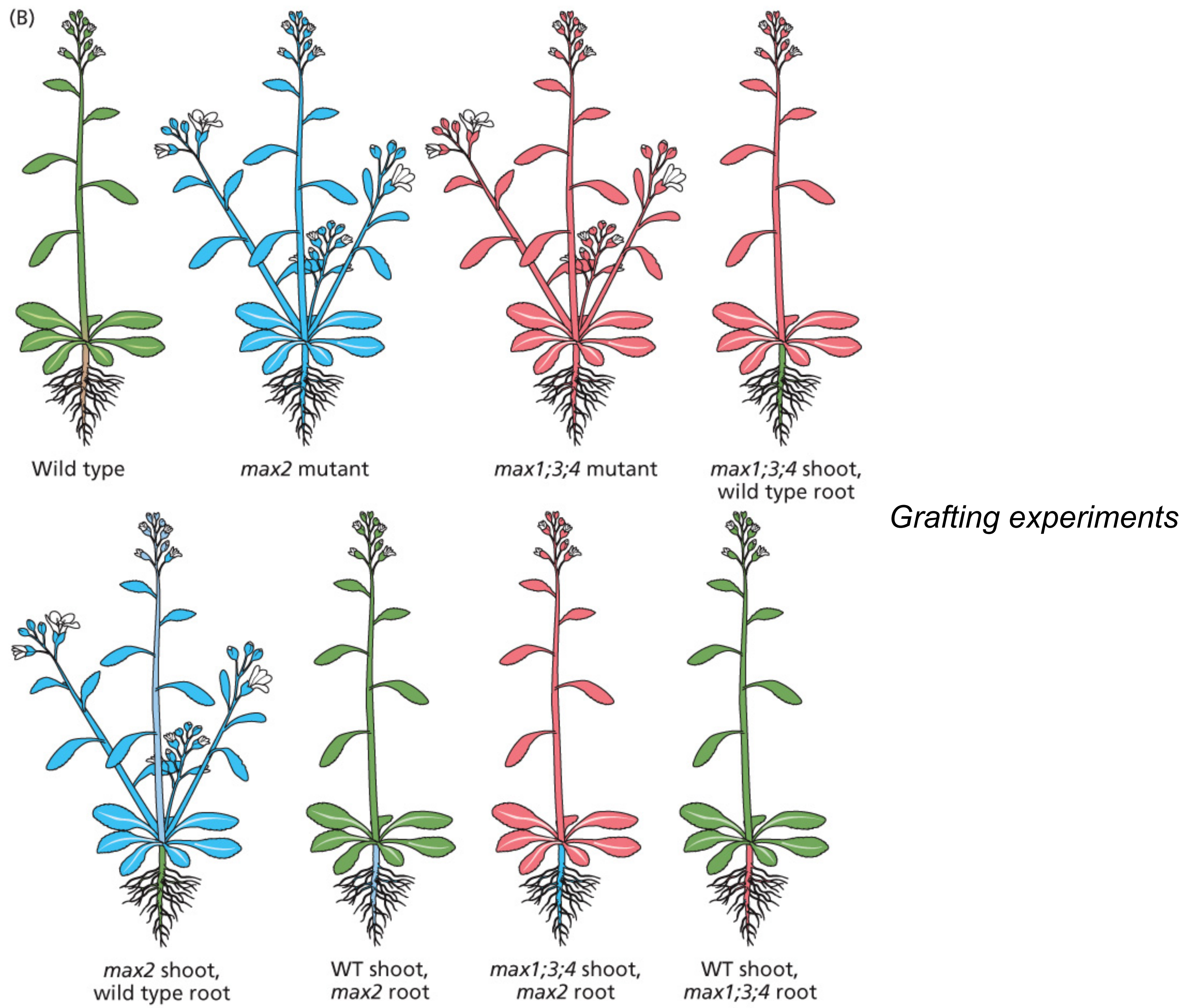


***PLANT PHYSIOLOGY AND DEVELOPMENT 6e*, Figure 15.25**

Figure 19.30 Axillary bud outgrowth is inhibited by auxin and strigolactones

max2
- SL signaling mutant

