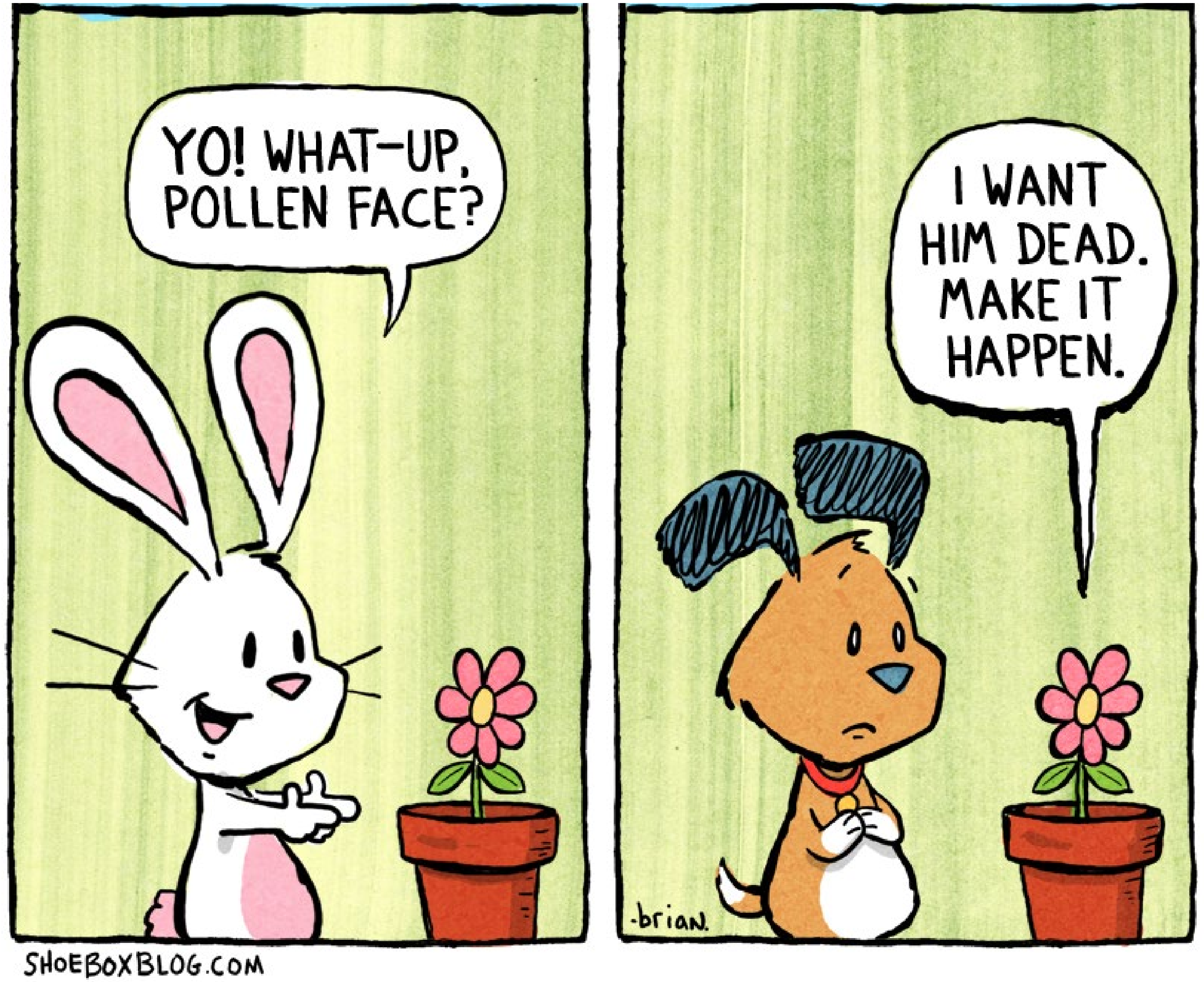
Plant communication part I



Plant-feeding insects damage plants and act as vectors for plant diseases

- Plant-associated insects show host preferences
- Preferences can be positively or negatively affected by plant health and disease status

Hopperburn in rice caused by the brown planthopper (BPH), *Nilaparvata lugens*

Once a minor pest – now one of the most damaging pests of rice

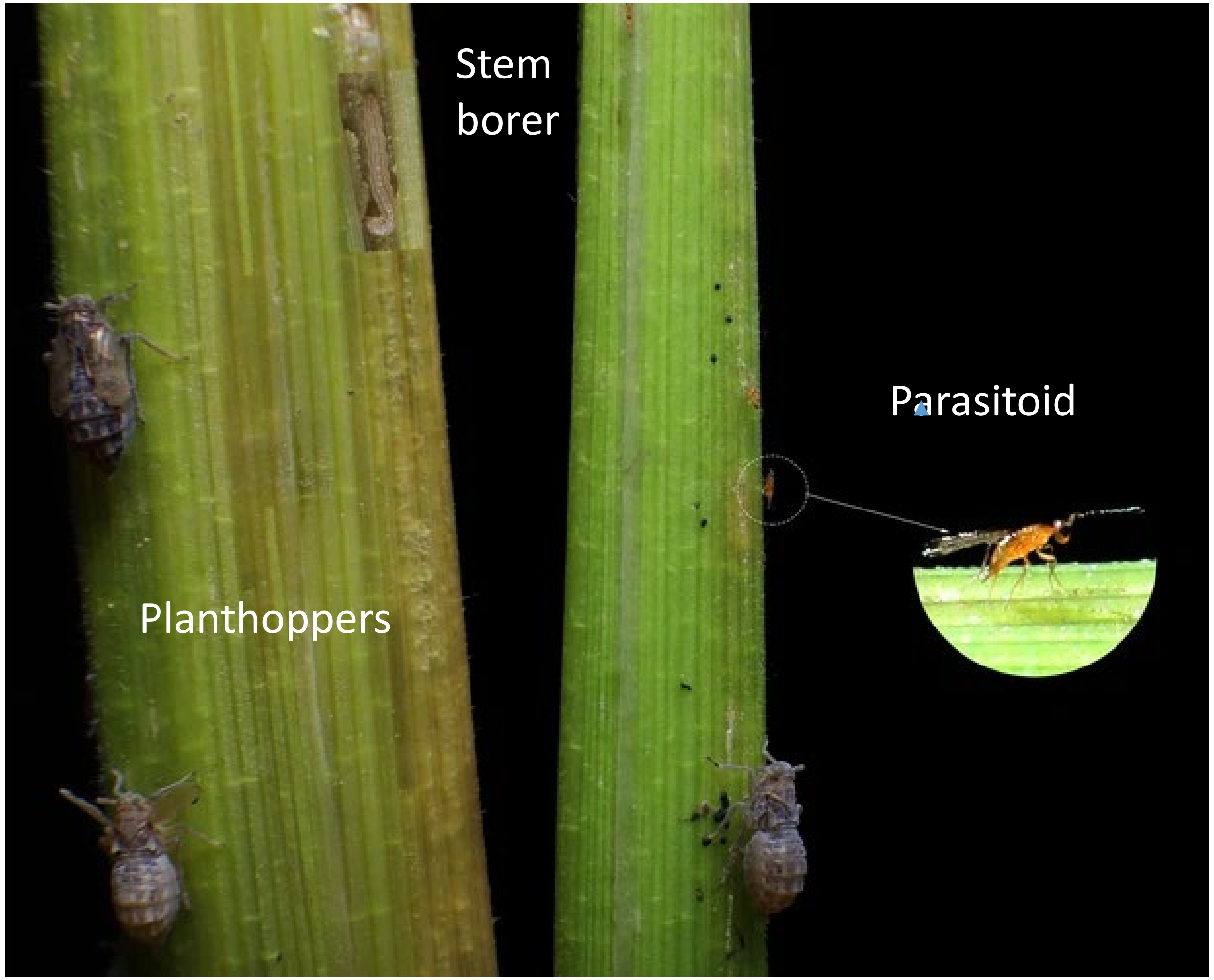
Nitrogen fertiliser treatment increases susceptibility

Feeding damage (hopperburn) = 400+ nymphs per plant

BPH is also a viral vector & causes increased predisposition to disease through wounding

http://www.knowledgebank.irri.org/training/fact-sheets/pest-management/insects/item/planthopper

Brown plant hoppers (BPH) preferentially oviposit on rice plants infested by the rice striped stem borer (SSB; *Chilo suppressalis*) – another major pest of rice.



SSB infested plants are avoided by the BPH parasitoid *Anagrus nilaparvatae*

Stem borers also prefer to lay eggs on BPH infested plants - BPH suppresses plant defences against stem borers and reduces attractiveness to stem borer parasitoids

How do stem borer infected plants attract BPH and repel parasitoids (or vice versa)?

Can we make crops less attractive to pests and more attractive to parasitoids?

Hu et al. 2020 eLife, Liu et al. 2021 Nature Comms

Overview

- How plants communicate with other organisms
- Basics of biological communication
- Chemical signalling between plants and other organisms
- Volatile organic compounds (VOCs) as agents of plant communication
- Using knowledge of VOC signalling to benefit plant health

Plant communication

Who do plants talk to?

1. Pollinators
2. Seed-dispersing organisms
3. Herbivores & pathogens
4. Symbionts
5. Guardians
6. Prey
7. Predators
8. Themselves
9. Other plants

How do plants communicate?

Appearance (vision)

Touch (mechanoreception)

Mouthfeel (texture)

Chemicals (chemoreception)

Taste (gustation)

Smell (olfaction)

Toxicity (nociception and interoception)

Temperature (thermoception)

Electricity (electroception)

Acoustics

Over 200 species of plants coat themselves in sand, which makes them less appealing to herbivores "psammophory"

Experiments using “green sand” to increase apparency show that it may be the abrasive nature of sand that deters herbivory – rather than sand acting as camouflage

LoPresti and Karben, 2016

Critical analysis of plant communication experiments

- Are you convinced by the authors’ explanation of their observations?
- Could there be alternate explanations?
- Is the data provided conclusive or correlative?
- What other experiments might you want to do, or what other data might you want to gather to more conclusively demonstrate or refute a hypothesis?

Definition of biological communication?

“Information transmission that is fashioned and/or maintained by natural selection”

What is a signal?

“Signals are traits whose value to the signaler is that they convey information to receivers”

Communication—if signaling plant derives a fitness benefit from conveying information to others

(a)

Ecological effect on organism A

Ecological effect on organism B

	+	−	0
+	Mutualism	Exploitation (predation, parasitism)	Commensalism
−		Competition	Amensalism
0			Neutralism

(b)

Change in fitness of receiver

Change in fitness of sender

	+	−
+	Cooperation	Deceit
−	Exploitation	Spite

Kessler, New Phytologist 2018

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Electricity (electroception)

Acoustics

A ***semiochemical*** (semeon = signal (Greek)) is a generic term used for a chemical substance or mixture that carries a message

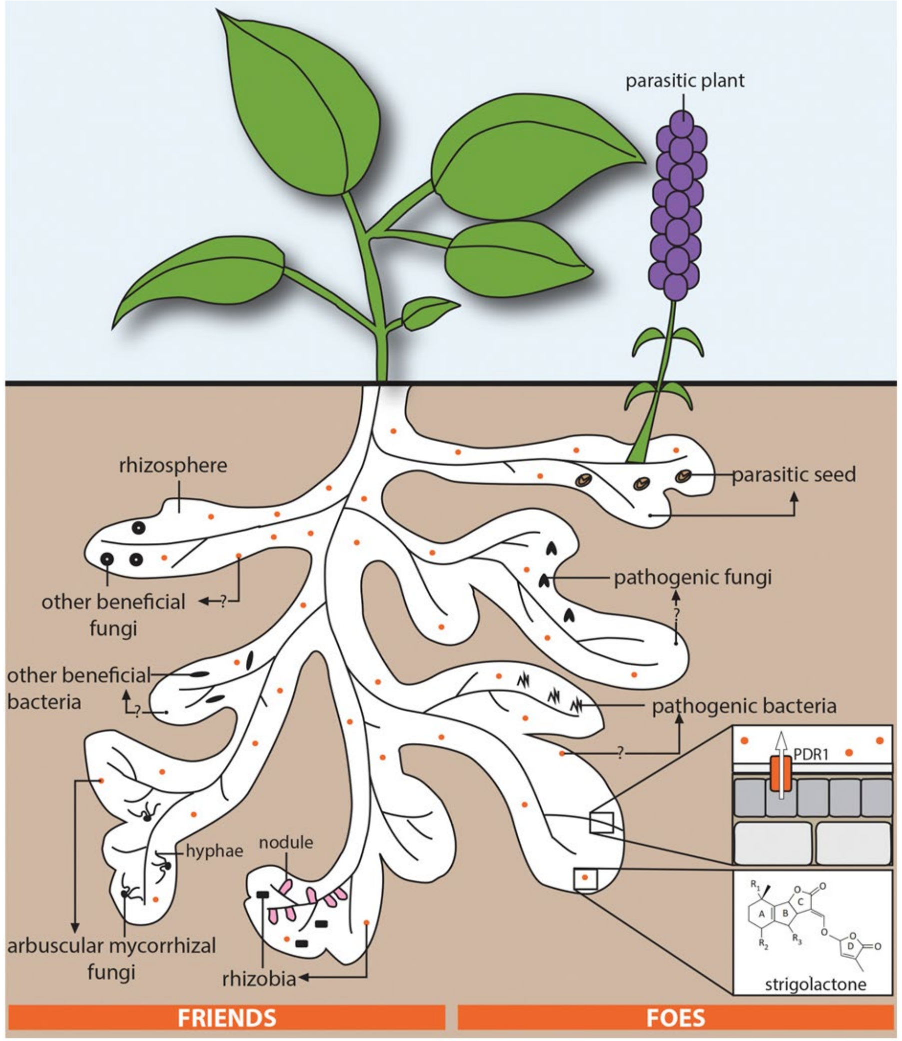
Hormone – a semiochemical produced in one part of an organism that exerts an effect in another part of an organism

Allomone - a semiochemical produced and released by a living organism that benefits the donor (signal producer)

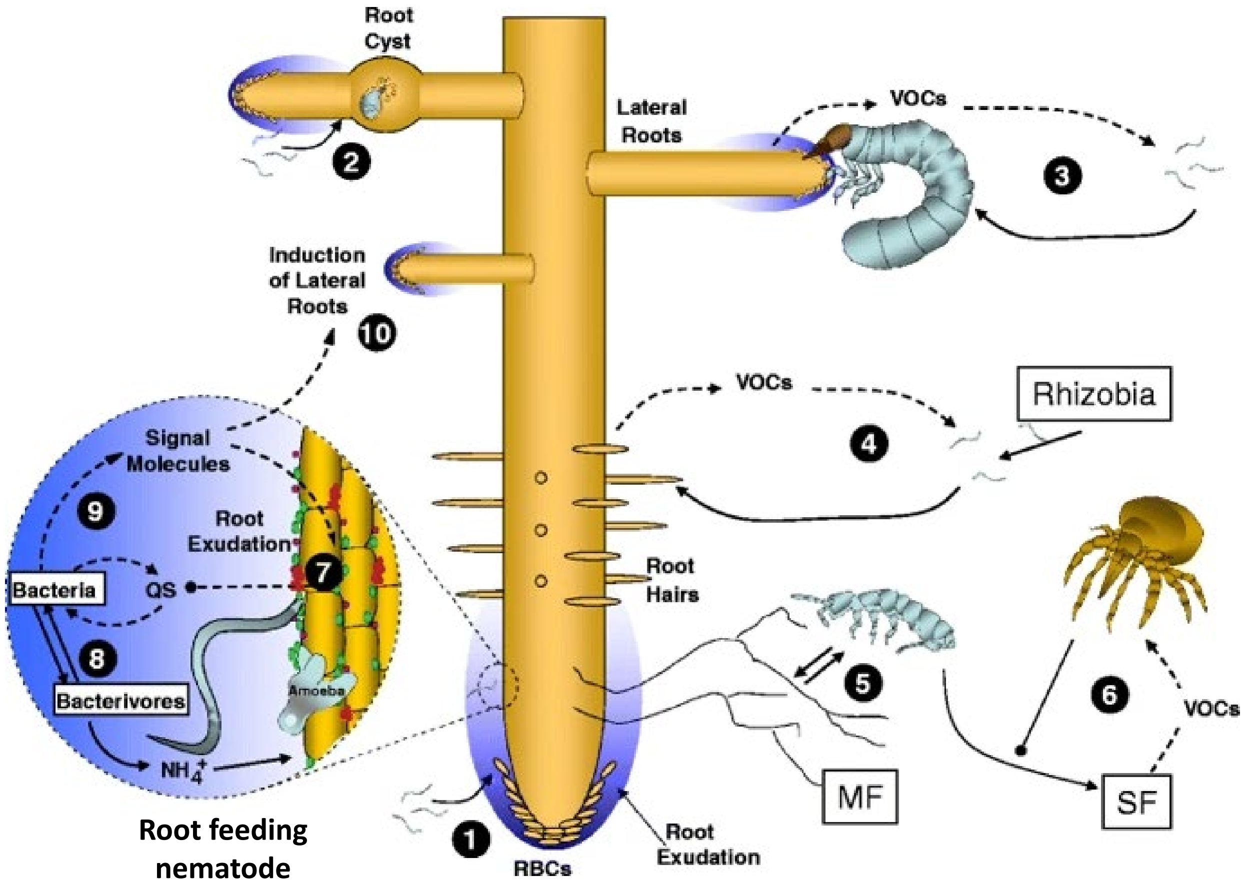
Kairomone - a semiochemical produced and released by a living organism that benefits the receiver

Synomone - a semiochemical that is adaptively advantageous to both the emitting and the receiving organism

Chemical signalling in the rhizosphere affects the outcome of plant interactions with microbes, parasites and soil fauna



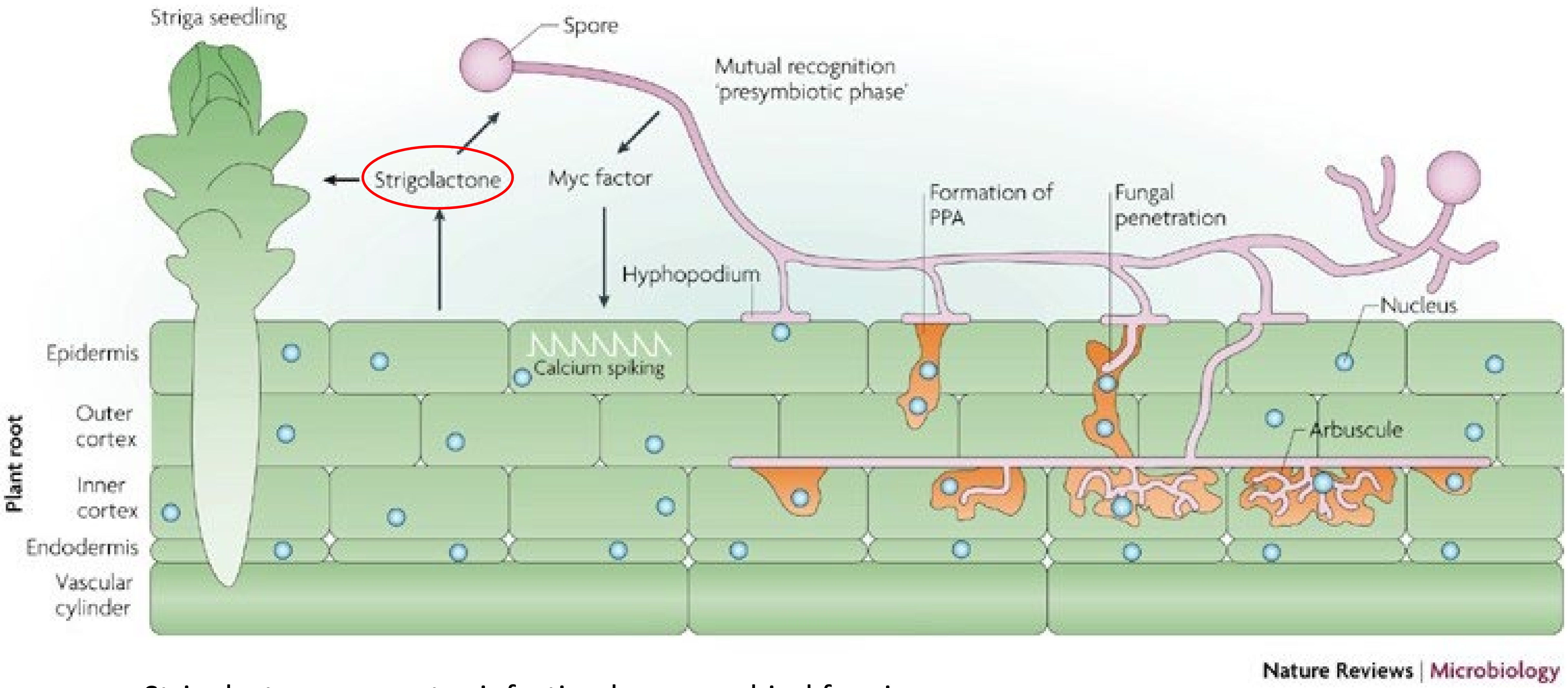
Previous lectures (Nod factors, Myc factors, Strigolactone)