max1,3,4
- SL synthesis mutants

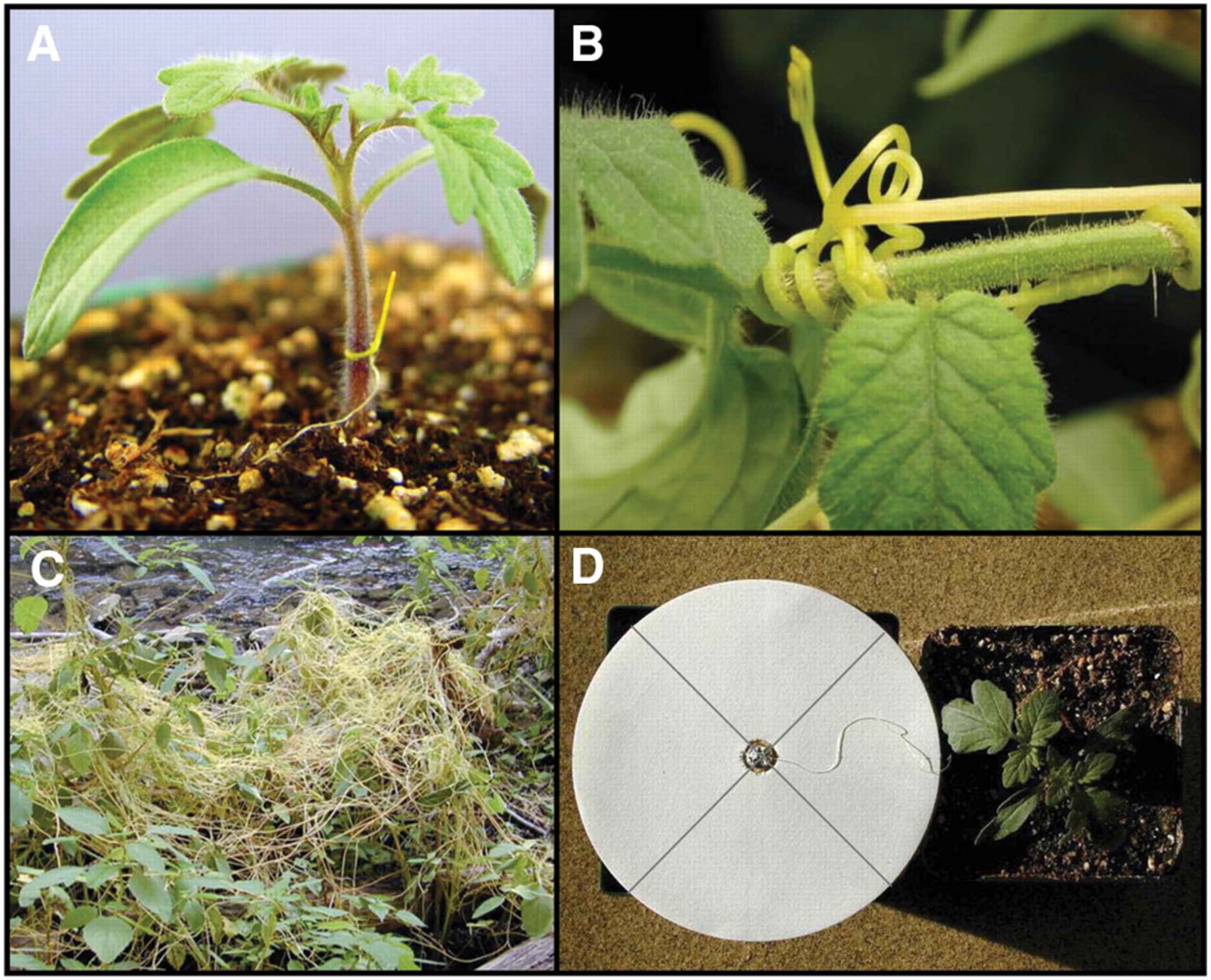


***PLANT PHYSIOLOGY AND DEVELOPMENT 6e*, Figure 19.30 (Part 2)**

Parasitic plants – *Cuscuta pentagona* (dodder) (morning glory family)