Bonkowski et al. Plant Soil 2009

De Cuyper et al. MPMI 2017

Chemical signalling is rarely restricted to a single pair of organisms

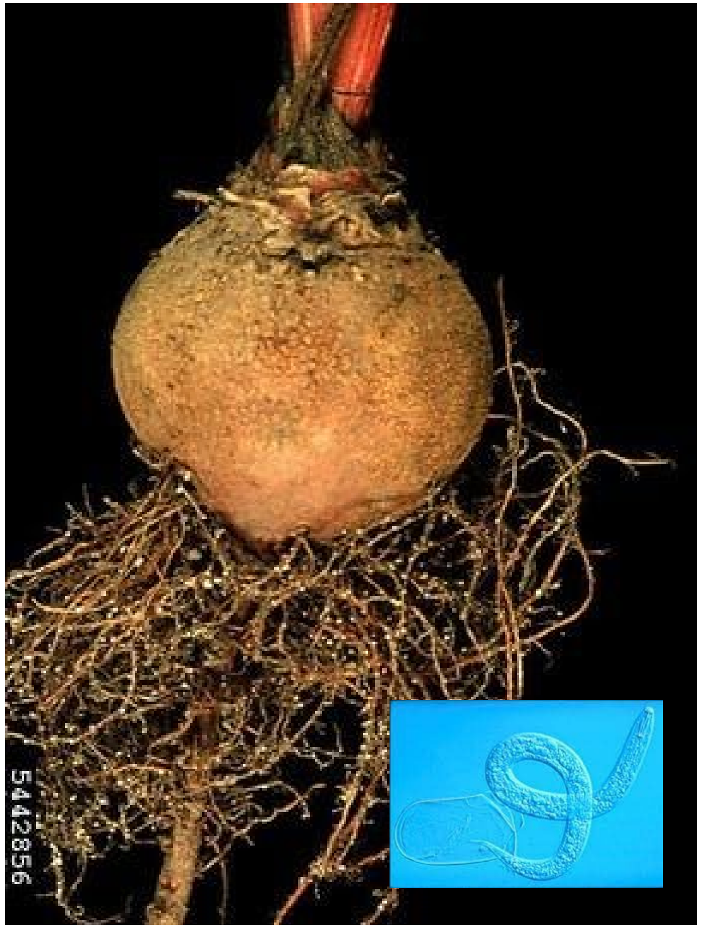


Strigolactone promotes infection by mycorrhizal fungi
<u>and</u> parasitic plants such as *Striga*

Parniske, Nature Rev. Microbiol (2008)
Waters et al. Annu Rev. Plant Biol (2017)

The pitfalls of signalling mechanisms – chemicals such as strigolactone can act as invasion signals for symbionts, pathogens and parasites…

Striga – “Witchweed”



Cyst nematode

Orobanchaceae

Escudero Martinez (2019) Eur J Plant Pathol

VOCs are key agents of chemical communication for plants

Volatile organic compounds (VOCs) are compounds that have a high vapor pressure and low water solubility

Up to 36% of assimilated carbon may be released by plants as complex bouquets of VOCs

Some VOCs (e.g. ethylene, methyl jasmonate, methyl salicylate) - may be used in signalling processes both intra- (within) and inter- (between) organisms

Some VOCs detected when researchers study VOCs released by plants are actually generated by microorganisms present in the plant microbiome

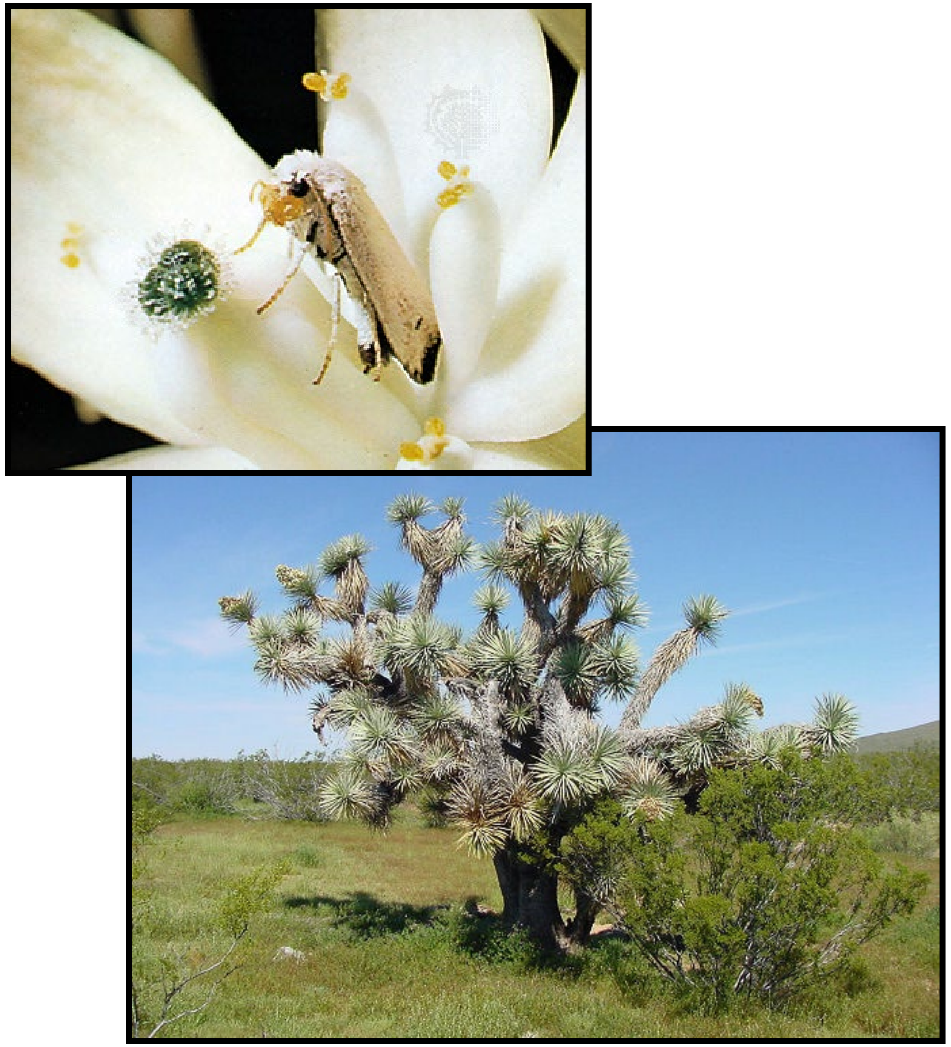
VOCs as inter-kingdom signals

Who do plants talk to using VOCs?

1. Pollinators
2. Seed-dispersing organisms
3. Herbivores
4. Guardians
5. Prey
6. Predators

Symbionts & pathogens (see other lectures)

1. Attracting pollinators



Yucca brevifolia (moth-pollinated)

Rafflesia amoldii (fly-pollinated)

VOCs act in conjunction with other signals such as flowers or temperature to communicate messages to pollinators

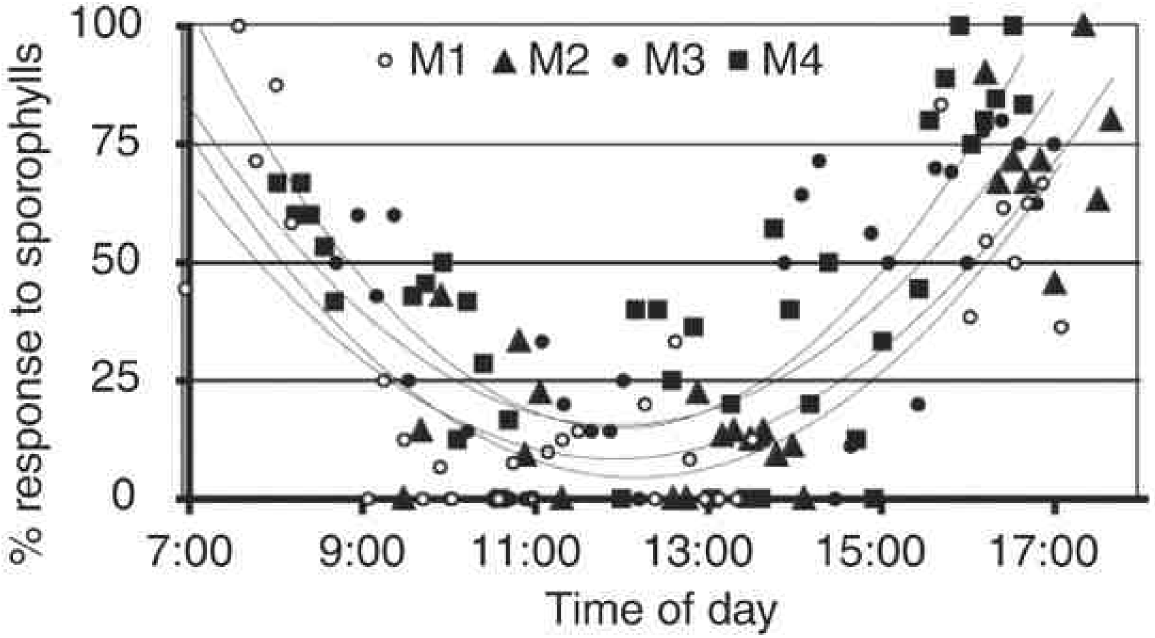
Titan arum

(corpse flower)

Harrap et al. eLife 2017

Cycles of thermogenesis and volatile production modify pollinator behaviour in cycads

% of insects going to sporophylls of four mid-pollination-stage male cones (M1 to M4) versus controls



Pollen-laden thrips leave male cycad cones during the daily thermogenic phase. Cone temperatures and volatile emissions increase dramatically and thrips are repelled.

As thermogenesis declines, total volatile emissions diminish. Cones attract thrips, resulting in pollination of female cones.

Terry et al. (2007). Science *318*, 5847.

Plant manipulation of acoustic perception

Marcgravia evenia has evolved dish-shaped leaves with conspicuous echoes that enable nectar-feeding bats to find its flowers through echolocation

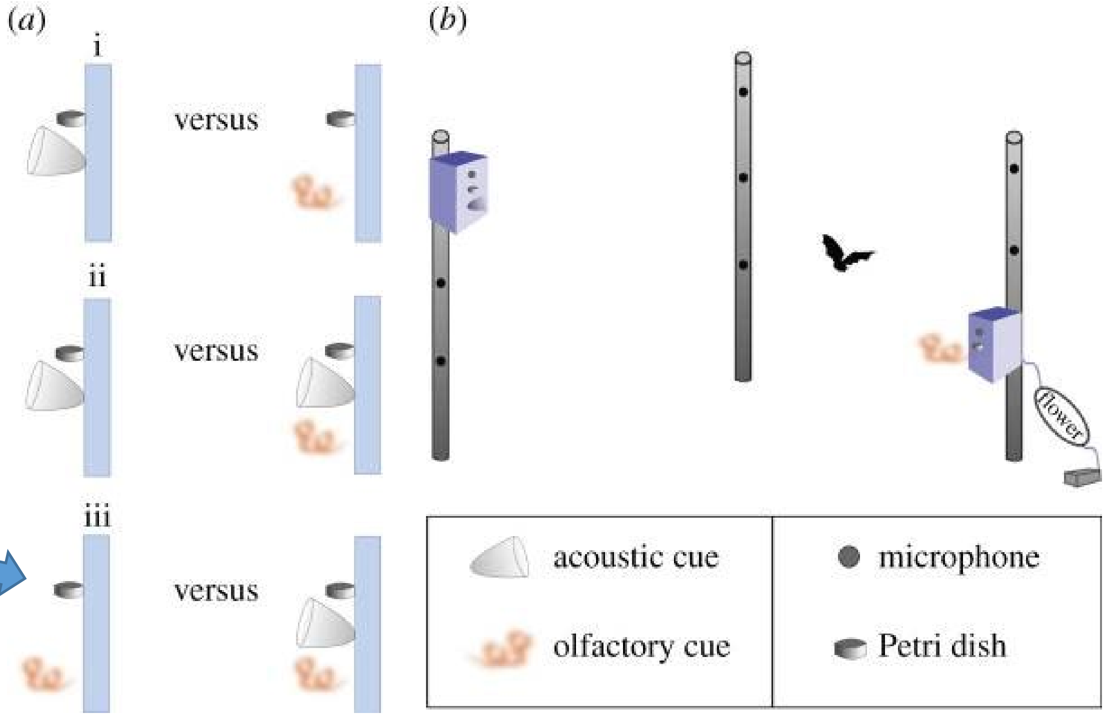
R. Simon, M. W. Holderied, C. U. Koch, O. von Helversen. **Floral Acoustics: Conspicuous Echoes of a Dish-Shaped Leaf Attract Bat Pollinators**. *Science*, 2011; 333 (6042): 631

Bats use a combination of scent and echolocation to find flowers…

acrylic paraboloid

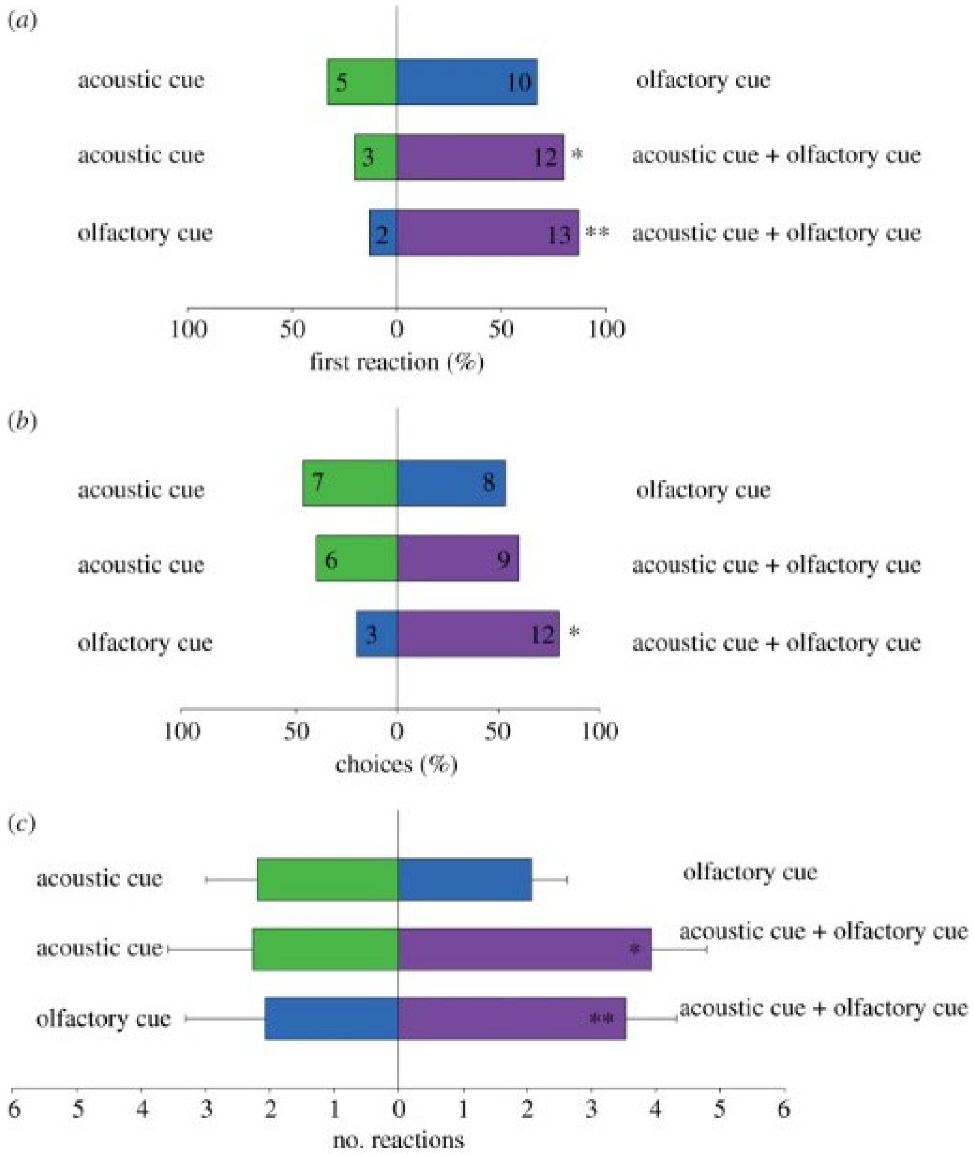
food reward

floral scent of the bat-pollinated cactus *Pachycereus pringlei*



Gonzalez-Terrazas, 2016

In choice assays bats respond more to the combined acoustic and olfactory cue than to either cue alone…



Gonzalez-Terrazas, 2016

(a) **Ecological effect on organism A**

Ecological effect on organism B	+	–	0
+	Mutualism	Exploitation (predation, parasitism)	Commensalism
–		Competition	Amensalism
0			Neutralism

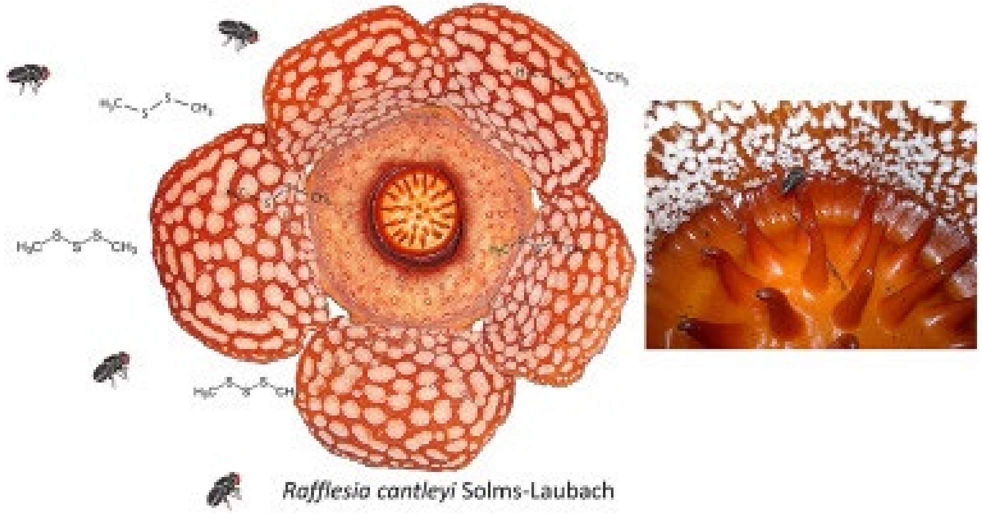
(b) **Change in fitness of receiver**

Change in fitness of sender	+	–
+	Cooperation	Deceit
–	Exploitation	Spite

Are there examples of plant signalling interactions that involve deceit?

Kessler, New Phytologist 2018

Deceitful plants?



Rafflesia cantleyi
(fly-pollinated)

Potential rewards offered by plants to pollinators

- Food (e.g. nectar, pollen, plant tissue)
- Takeaway food for young organisms
- Egg laying site
- Nest building material
- Shelter
- Warmth
- Fragrance to use in mating displays

- *Rafflesia* attracts but does not benefit female flies
- Rendezvous location – mating opportunities for male flies?

Wee et al., Phytochemistry 2018

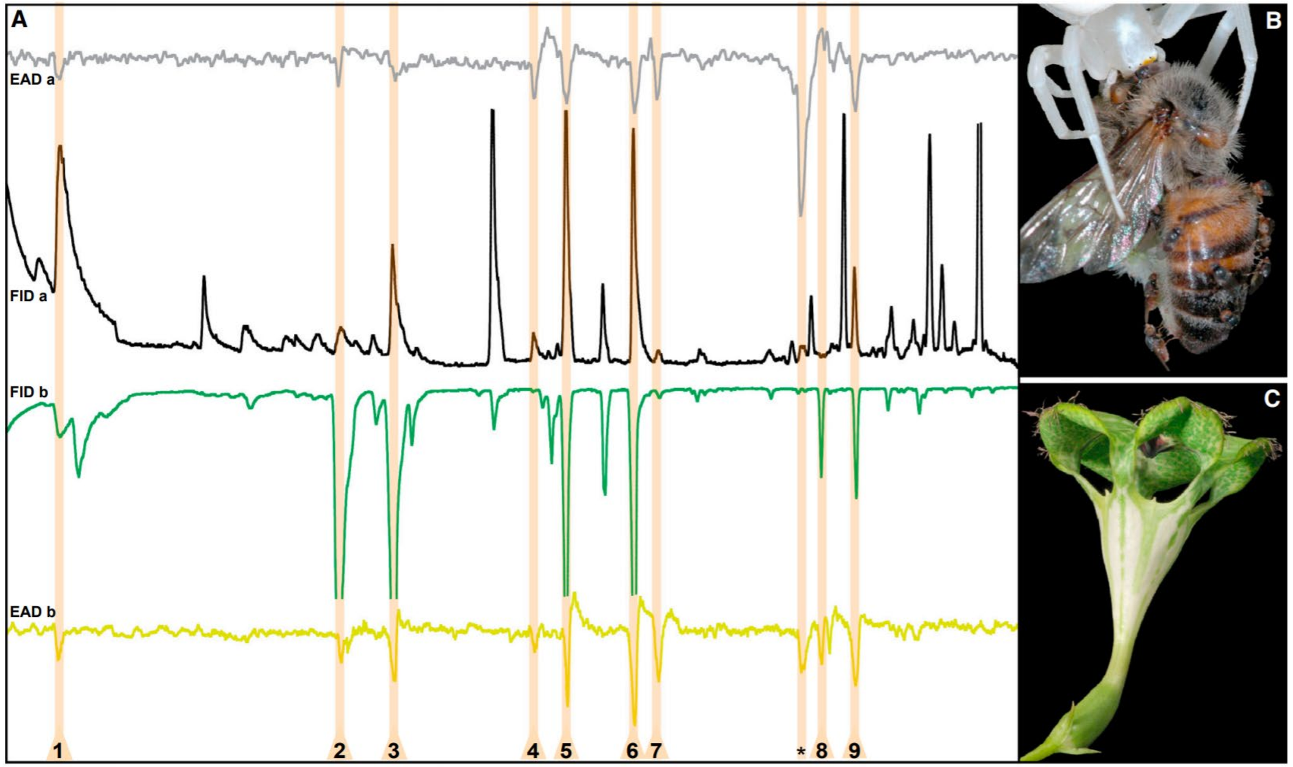
Trap flowers lure pollinators with false signals

- An estimated 4-6% of plants are thought to attract pollinators by deception

- *Ceropegia sandersonii* emits VOCs similar to those emitted by honeybees being attacked by predators

- This attracts “kleptoparasitic” flies, which normally feed on the prey of other organisms

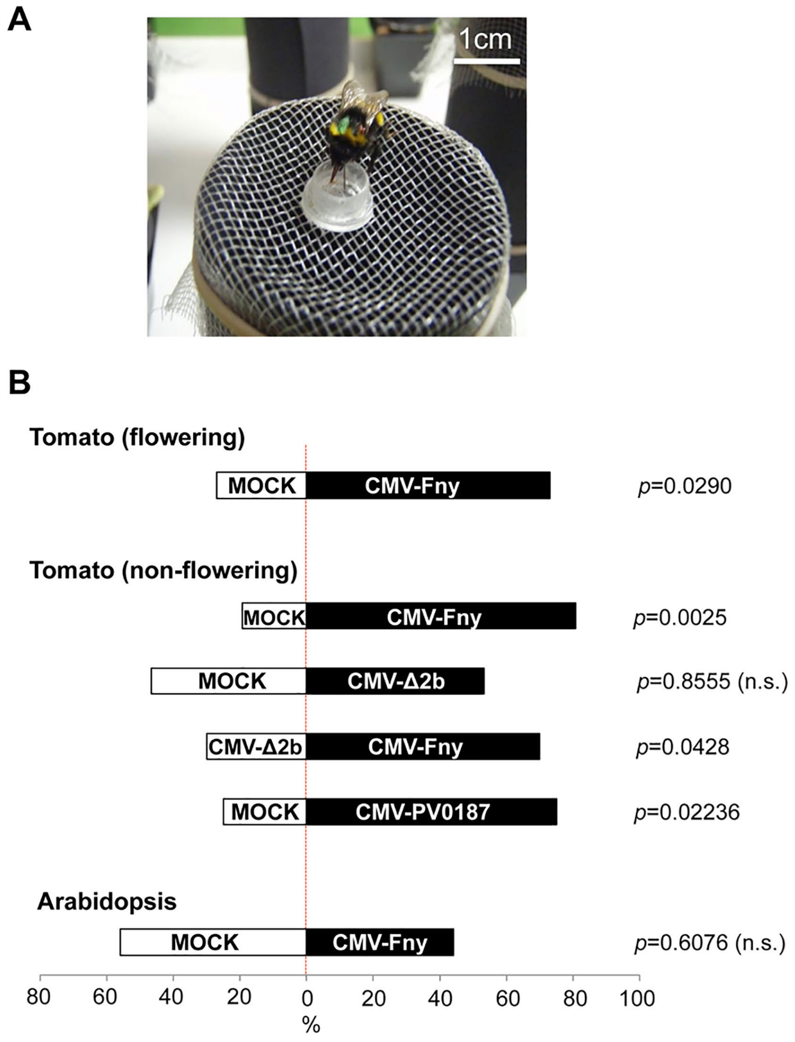
- The plant lures the flies to a pitfall trap, which enables pollination



- Antennal responses of female *Desmometopa sordida* to VOCs released by honeybees under simulated attack (top) and to the flower scent of *Ceropegia sandersonii* (bottom).
- The image at the top right shows kleptoparasitic flies on the body of a bee that is being attacked by a spider

Heiduk et al. Curr Biol 2016

Some pathogens increase plant attractiveness to pollinators



Bumblebees prefer volatiles emitted by Cucumber Mosaic Virus (CMV)-infected tomato plants

Bees are not viral vectors – is this a payback for susceptible viral hosts?

Groen et al. 2016, PLoS Pathogens

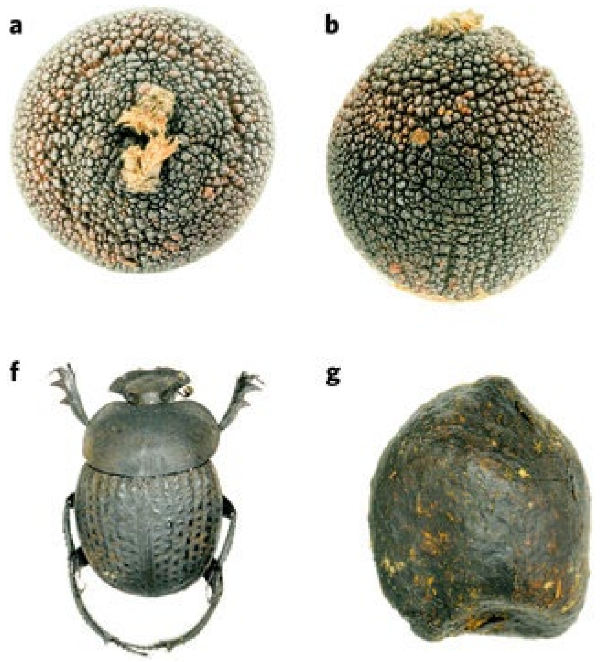
2. Seed dispersal

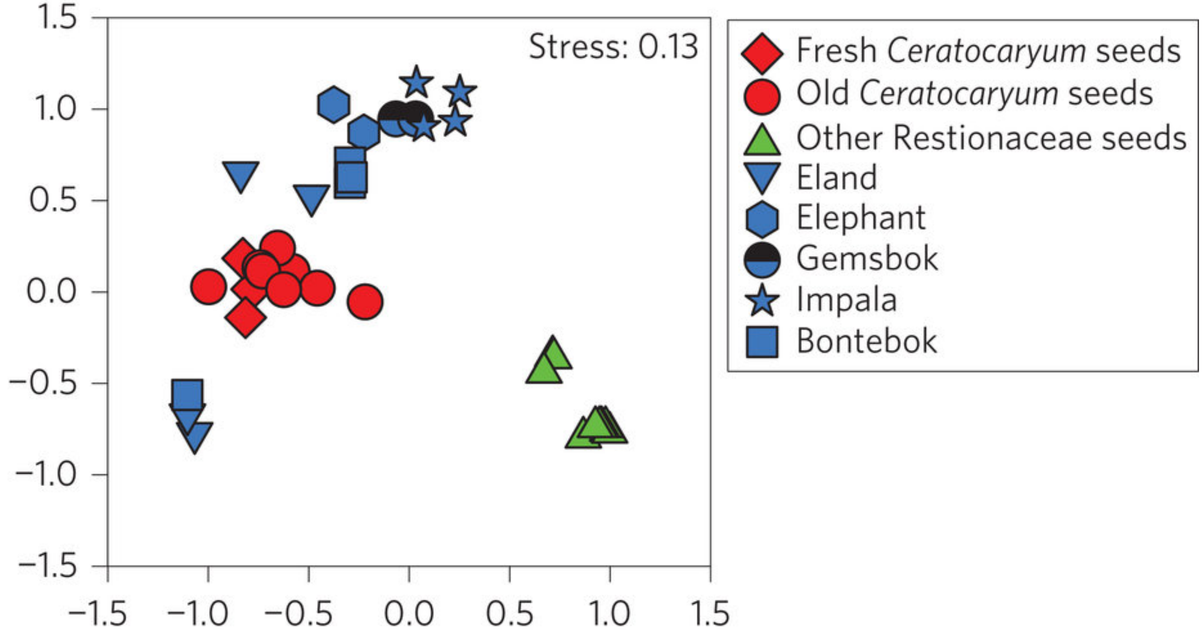
The size, shape, colour and odour of seeds and fruit attracts organisms that act to disperse seeds – odour can be particularly important for nocturnal animals

Leptonycteris curasoae: Lesser long-nosed bat feeding on saguaro (*Carnegiea gigantea*)

Grey mouse lemur (*Microcebus murinus*)

Faecal mimicry by seeds ensures dispersal by dung beetles





Vertical (a) and side (b) views of a *C. argenteum* seed.
(f) *E. flagellatus*. (g) Bontebok faeces

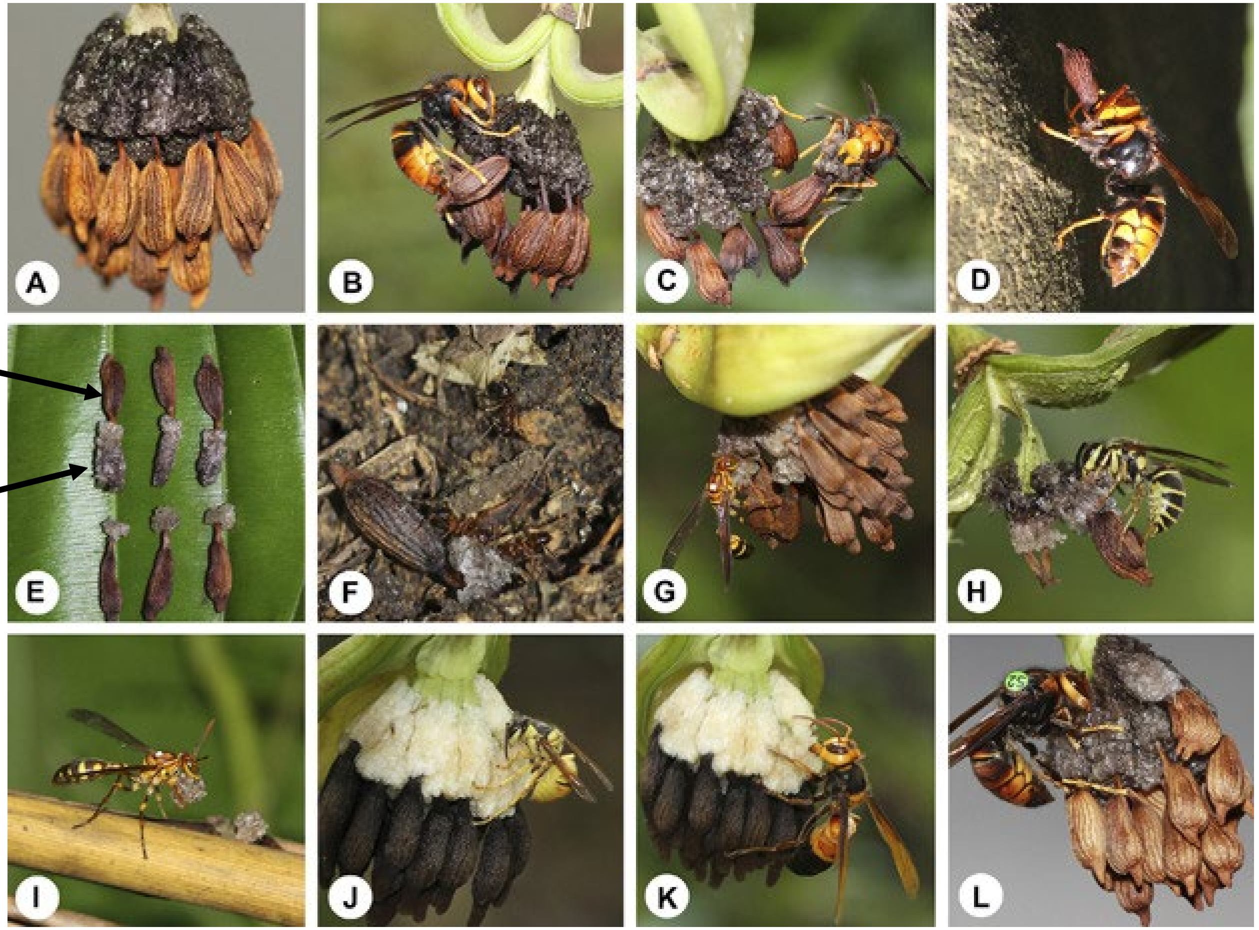
The composition of scent sampled from *Ceratocaryum* seeds is very similar (R = 0.75, P = 0.33) to that of dung of local herbivores (eland and bontebok), but differs markedly (R = 1.0, P = 0.028) from that of seeds of other Restionaceae (nested ANOSIM permutation test).

Midgley et al. Nat Plants 2015

Volatile signals attract hornets (and ants) to disperse seeds of myrmecochorous plants

Seed

Nutrient-
rich
Eliaosome



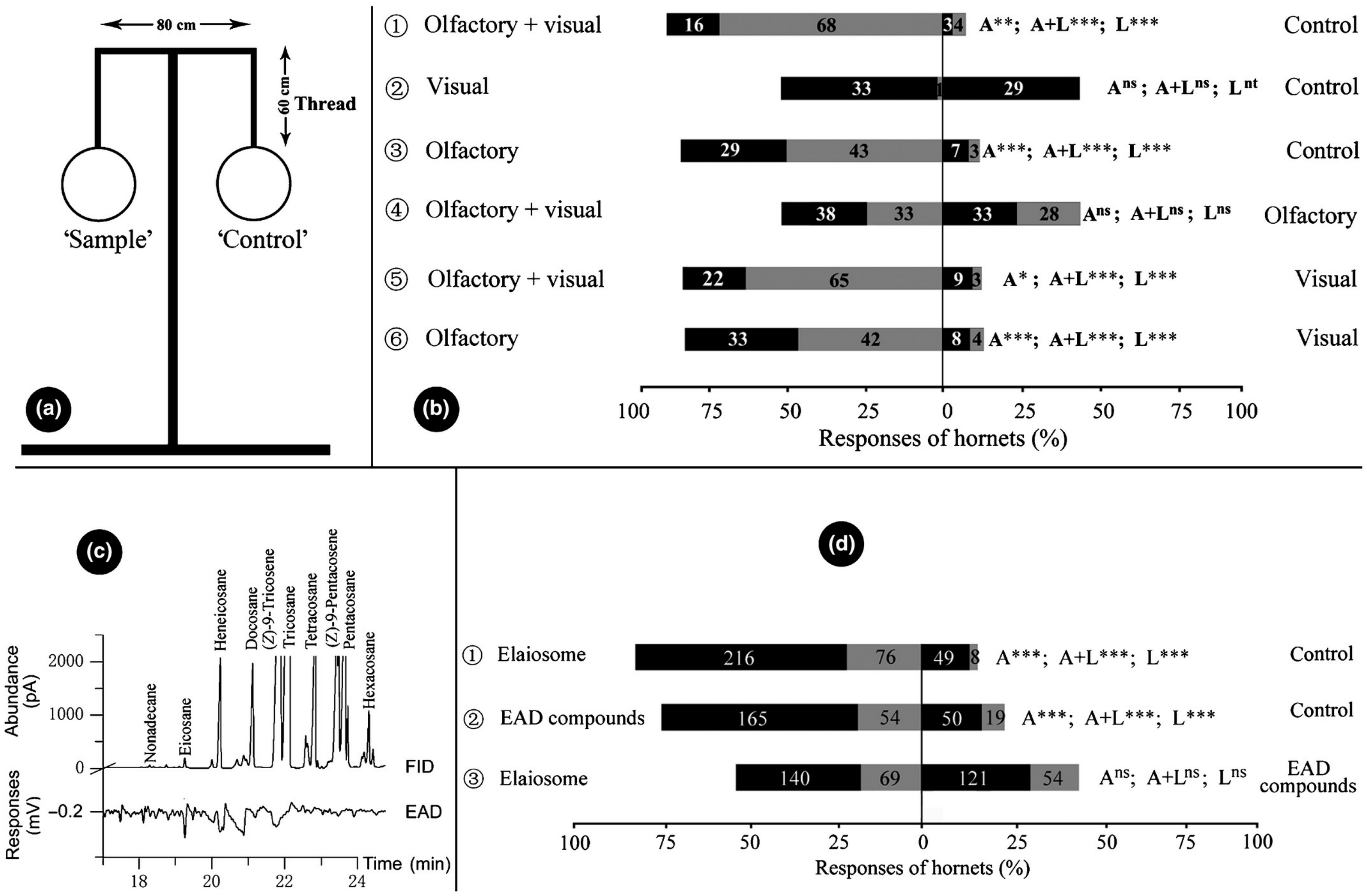
Myrmecochory =
dispersal by ants

Movie S1
Movie S2

https://onlinelibrary.wiley.com/doi/full/10.1111/jipb.12568

Chen et al. J. Intr Plant Biol. 2017.

Hornets are attracted by volatile signals released by the elaiosome

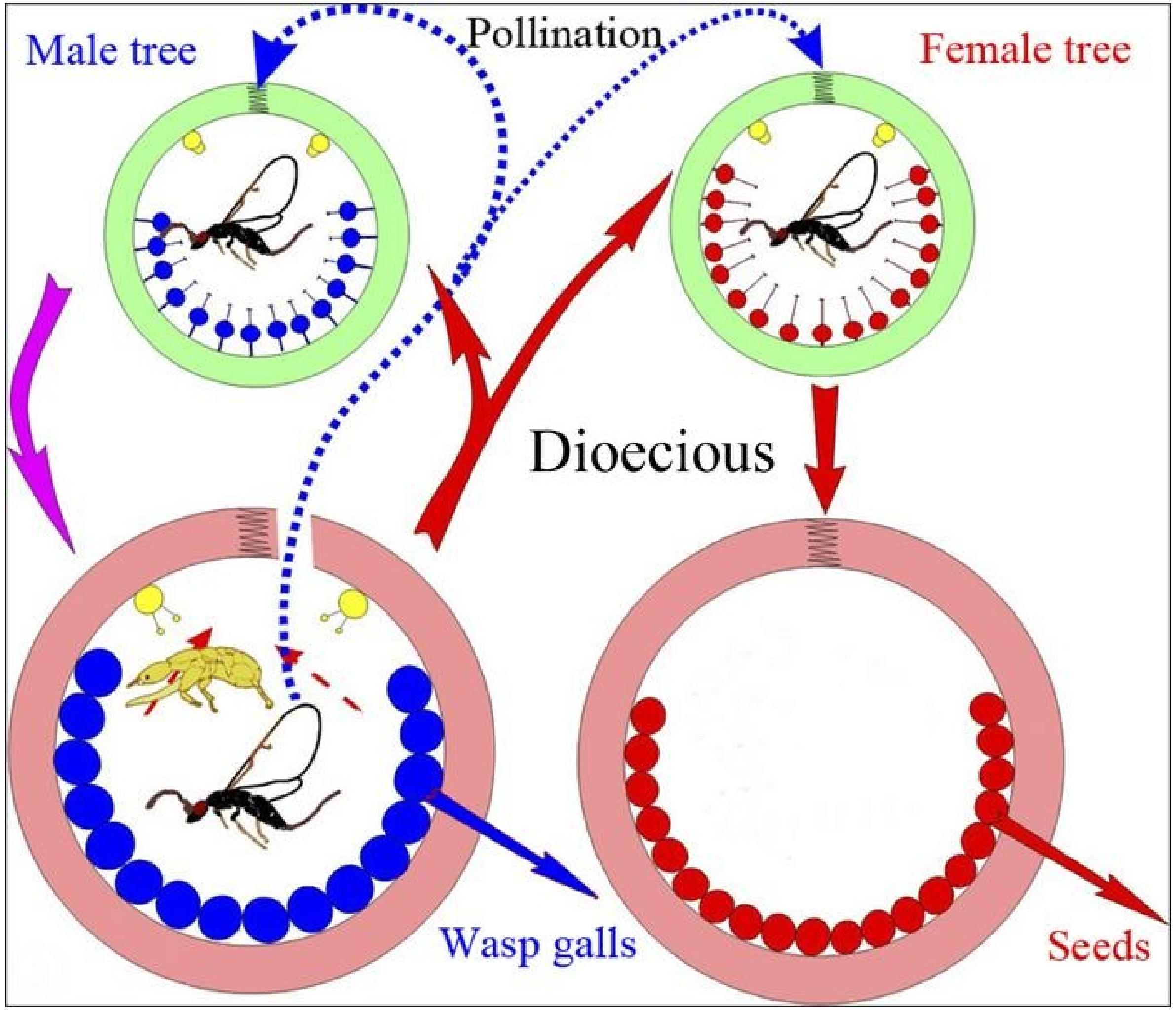


Chen et al. 2017

VOCs promote pollination and seed dispersal in figs

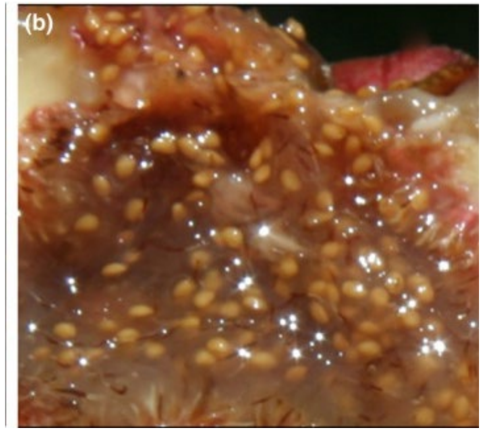
VOCs attract pollinating female wasps

Repels seed dispersers



http://www.figweb.org/Interaction/Life_cycle/dioecious.htm

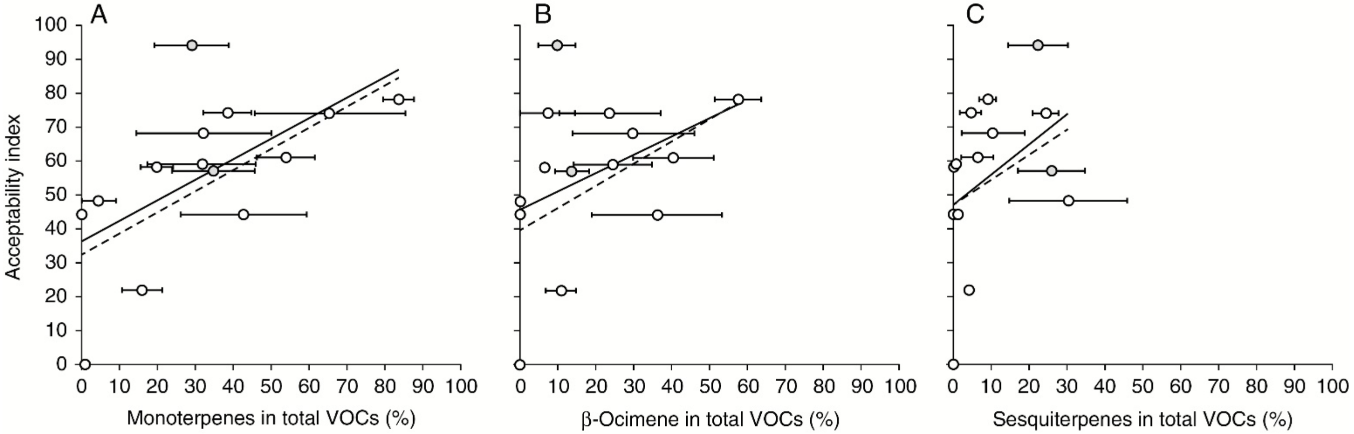
Attracts seed dispersers (e.g. bats, birds, primates)