http://www.ipm.ucdavis.edu/PMG/C/W-CV-CSPP-YP.001.html

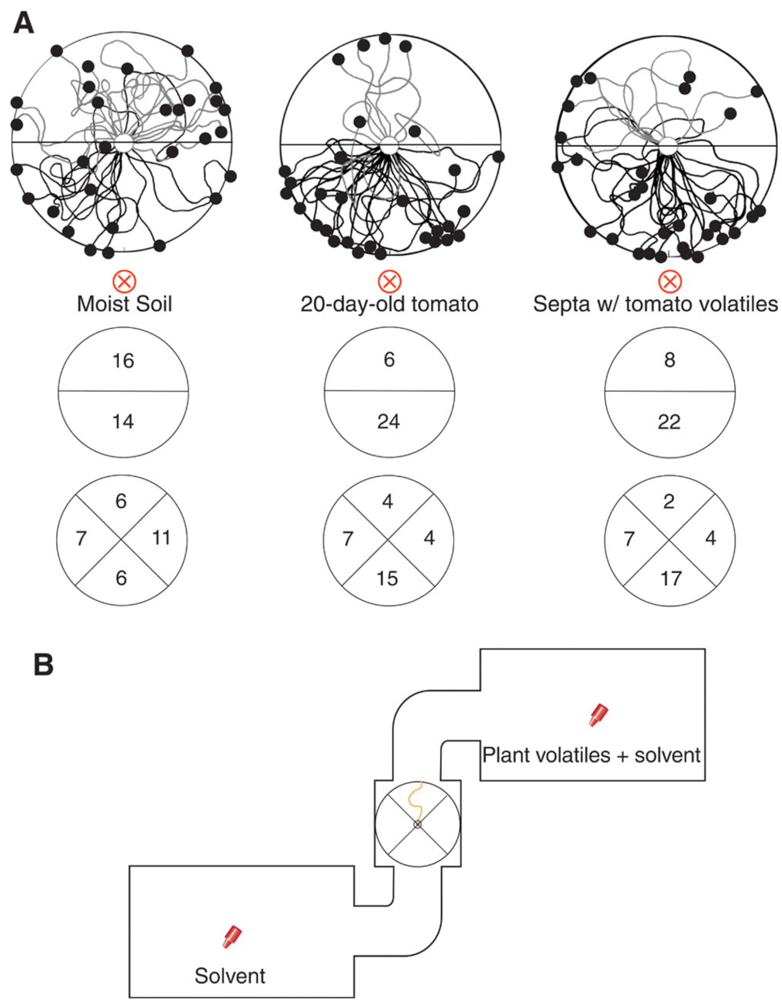
How does Cuscuta pentagona find its host?



Dodder
Cuscuta pentagona

J. B. Runyon et al., Science 313, 1964 -1967 (2006) LINK

Foraging by *Cuscuta pentagona* seedlings



J. B. Runyon et al., Science 313, 1964 -1967 (2006)

Published by AAAS

Foraging by Cuscuta pentagona seedlings

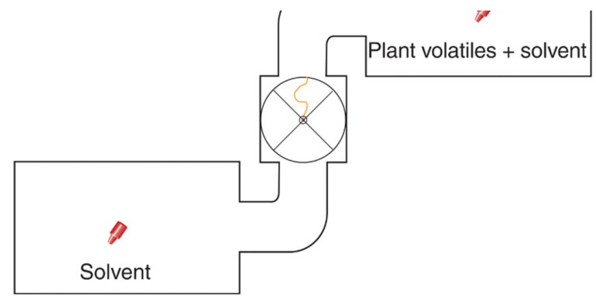
Table 4. Foraging of *Cuscuta pentagona* seedlings on filter paper discs to individual tomato (top) and wheat (bottom) volatiles released from rubber septa.