Borges et al 2008
Functional Ecology

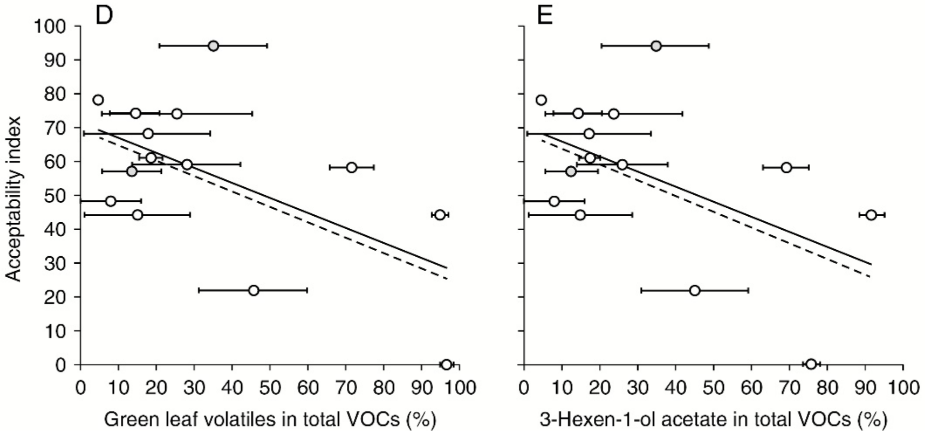
3. Herbivores

Specific VOCs can affect attractiveness to specific herbivores



Relationship between seedling acceptability (AI) and the relative proportion (% in total profile) of major VOCs produced by the seedlings of 14 grassland plant species.

Cornu aspersum



Preferred species produce high levels of monoterpenes, beta-ocimene and sesquiterpenes, but lower levels of green leaf volatiles and 3-hexen-1-ol acetate.

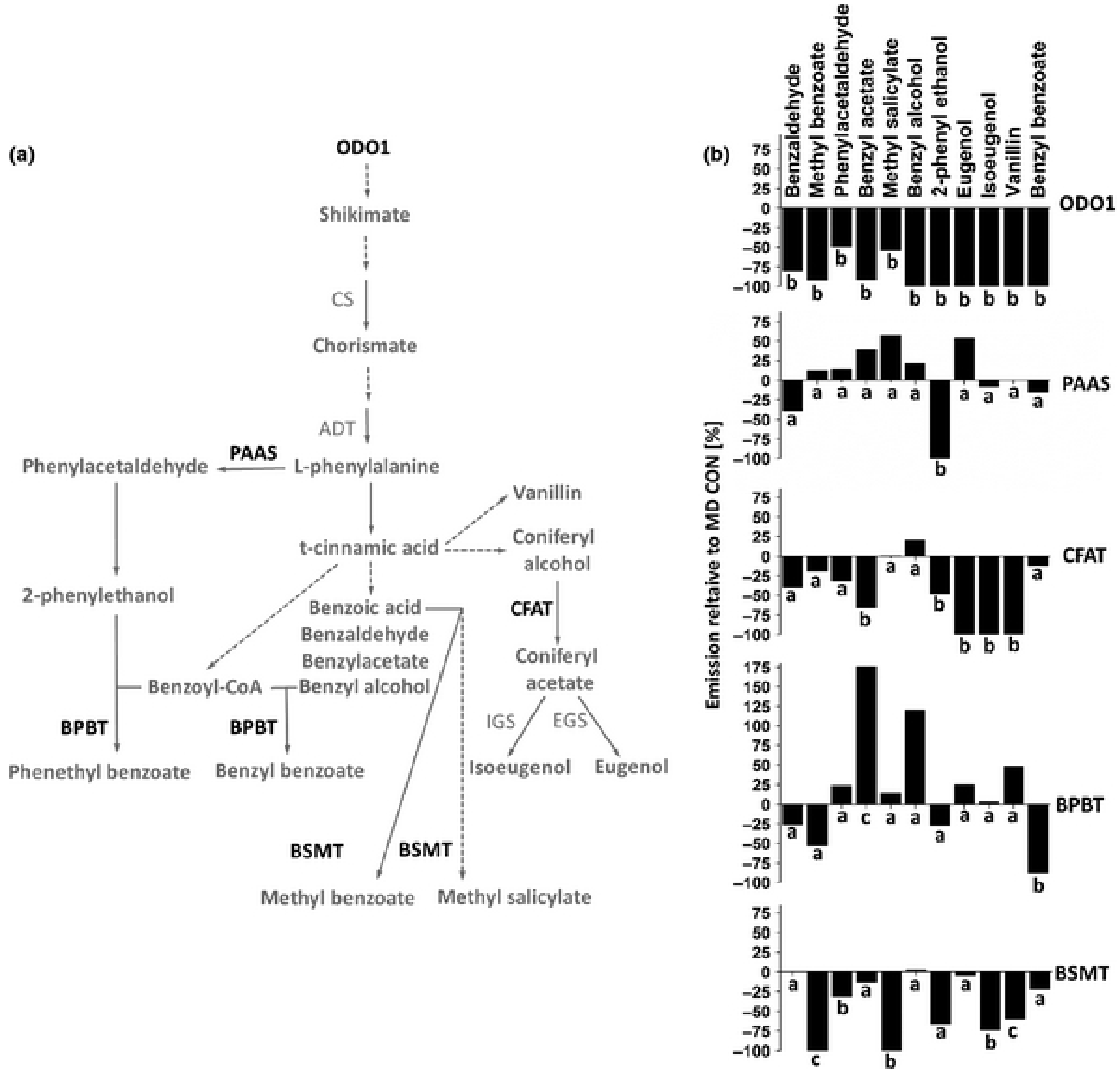
Hanley et al. 2018, Annals of Botany

Volatile compounds can also act to deter oviposition by females

Nicotiana attenuata
deters oviposition by
Manduca sexta

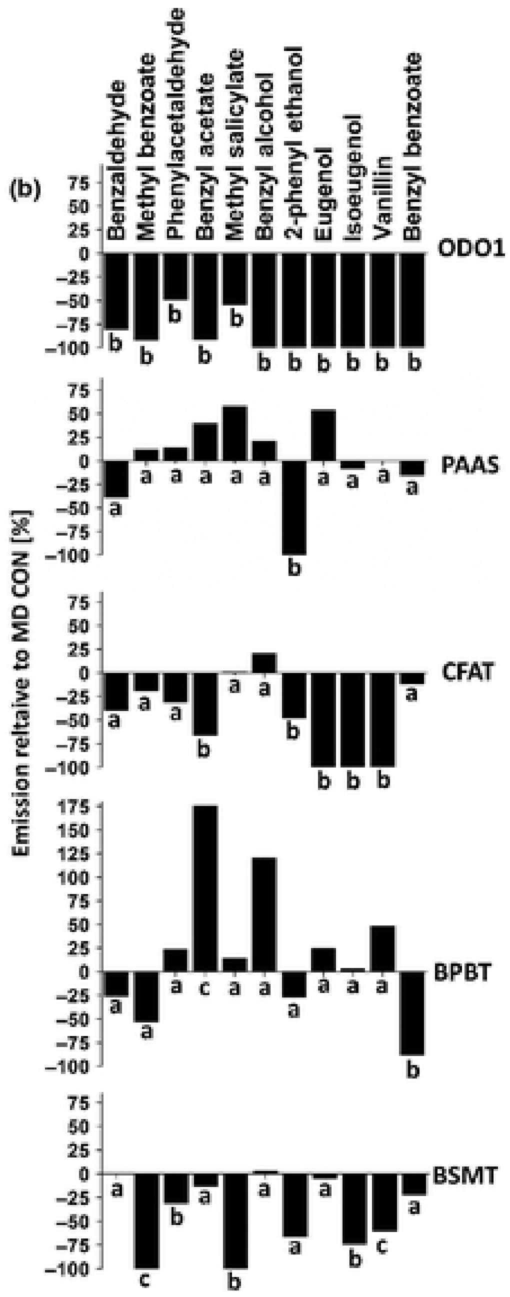
Kessler and Baldwin. 2001. Science

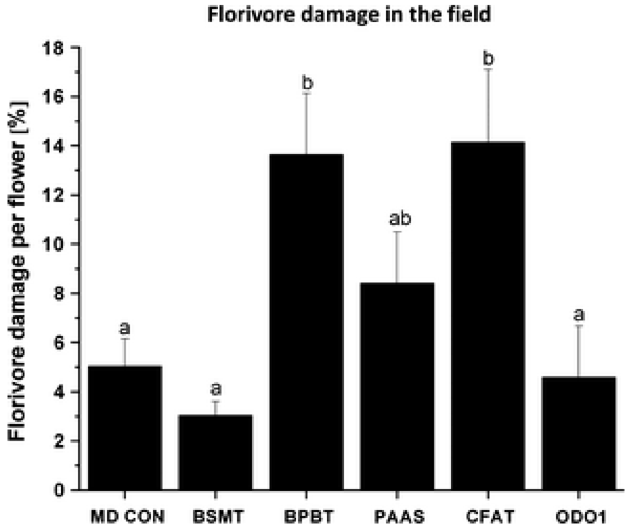
The floral VOC cocktails emitted by *Petunia* can be altered by silencing specific genes…



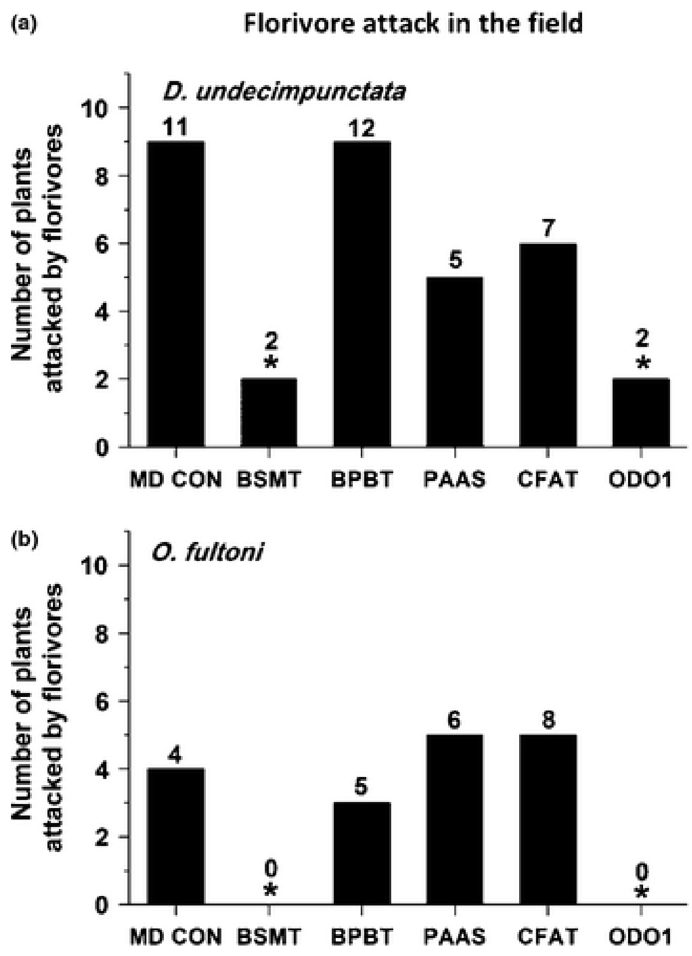
Kessler et al., 2013

Petunia flowers with altered levels of volatiles are subject to differing levels of damage by florivores





The presence of specific florivores on *Petunia* flowers depends on the emission of specific floral volatiles..



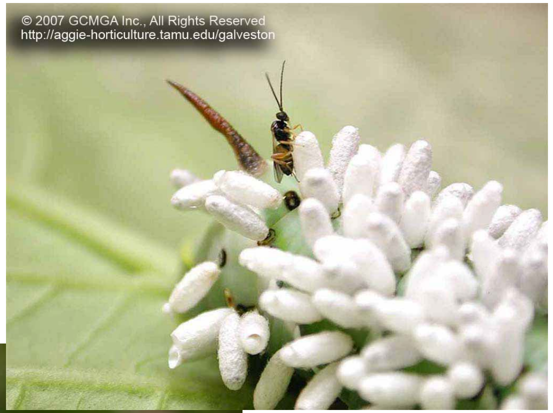
Diabrotica undecimpunctata

Oecanthus fultoni

4. Guardians

Attract air-borne parasitoids

Diaeretiella rapae attacking
Myzus persicae on
Arabidopsis



Tobacco Hornworm
(Manduca sexta)
parasitized by
braconid wasps

Parasitoids recognise the chemical signals associated with specific types of herbivore damage

Spodoptera littoralis

Spodoptera littoralis larva.

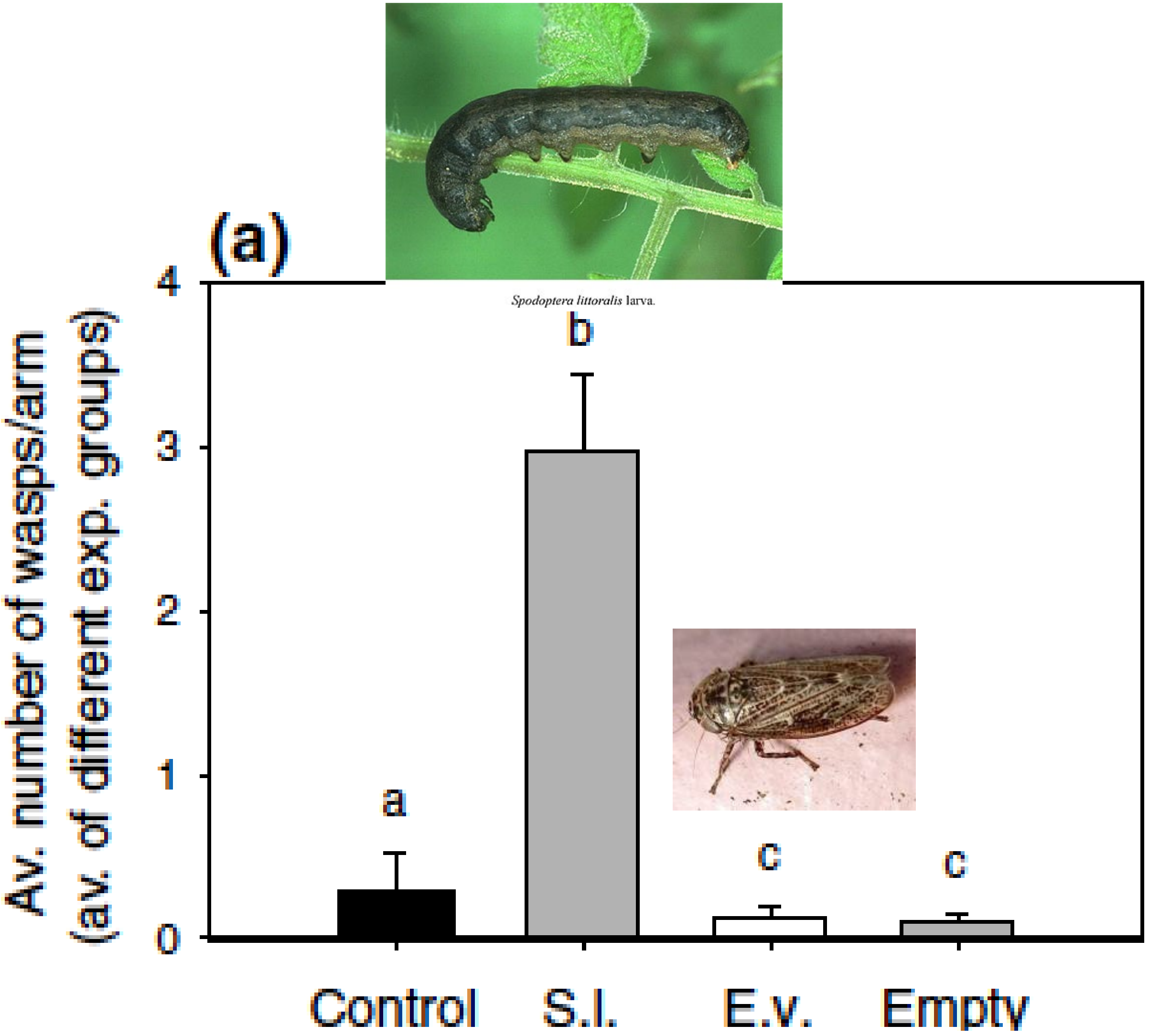
Herbivore 1
(chewing)

Euscelidius variegatus

Herbivore 2
(piercing sucking)

Cotesia marginiventris

Parasitoid of
herbivore 1



Costesia marginivenis (parasitoid) is specifically attracted by the volatile signals emitted by plants when they are attacked by *Spodotora litteralis* (host organism)

Erb et al BMC Plant Biol 2010

Sucking and piercing insects induce a distinctive set of plant volatile compounds, which attract specific parasitoids of these insects

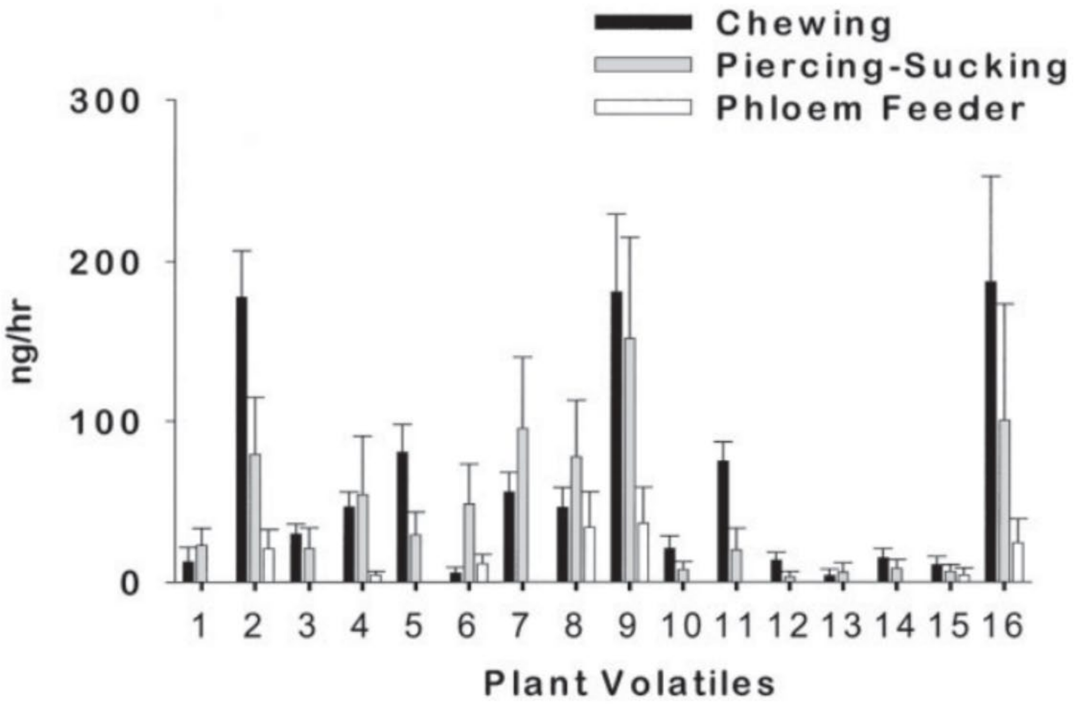
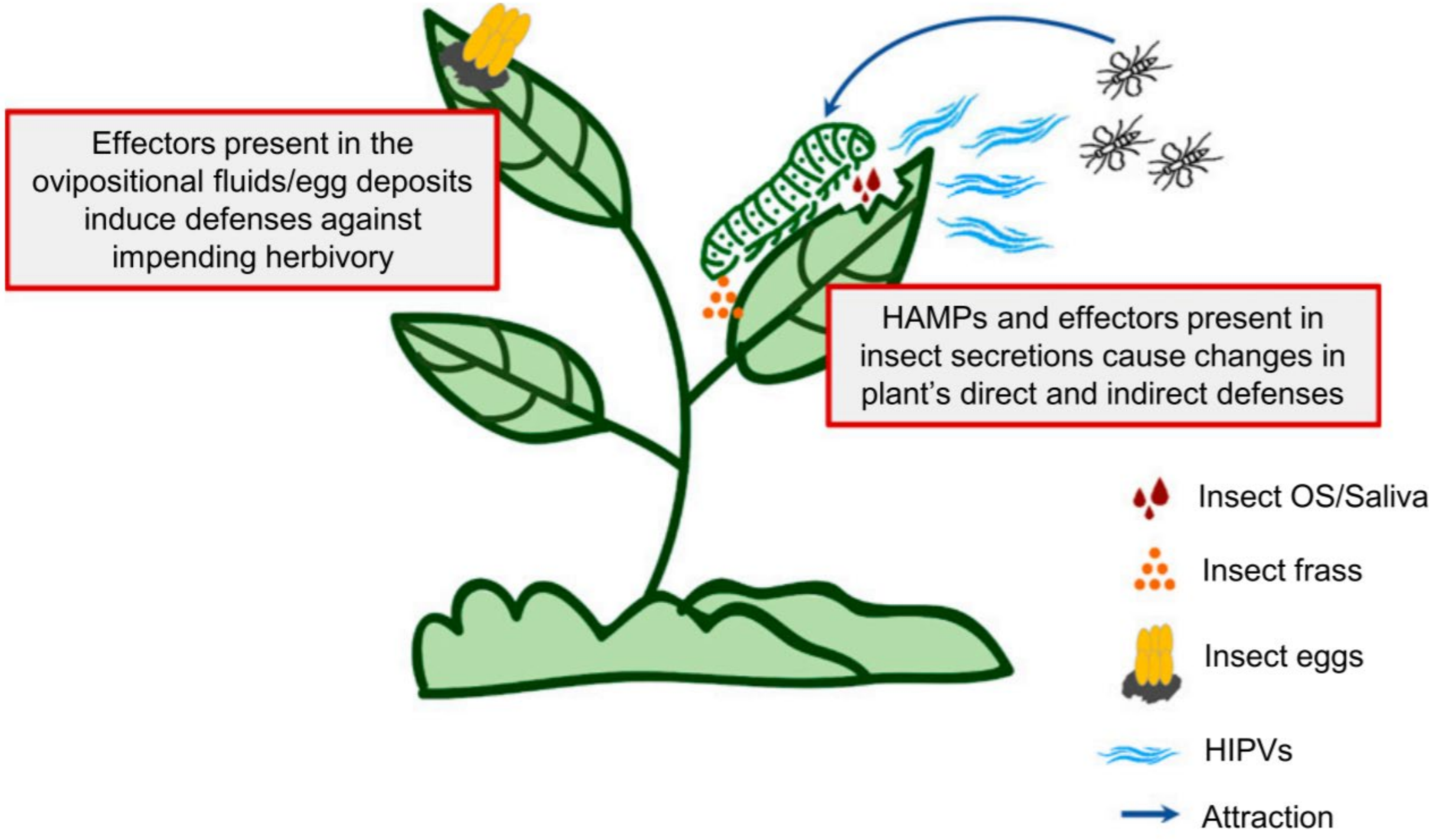


Fig. 1. Headspace volatile emissions from cotton plants injured by three species of herbivores with different feeding habits: the chewing caterpillar *Spodoptera exigua*, the piercing-sucking bug *Lygus hesperus*, and the phloem feeder *Bemisia tabaci*. Volatile compounds are: 1 = (*E*)-2-hexanal, 2 = α-pinene, 3 = β-pinene, 4 = myrcene, 5 = (*Z*)-3-hexenyl acetate, 6 = limonene, 7 = (*E*)-β-ocimene, 8 = linalool, 9 = (*E*)-4,8-dimethyl-1,3,7-nonatriene, 10 = indole, 11 = (*E*)-β-caryophyllene, 12 = α-humulene, 13 = (*E*)-β-farnesene, 14 = (*E,E*)-α-farnesene, 15 = nerolidol, 16 = (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. Bars represent the mean + 1 SE. Data extracted from Rodriguez-Saona et al. (2002, 2003).

The composition of the volatiles released is affected by the type of damage, and by chemicals present in insect saliva

Williams et al. Arch Insect Biochem Physiol. 2005

A cry for help…?



Herbivore associated molecular patterns (HAMPs) which induce plant responses can arise from:

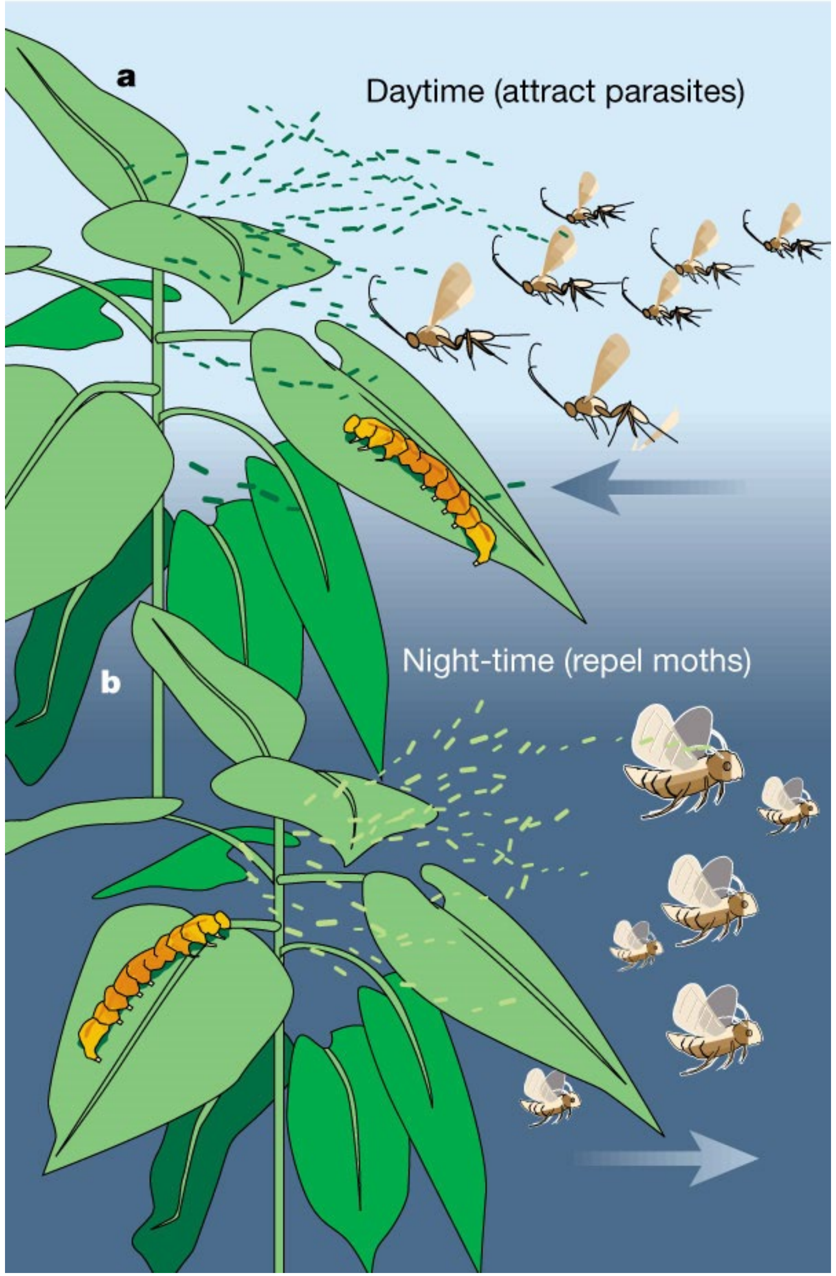
- Oral secretions (OS) (regurgitant)
- Saliva
- Ventral eversible gland (VEG) secretions
- Digestive waste products (e.g., frass)
- Ovipositional fluids
- Herbivore-associated endosymbionts

Plant responses to herbivores can be divided into direct responses – which act directly on the herbivore and indirect responses, such as the attraction of parasitoids

Basu et al. MPMI 2018

A nocturnal warning?

- Tobacco plants (*Nicotiana tabacum*) release herbivore-induced volatiles during both night and day.
- Several volatile compounds are released exclusively at night and are highly repellent to female moths (*Heliothis virescens*).
- The plant also makes chemicals that attract predatory insects during the day, so it could be advantageous for the moths to keep away.



Ryan (2001), Nature

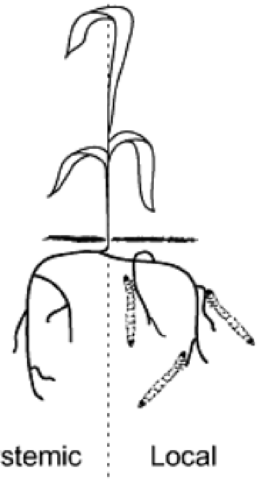
De Moraes et al (2001) *Nature*

Crying for help below ground?

Western corn rootworm
Diabrotica virgifera virgifera

Entomopathogenic
nematode (EPN)

Split root system

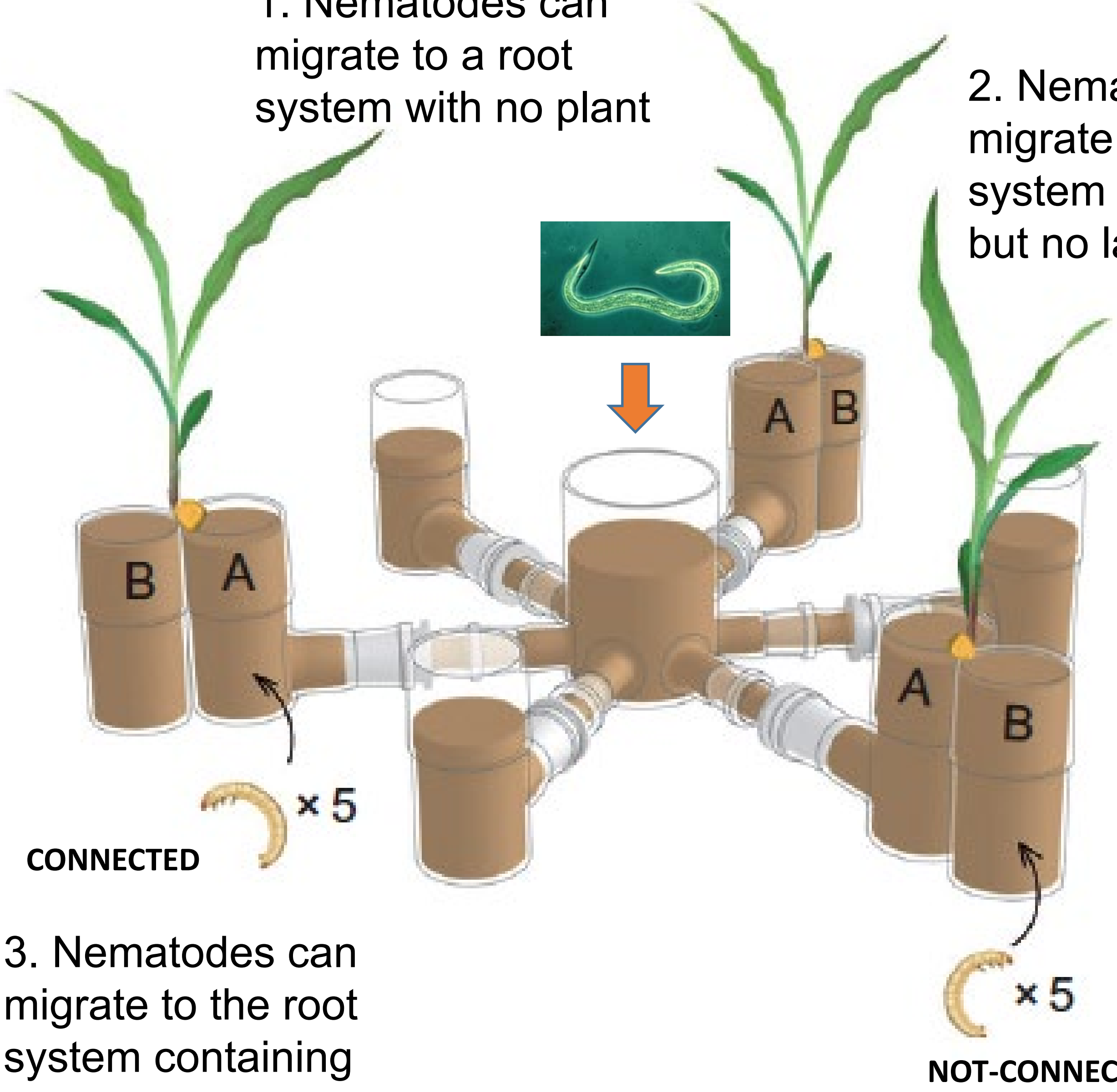


Systemic responses to larvae

Larvae

1. Nematodes can migrate to a root system with no plant

2. Nematodes can migrate to a root system with a plant but no larvae



3. Nematodes can migrate to the root system containing larvae (A)

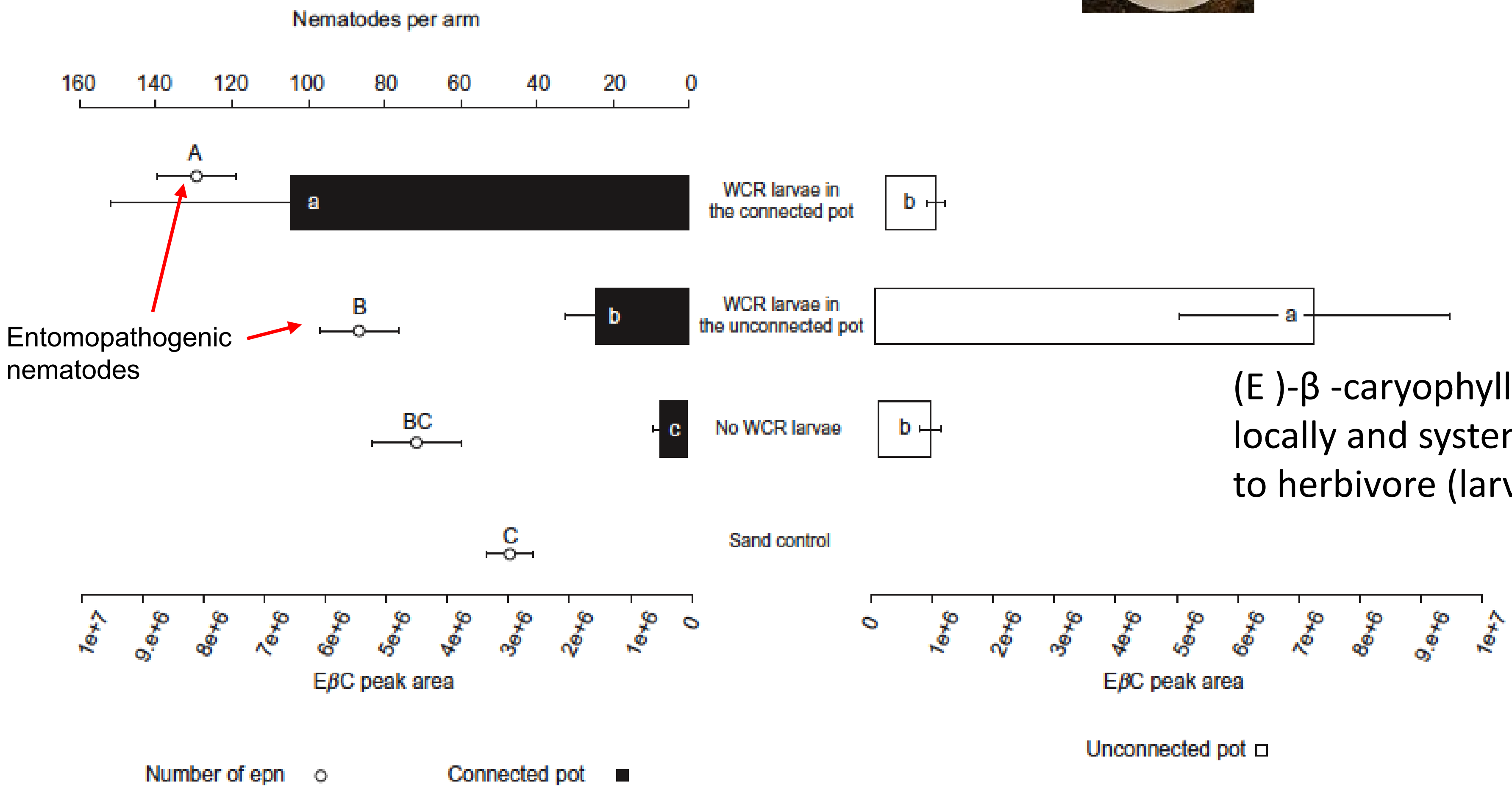
4. Nematodes can migrate to the roots of a plant that is being attacked by larvae. But nematodes and larvae are separated

Hiltpold et al Plant Cell Env 2011

Attack by western corn rootworm larvae attracts entomopathogenic nematodes

Nematodes

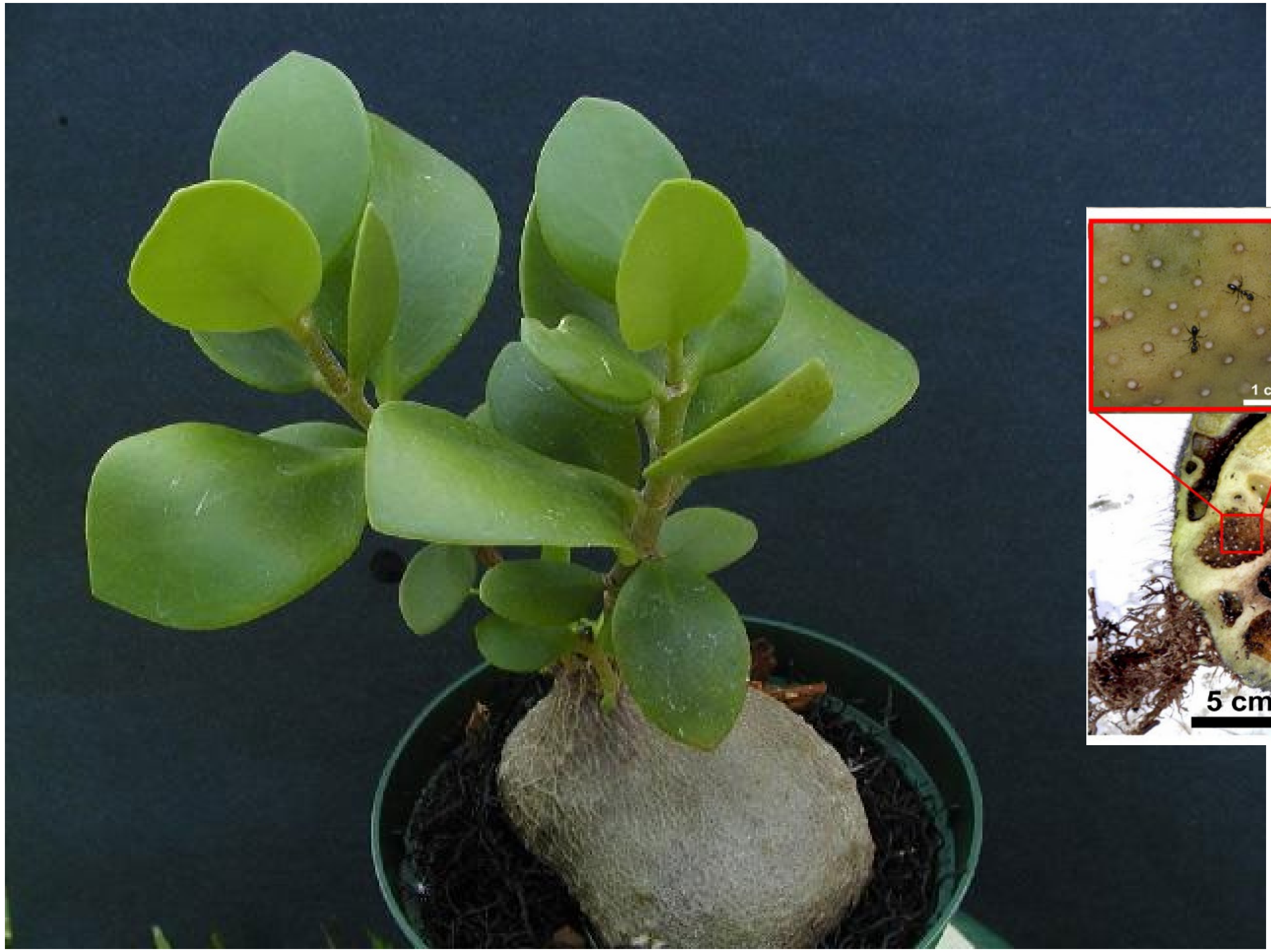
Larvae

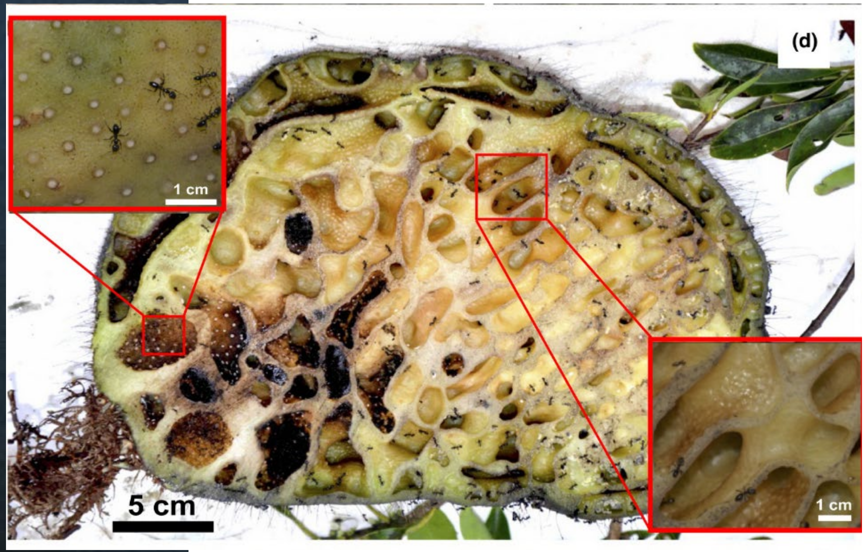


(E)-β -caryophyllene is produced locally and systemically in response to herbivore (larvae) damage