Volatile compound	Seedlings choosing disc half with or without volatile					Seedlings choosing quadrants (direction relative to volatile)				
	No. with volatile	No. without volatile	% with volatile	% without volatile	χ^2 (*P* value)	A (away)	B (side)	C (side)	D (toward)	χ^2 (*P* value)
➡ α-Pinene	23	11	68	32	4.23 (0.039)	6	8	9	11	1.53 (0.676)
➡ β-Myrcene	21	9	70	30	4.80 (0.029)	6	6	4	14	7.87 (0.049)
2-Carene	14	20	41	59	1.06 (0.304)	11	9	8	6	1.53 (0.676)
p-Cymene	17	13	57	43	0.53 (0.465)	5	7	9	9	1.47 (0.690)
➡ β-Phellandrene	21	9	70	30	4.80 (0.029)	5	6	6	13	5.47 (0.141)
Limonene	16	14	53	47	0.13 (0.715)	9	6	5	10	2.27 (0.519)
TMTT*	14	16	47	53	0.13 (0.715)	8	8	5	9	1.20 (0.753)
➡ (*Z*)-3-Hexenyl acetate	11	23	32	68	4.23 (0.039)	13	5	9	7	4.12 (0.249)
(*Z*)-3-Hexen-1-ol	15	19	44	56	0.47 (0.493)	13	6	6	9	3.88 (0.275)
(*E*)-β-Ocimene	16	14	53	47	0.13 (0.715)	3	7	10	10	4.40 (0.221)
Linalool	14	16	47	53	0.13 (0.715)	9	8	9	4	2.27 (0.519)
Decanal	22	12	65	35	2.94 (0.086)	8	7	9	10	0.59 (0.899)
Nonanal	17	17	50	50	0.00 (1.000)	6	15	6	7	6.71 (0.082)