Hiltpold et al Plant Cell Env 2011

Volatiles are also used as signals in mutualistic associations with herbivores



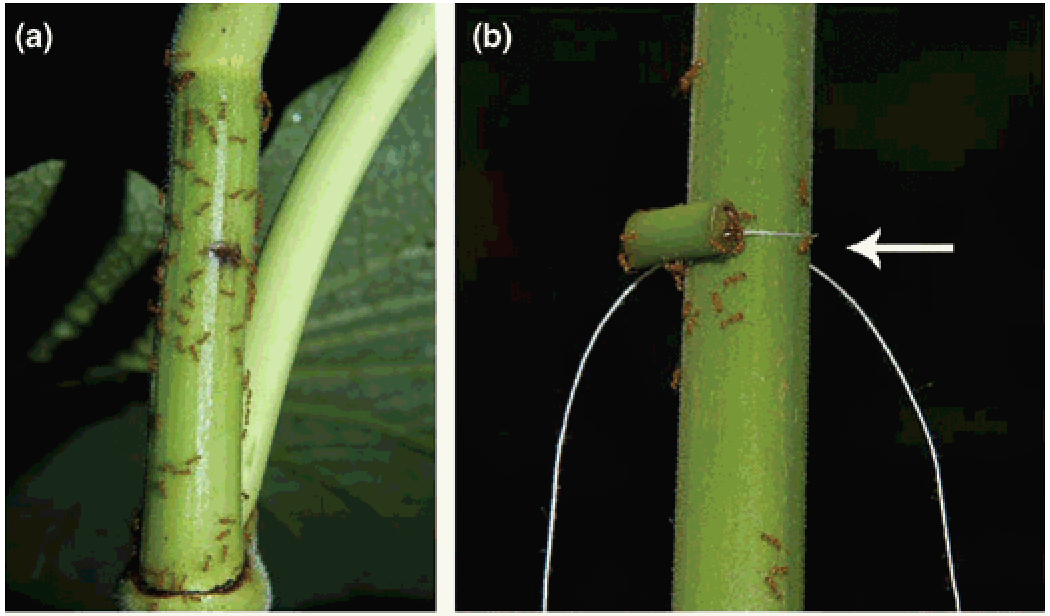


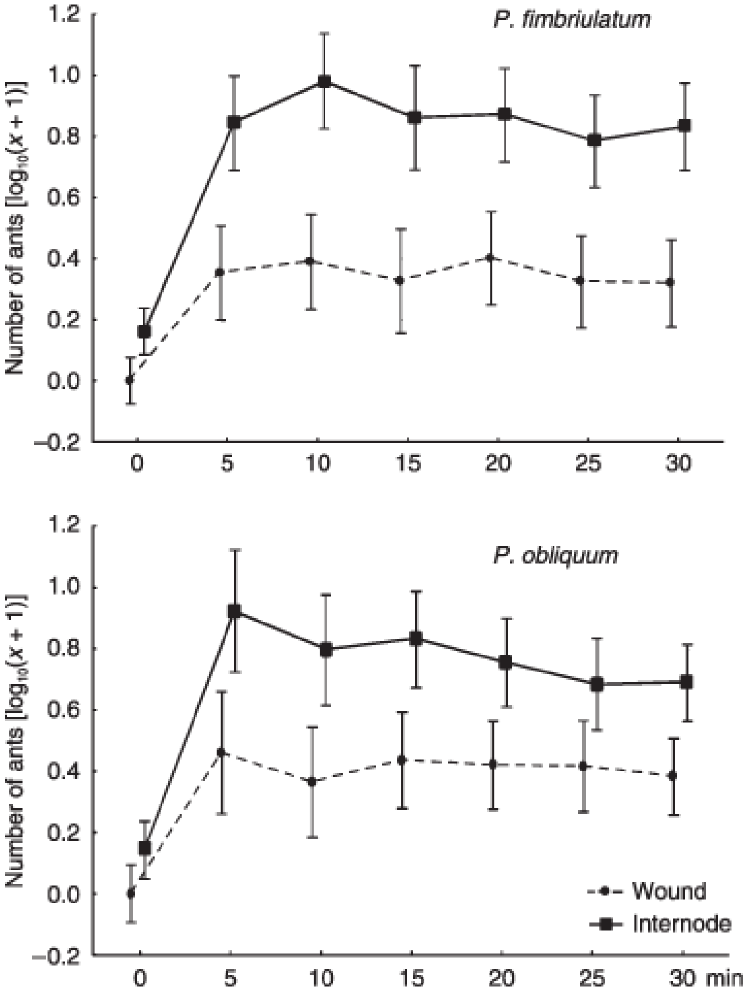
Hydnophytum

Chomicki, G et al. *Plants, People, Planet*. 2019; 1: 302– 305.


Acacia

Guardians are attracted by plant volatiles to damage to their host plant…



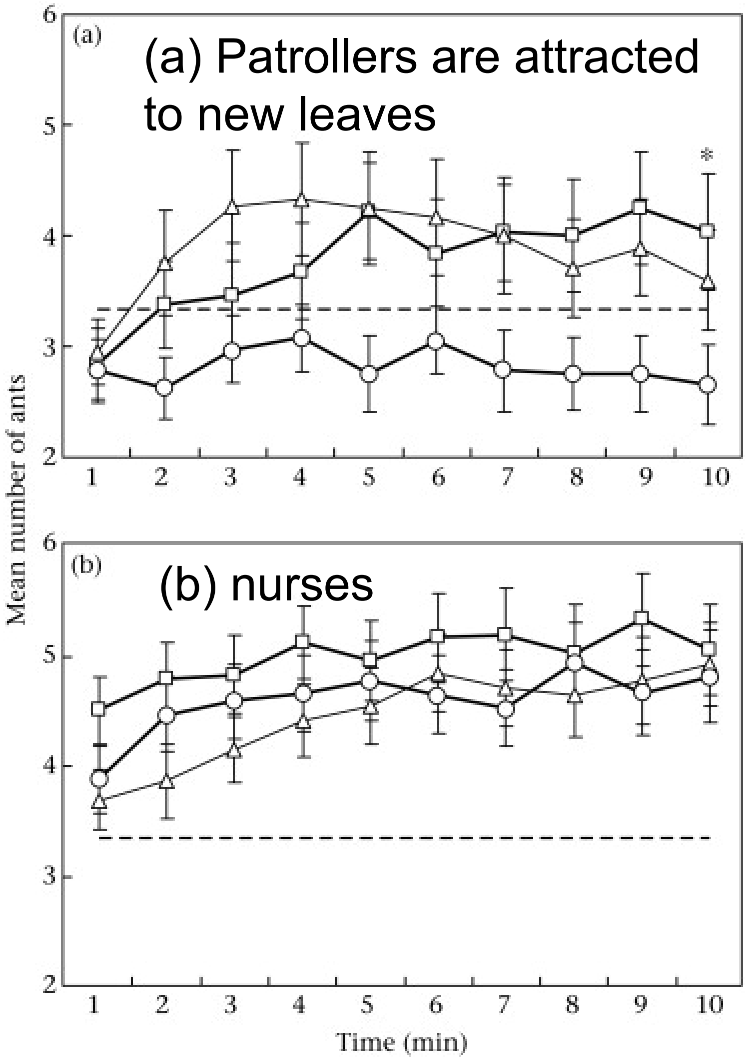


Mayer, V., D. Schaber, and F. Hadacek. 2008. Volatiles of myrmecophytic *Piper* plants signal stem tissue damage to inhabiting *Pheidole* ant-partners. J. Ecol. **96**:962-970.

Chemical signals also modify the distribution of guardians – e.g. to protect new shoots

Nurse workers and brood

Patroller workers on new shoot



Mean number of worker ants attracted to filter papers containing new-leaf (□), mature-leaf (○), and pure hexane (Δ) extracts

Edwards et al. Animal Behaviour, 2007

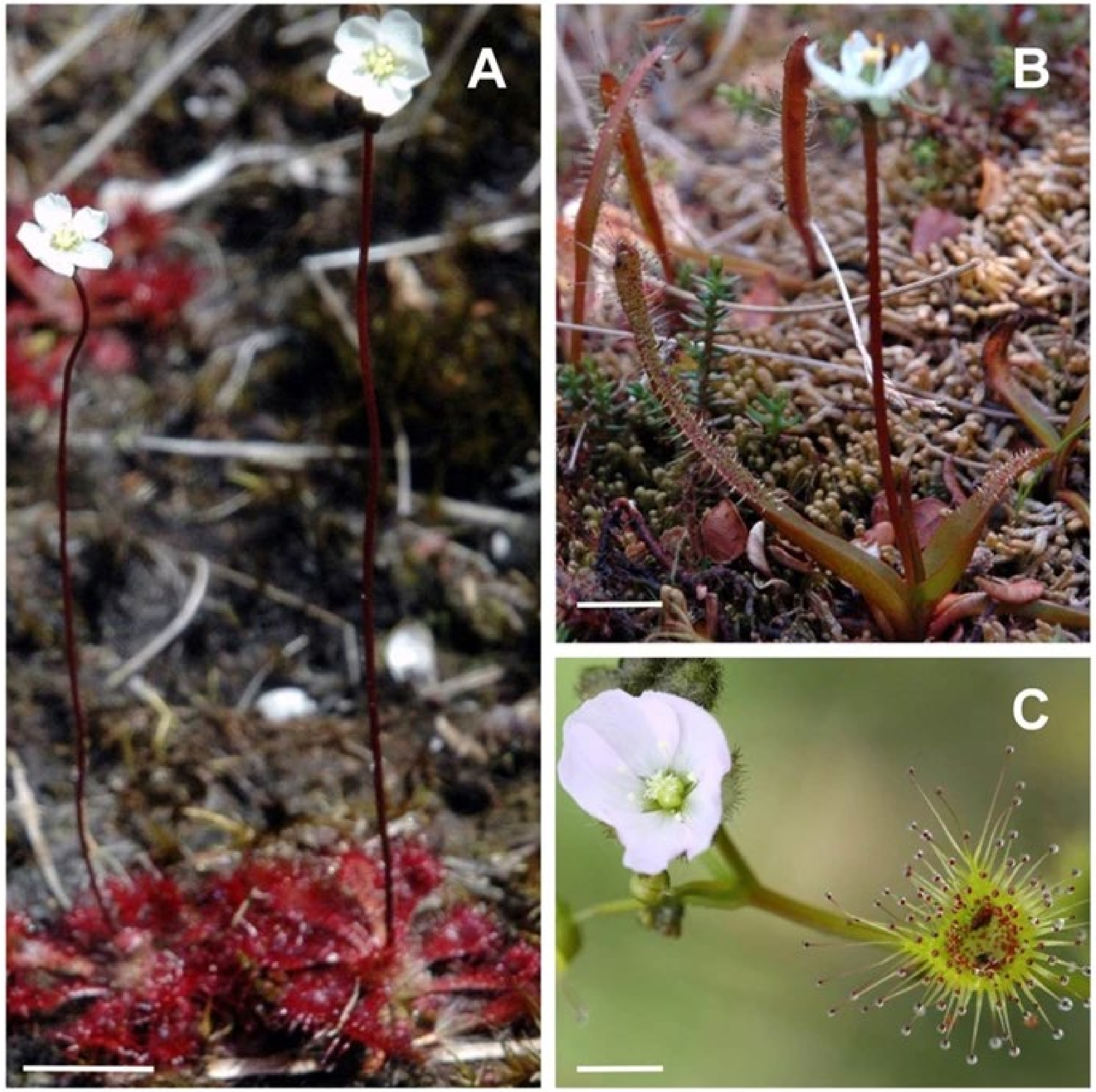
5. Prey

Carnivorous plants use scent to attract prey…

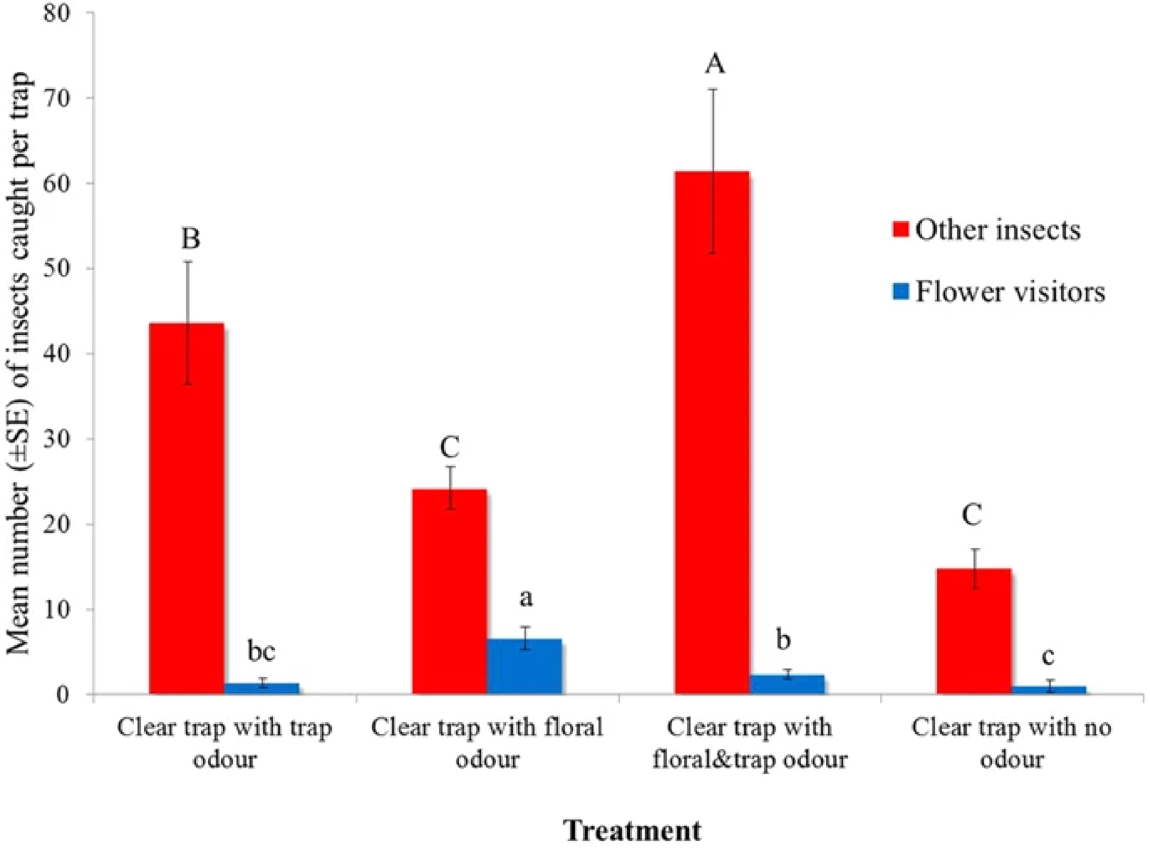
Venus fly trap

Pitcher plant

Carnivorous plants attract pollinators to flowers and prey to traps



Flower trap arrangement in *Drosera spatulata* (A), *Drosera arcturi* (B) and *Drosera auriculata* (C). Scale bar = 1 cm.

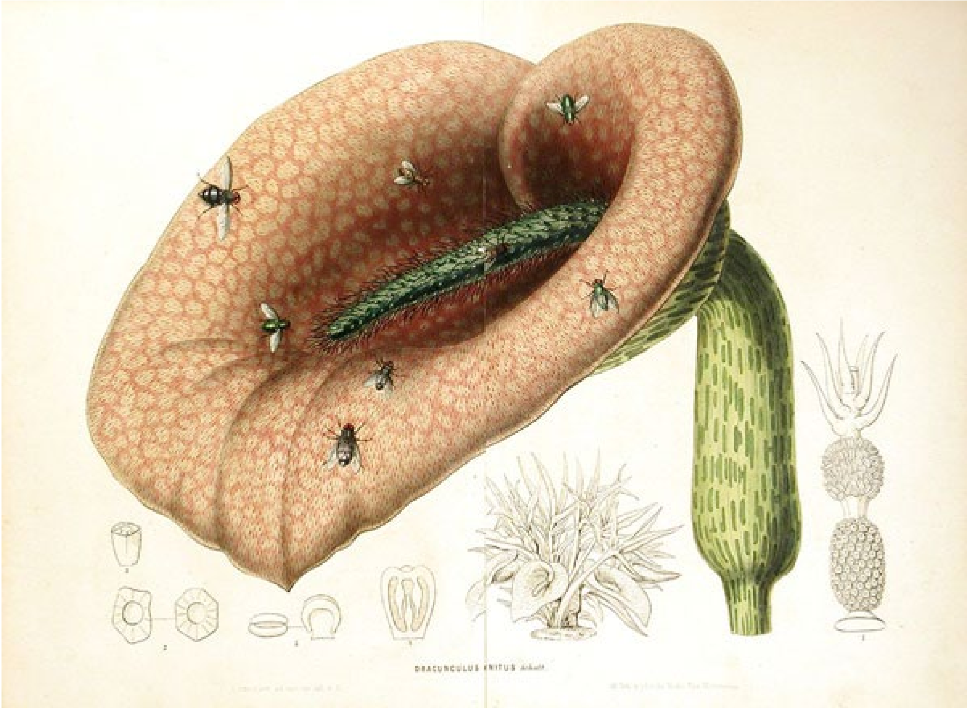


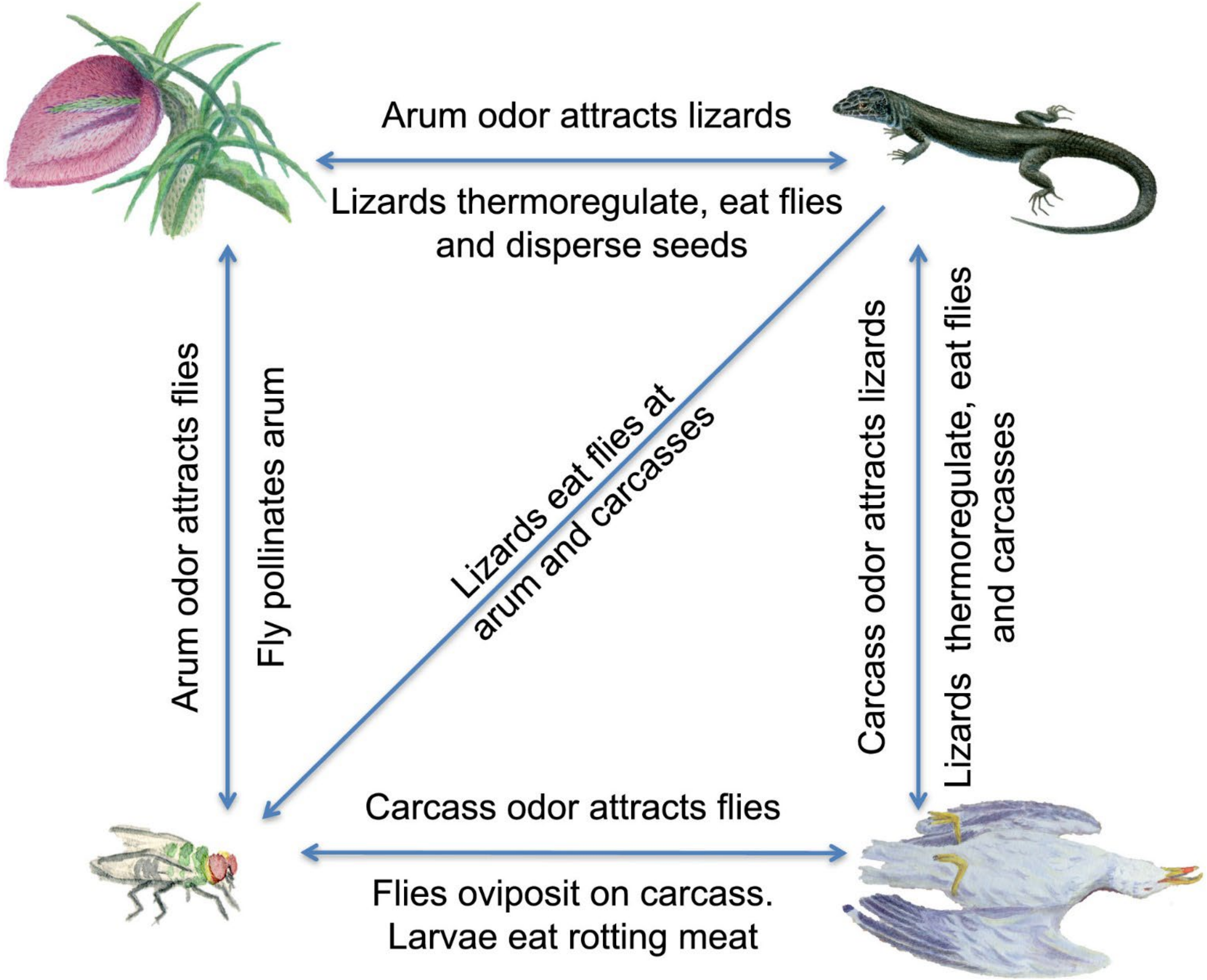
Traps with trap odour attract a range of insects, but floral visitors are attracted more to traps with floral odour

El-Sayed et al. Sci Reports 2016

6. Predators may also use plants to attract prey – while plants can exploit predators for seed dispersal

Dead horse arum and *Podarcis lilfordi* (Balearic lizard)



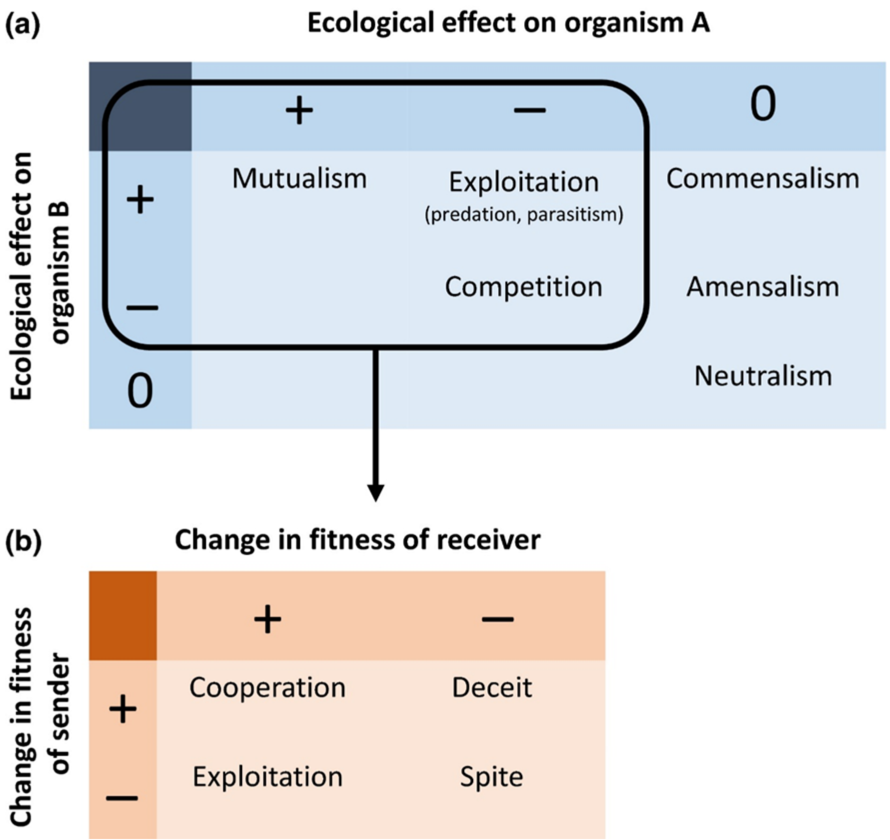


Perez-Cembranos et al. 2018

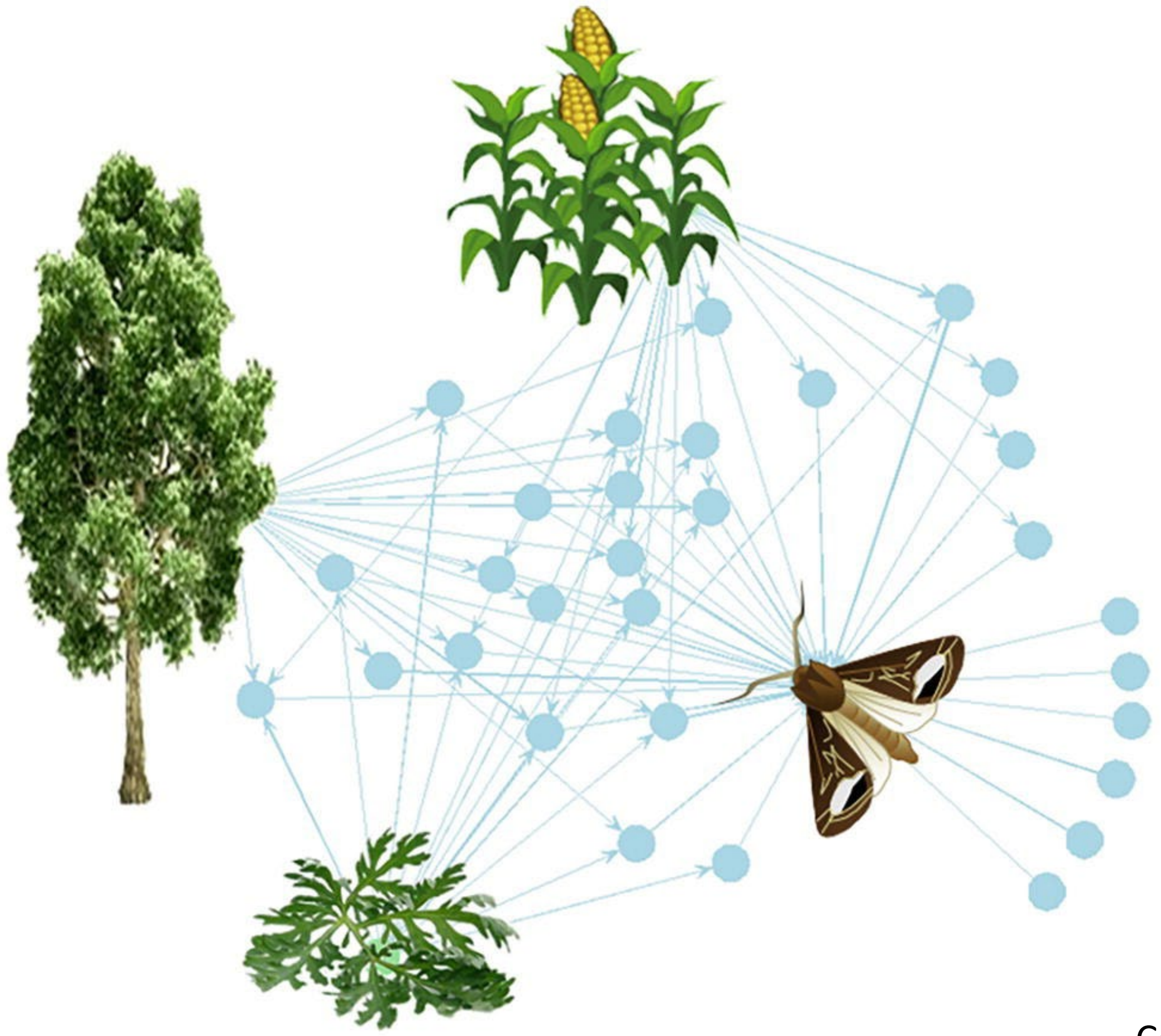
VOCs as inter-kingdom signals

Who do plants talk to?

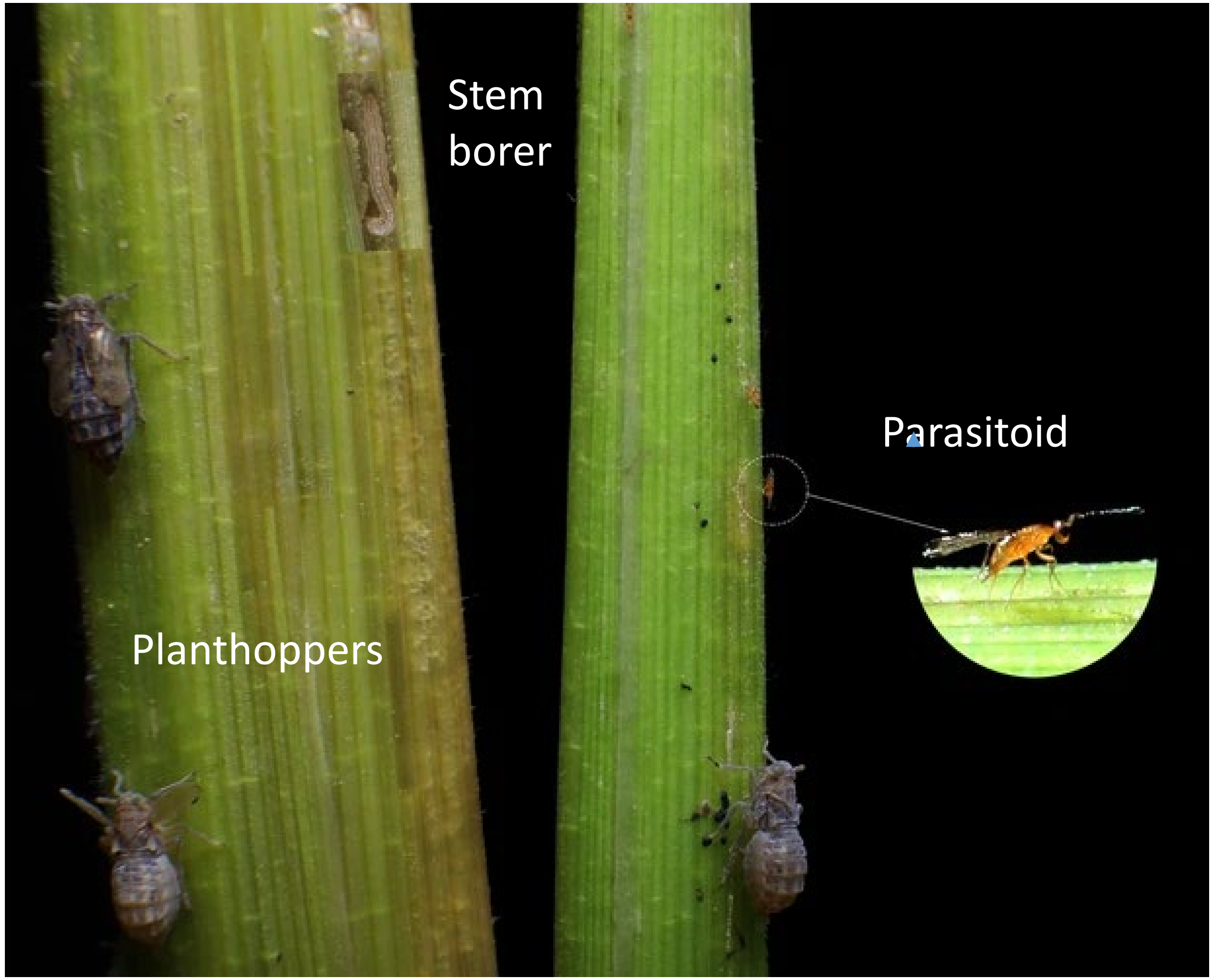
1. Pollinators
2. Seed-dispersing organisms
3. Herbivores, parasites and symbionts
4. Guardians
5. Prey
6. Predators



Can we use knowledge of plant communication mechanisms to enhance pest and disease control?



Conchou et al. (2019) Front Physiol



The brown planthopper *Nilaparvata lugens*, the rice-striped stem borer *Chilo suppressalis*, and the egg parasitoid *Anagrus nilaparvatae*.

Can we make crops less attractive to pests and more attractive to parasitoids?

GM strategies to alter volatile production?

Hu et al. 2020 eLife

Modern crop varieties often have significantly reduced volatile-mediated signalling relative to their wild relatives or landraces

- Modern crop species have been reported to produce both a reduced quantity and diversity of volatile signals in response to pest damage

- Studies on cotton (*Gossypium hirsutum* L.), tomatoes (*Solanum lycopersicum*), and maize (*Zea mays*) have shown that natural enemies such as parasitoids are more attracted to the damage-induced VOCs of wild relatives and landraces than those of modern crop species

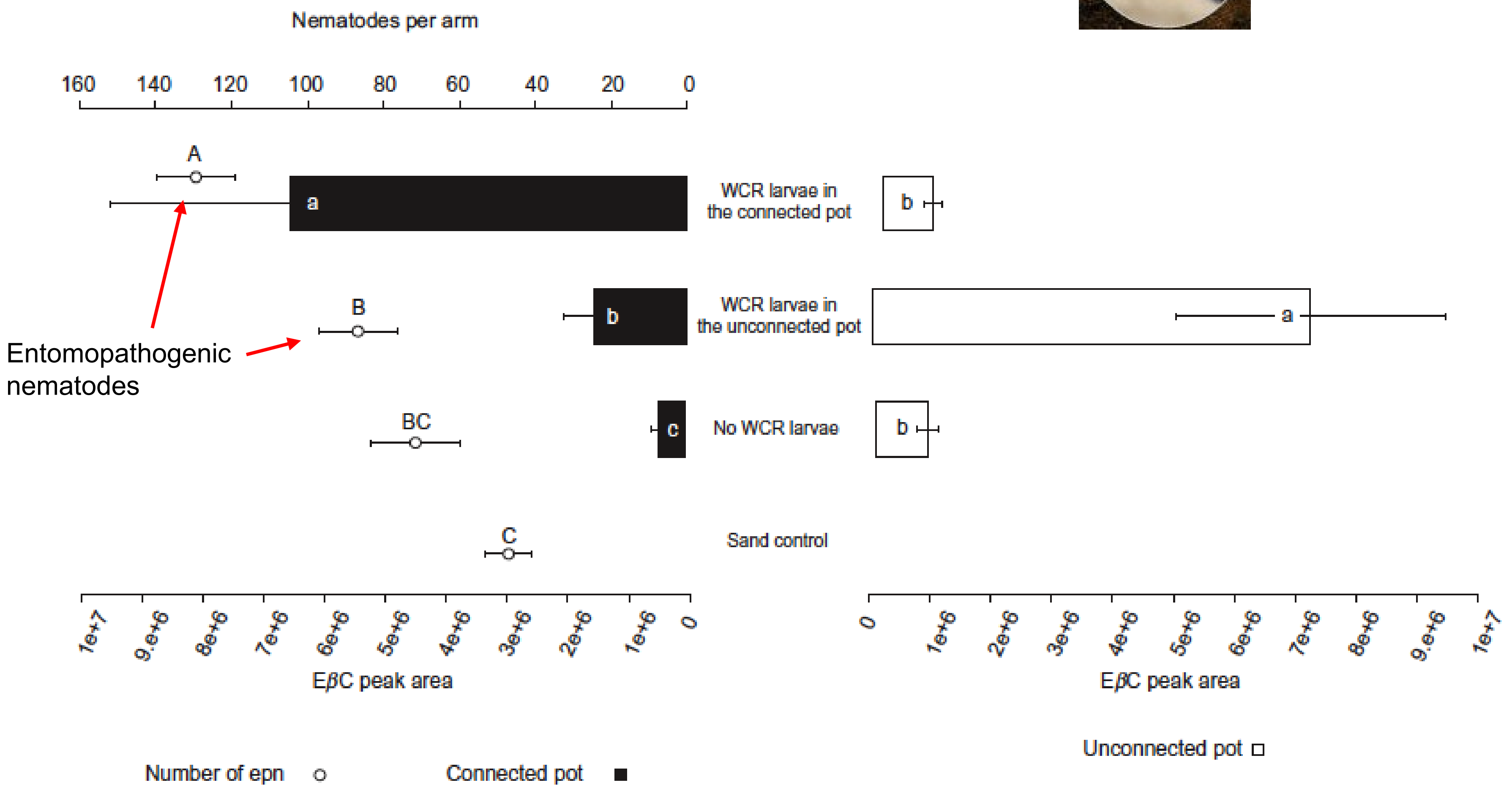
- Modern, high yielding rice varieties also show an altered volatile profile compared to traditional varieties, including a reduction in phenolics.

Loughrin et al. J. Chemical Ecology 1995, Chamberlain et al. J. Chemical Ecology 1996, Magara et al. Int. J. Sciences 2015, Li et al. Agricultural and Forest Entomology 2018, Ashokkumer et al. Frontiers Nutr 2020

Attack by western corn rootworm larvae attracts entomopathogenic nematodes

Nematodes

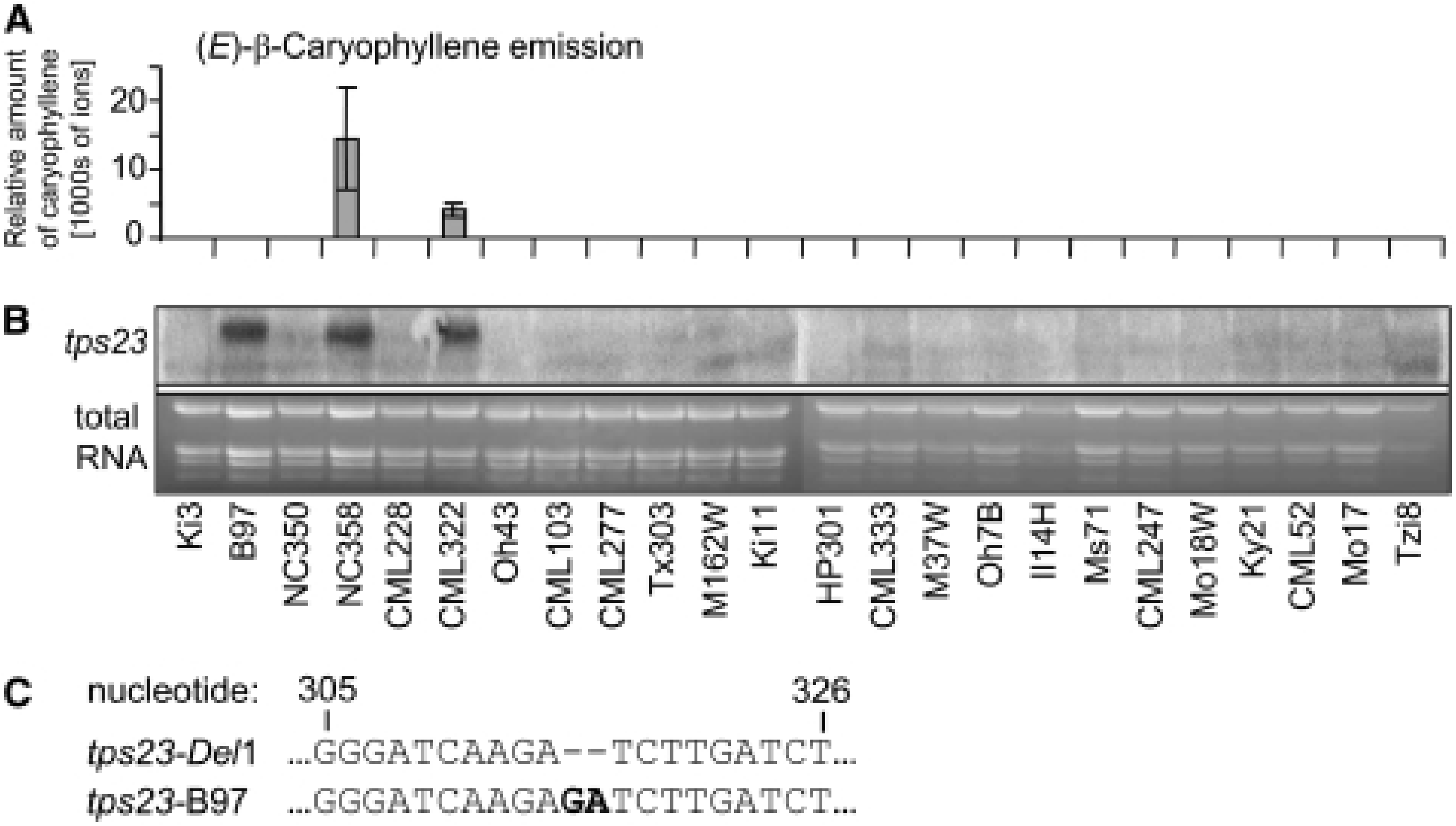
Larvae



(E)-β -caryophyllene (Eβ C) production increases in plants that are being attacked by larvae.