*(*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene

<u>attract</u>:
α-pinene,
ß-myrcene
α-phellandrene

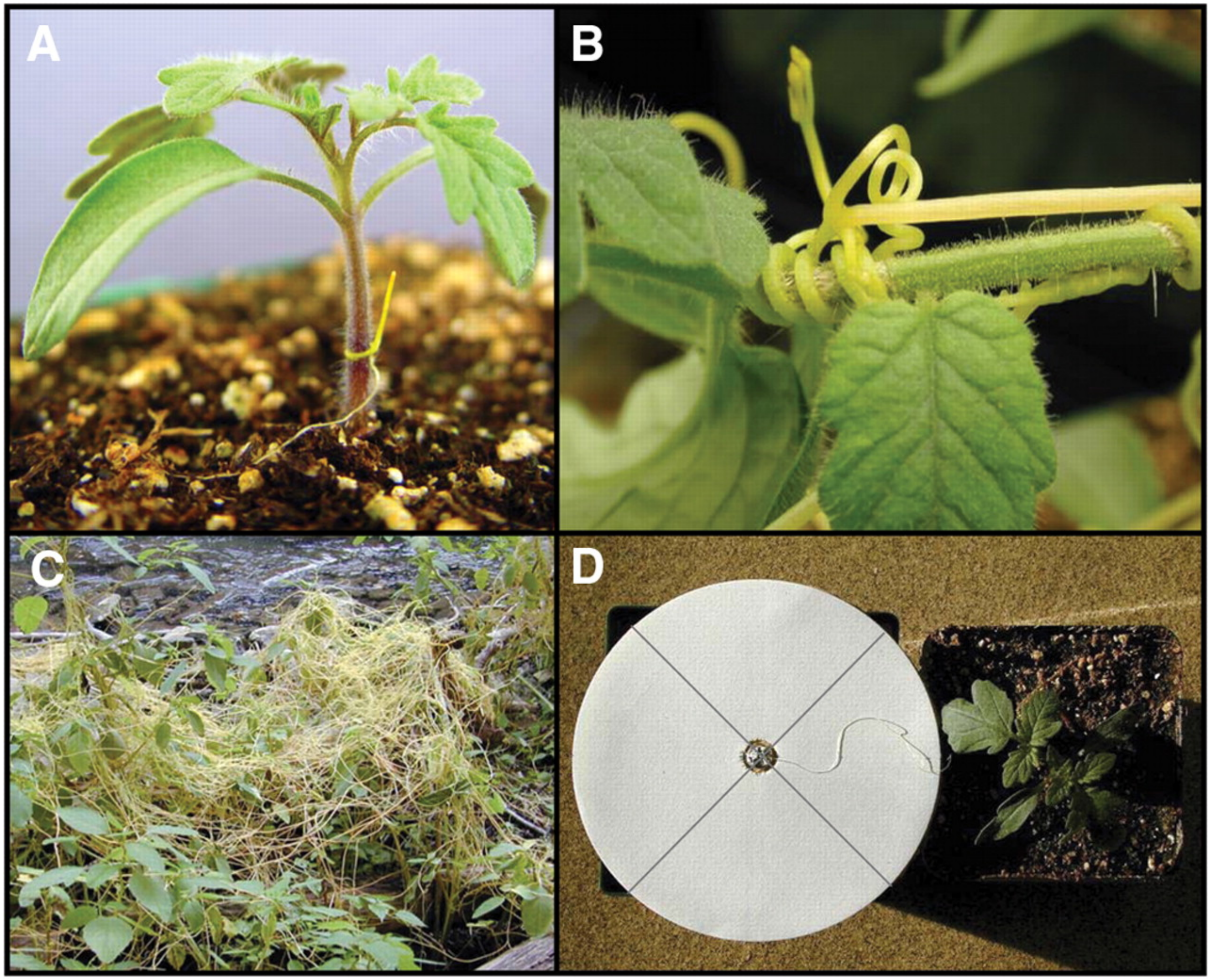
<u>repelled by:</u>
hexenyl acetate



J. B. Runyon et al., Science 313, 1964 -1967 (2006)

Published by AAAS

How does Cuscuta pentagona find its host?



Dodder
Cuscuta pentagona

J. B. Runyon et al., Science 313, 1964 -1967 (2006) LINK

i) Germination stimulants (phytochemicals) in root exudates

- *Striga* seeds need a **germination stimulant** (from host roots)
- identified as several **lactones** exuded from roots (ie strigol, sorgolactone)
- same compounds found as **mycorrhizal fungus** branching signals for arbuscular mycorrhizae
- led to discovery of role as and **endogenous shoot growth regulators** (carotenoid derived), called strigolactones.
- strictolactones are now know as root-generated regulators of shoot branching - phytohormones.

ii) Seedling foraging for host plants - Runyon et al. (2006) Science 313

- *Cuscuta pentagona* (dodder) (morning glory family)
- germinates on its own, needs to find host after
- "forages" for and finds living plants - *what does it track?*
- use circumnutation to grow towards tomato host
- cool experiments to identify the signals

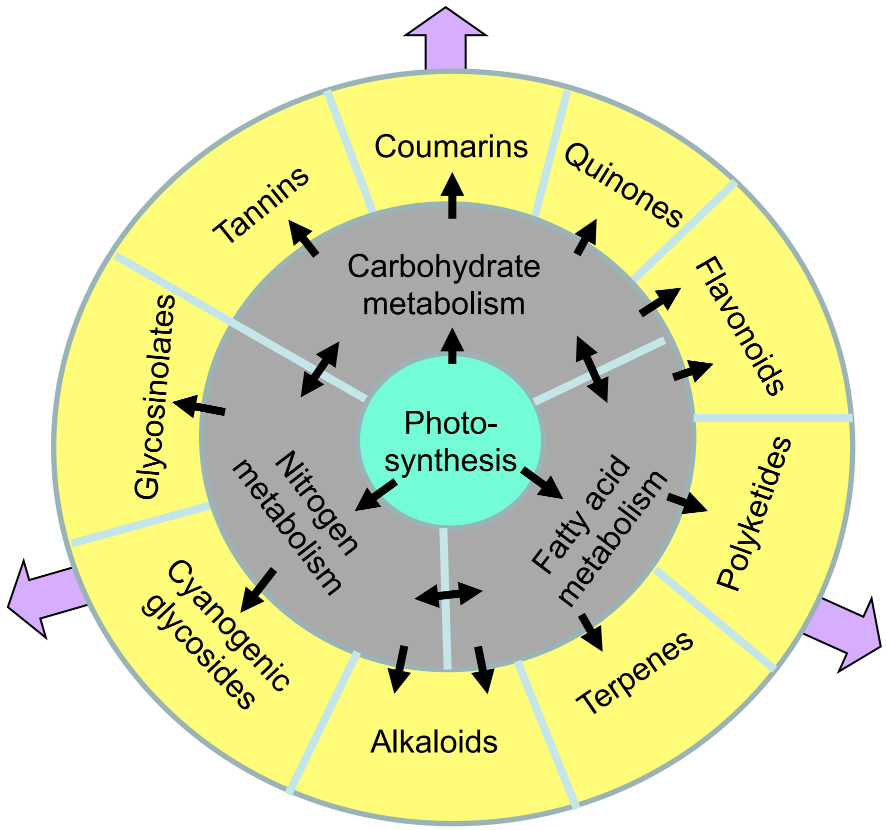
=> Therefore, several interacting organisms have learnt to ***'eavesdrop'*** *on plants via their phytochemistry*