Rasmann et al Nature 2005
Hiltpold et al Plant Cell Env 2011

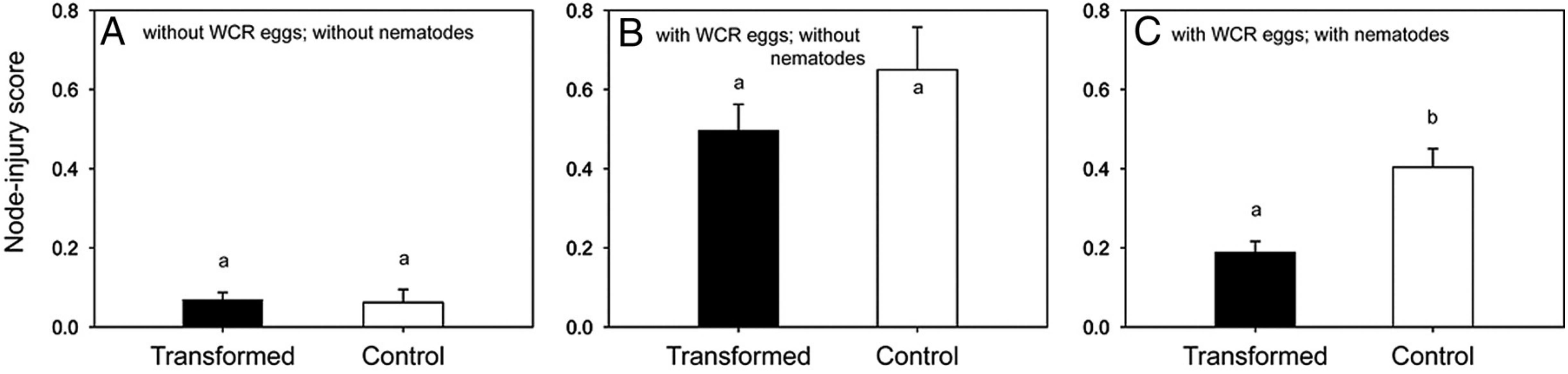
Maize lines of North American origin do not produce (E)-β-Caryophyllene



The *tps23* allele of the Eβc non-producing line B97 contains a 2-bp insertion at nucleotide 315 compared with *tps23*-Del, which results in an inactive enzyme.

Köllner et al. Plant Cell, 2008

Maize plants transformed to express the Eβc-synthase gene show reduced damage when western corn rootworm larvae and entomopathogenic nematodes are present



Restoring volatile production traits lost in domesticated or modern crops may increase pest and pathogen resistance

Degenhardt et al. PNAS USA 2009

Could enhancing scent production in commercially bred flowers enhance both appeal and pest/disease resistance?

Scented rose

Many commercially bred flowers have low scent production

(high yield, large flowers, long vase life = low scent = trade-off?)

"Fragrant Cloud"

volatile esters, aromatic and aliphatic alcohols, monoterpenes, and sesquiterpenes

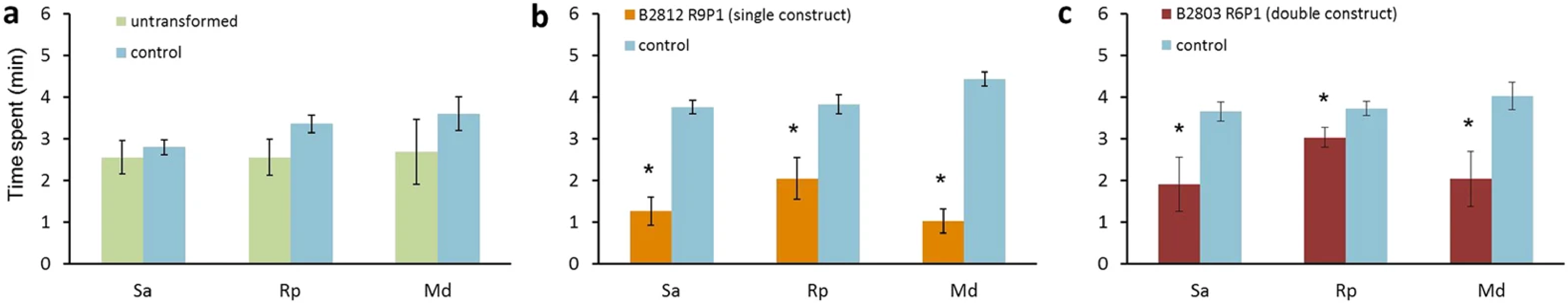
"Golden Gate"

nonscented methoxylated phenols

Guterman, I. *et al.* 2002 Plant Cell **14**:2325-2338.

Eckardt, N. A. 2002. Plant Cell **14**:2315-2317.

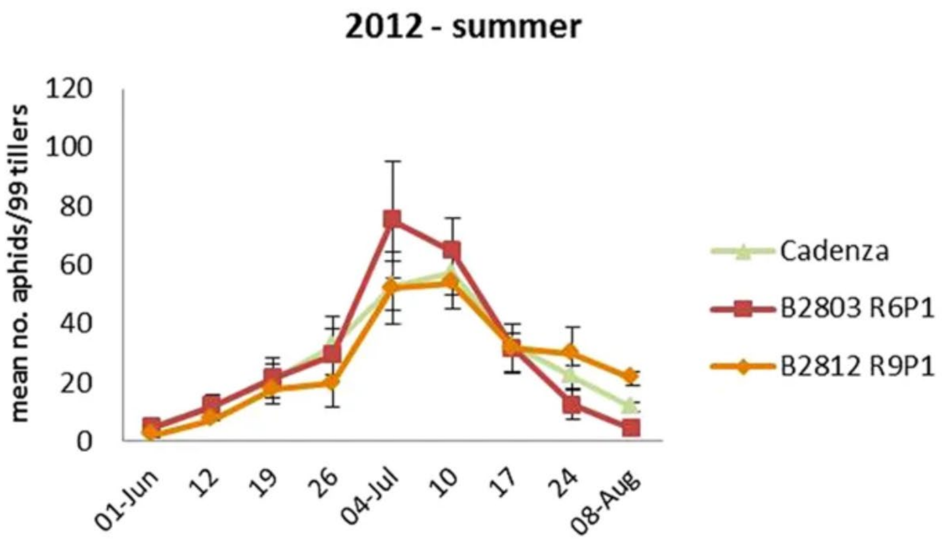
Wheat (*Triticum aestivum*) has been genetically engineered to produce the aphid alarm pheromone (E)-β-farnesene (Eβf), which repels aphids and attracts their natural enemies

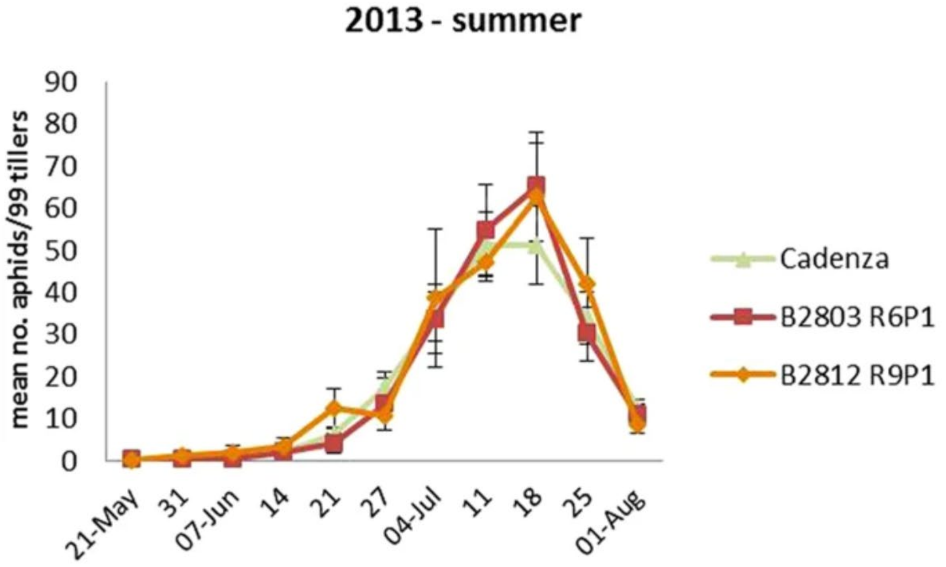


Aphids were observed to be repelled by the transformed wheat lines (B2812 R9P1 and B2803 R6P1) in the laboratory. Graphs show time spent (mean ± s.e.) by the cereal aphids *Sitobion avenae* (Sa), *Rhopalosiphum padi* (Rp) and *Metopolophium dirhodum* (Md) in different regions of a 4-arm olfactometer (n = 10).

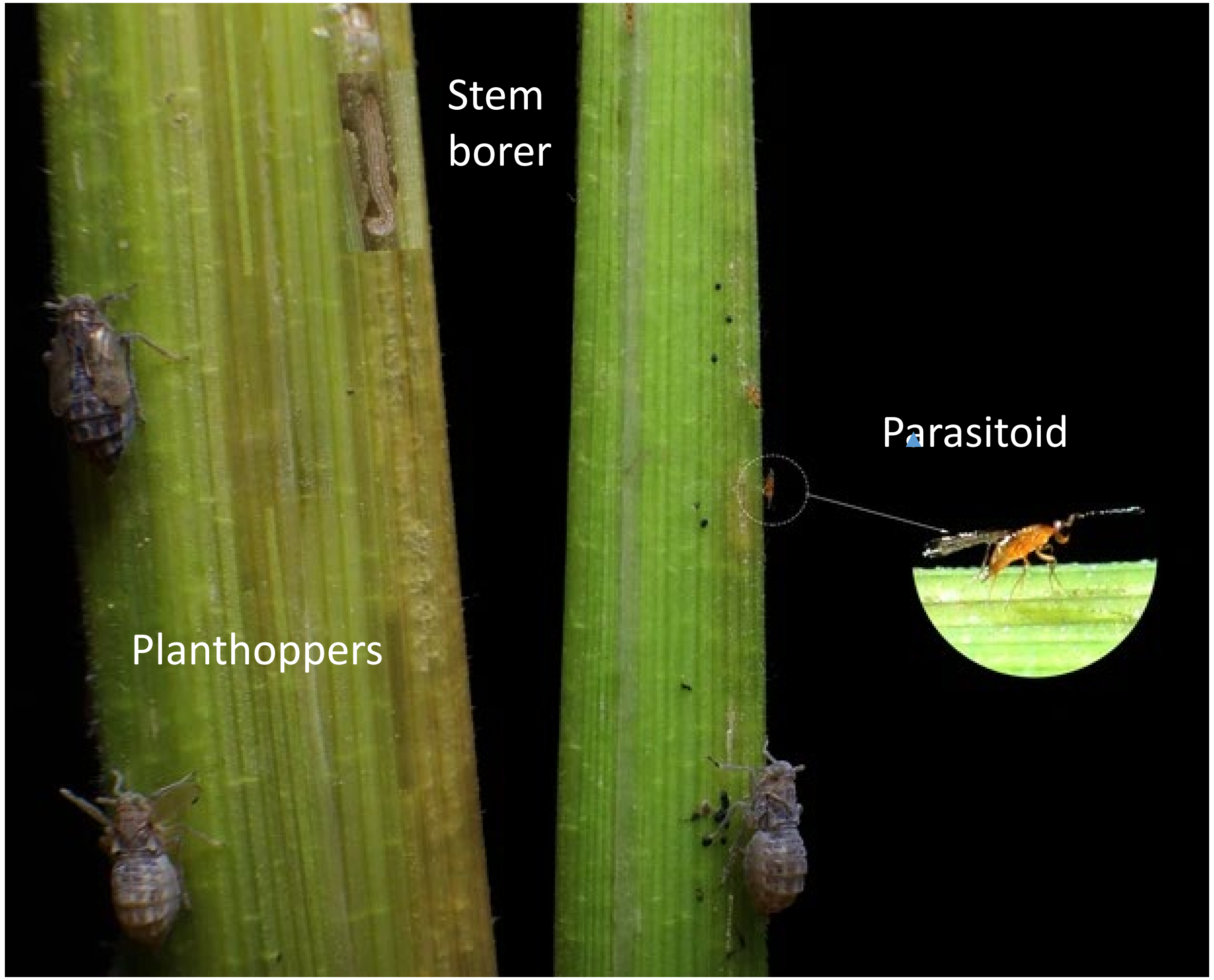
Bruce et al. Sci Reports, 2015

But the researchers did not observe a significant reduction in aphid numbers in the field





Bruce et al. Sci Reports, 2015



The brown planthopper *Nilaparvata lugens*, the rice-striped stem borer *Chilo suppressalis*, and the egg parasitoid *Anagrus nilaparvatae*.

Can we make rice less attractive to pests and more attractive to parasitoids?

GM strategies to alter volatile production?

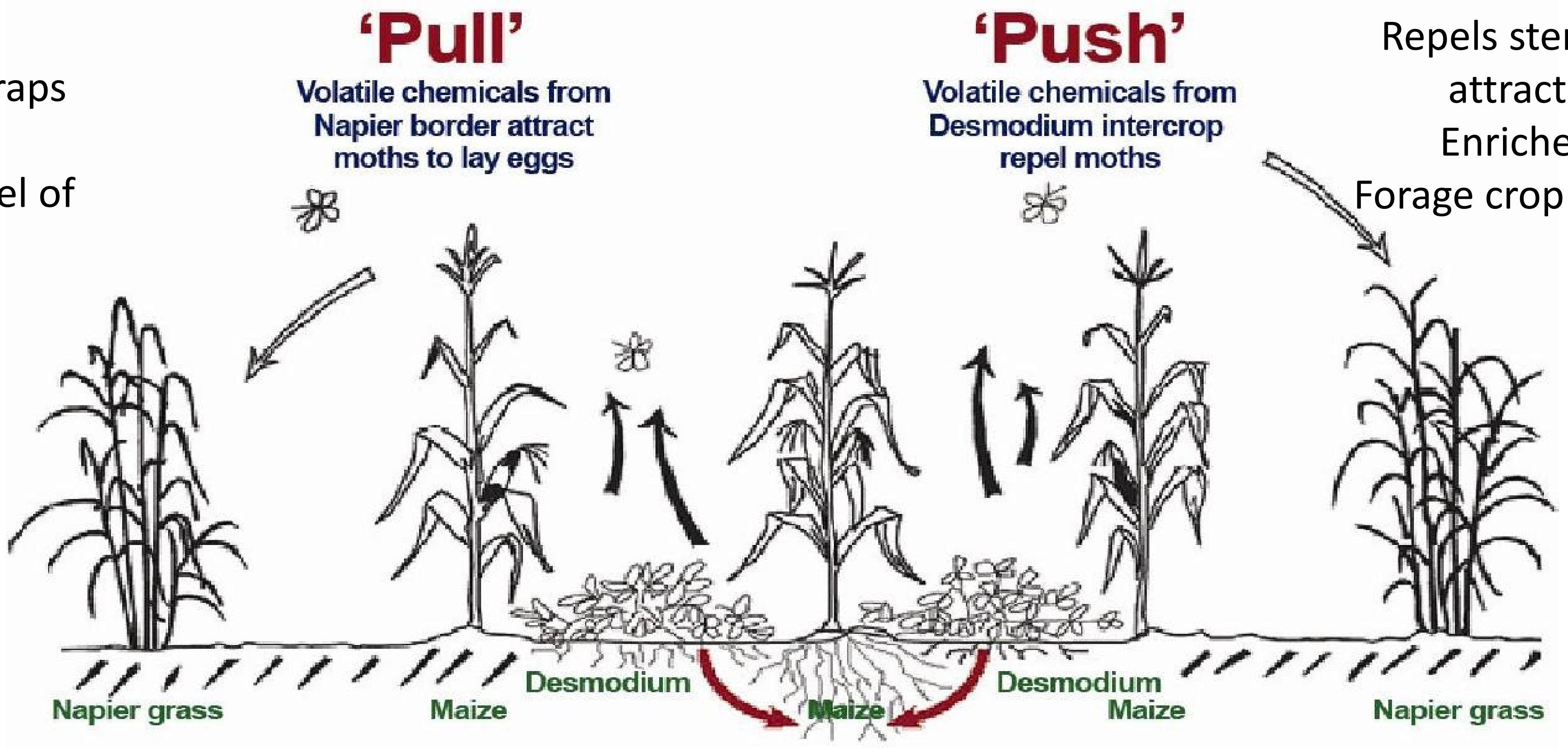
Other approaches?

Hu et al. 2020 eLife

Push-Pull technology to protect maize from insect pests

Napier grass:
Attracts and traps stemborers
Emits high level of VOCs at night

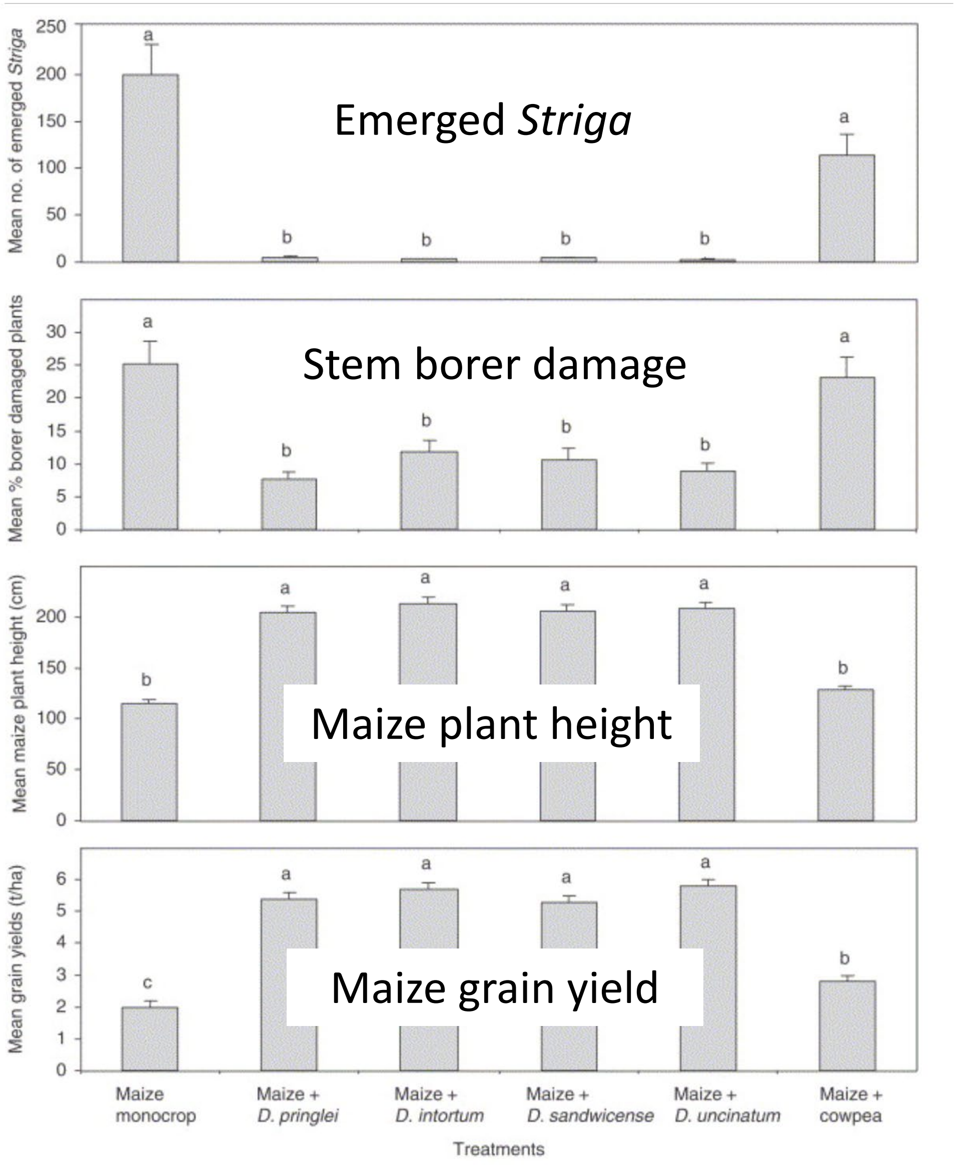
Desmodium:
Repels stemborers and attracts parasitoids
Enriches soil with N
Forage crop for livestock



http://www.push-pull.net/works.shtml

Desmodium intercropping also helps to control *Striga*

Desmodium secretes a C-glycosylflavonoid called Isoschaftoside in its root exudates which inhibits the growth of germinating *Striga.*



Khan et al. Crop Protection 2006

Vocabulary

- Semiochemical
- Hormone
- Allomone
- Kairomone
- Synomone
- Strigolactone
- Volatile organic compound
- Thermogenesis
- Choice assay
- Myrmecochory
- Oviposition
- Parasitoid
- Herbivore associated molecular pattern (HAMP)
- Push-Pull technology
- Intercropping