Themes in Secondary Plant Metabolism

Three structural classes of specialized metabolites

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

Although hugely diverse, specialized metabolites are derived from a few dozen highly versatile central intermediates, which are modified in lots of different ways



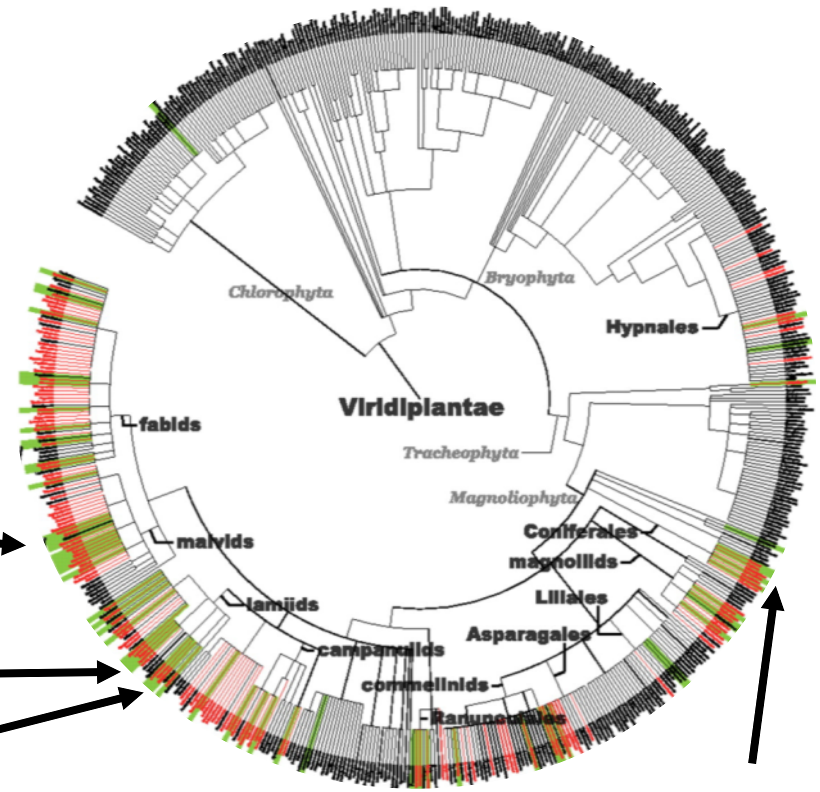
Alkaloids

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.

Medicinal compounds are unequally distributed in plant families

Plant families associated with drug-production are indicated in green, and red indicates families with endangered species



Myrtaceae (eucalyptus, clove)

Apocynaceae (periwinkle)

Solanaceae (tobacco, nightshade, peppers)

Papavaraceae (poppy)

Taxaceae (Pacific yew)

Zhu, F., Qin, C., Tao, L., Liu, X., Shi, Z., Ma, X., Jia, J., Tan, Y., Cui, C., Lin, J., Tan, C., Jiang, Y. and Chen, Y. (2011). Clustered patterns of species origins of nature-derived drugs and clues for future bioprospecting. Proc. Natl. Acad. Sci. 108: 12943-12948.