

Aboveground Plant Communication by Air Borne Signalling

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ABSTRACT

Plants are sessile but highly sensitive organisms, they are actively communicating among themselves for environmental stimuli/stresses both above and below the ground. As plants do not have organs that function as ears or mouths the idea that they can hear what might be spoken to them or speak to each other is by different ways of communication. Plants emit volatile organic compounds (VOCs) as a means of aboveground communication, they warn other plants of impending danger. Nearby plants exposed to the induced VOCs prepare their own defence weapons in response. Plants use Common Mycorrhizal Network (CMN) as a communicating media belowground; they use Common Mycorrhizal Network for sharing the nutrients and defence signals. In this review we are emphasising only on aboveground plant communication.

Key words: Volatile organic compounds (VOCs), Plant communication, Defence.

INTRODUCTION

Can plants talk? The answer is yes but plants developed their own ways of communication systems. In nature, plants are sessile organisms they cannot go and talk like us but plants continuously interact with other living organisms that share their environment, notably via the synthesis and release of volatile organic compounds (VOCs). When there is a stress either biotic or abiotic plants will sense and communicate to the neighbouring plants. Plants sends

warning/alarm signals to the healthy / undamaged neighbouring plants.

Plant Communication

Plants communicate their physiological condition to a diverse range of organisms in their community through the emission of VOCs. Plant volatiles can be produced by various plant organs (leaves, flowers, fruits and roots) and have been shown to be key mediators in biotic interactions both aboveground and belowground. VOCs are able to attract the beneficial insects and also able to repel the pests.

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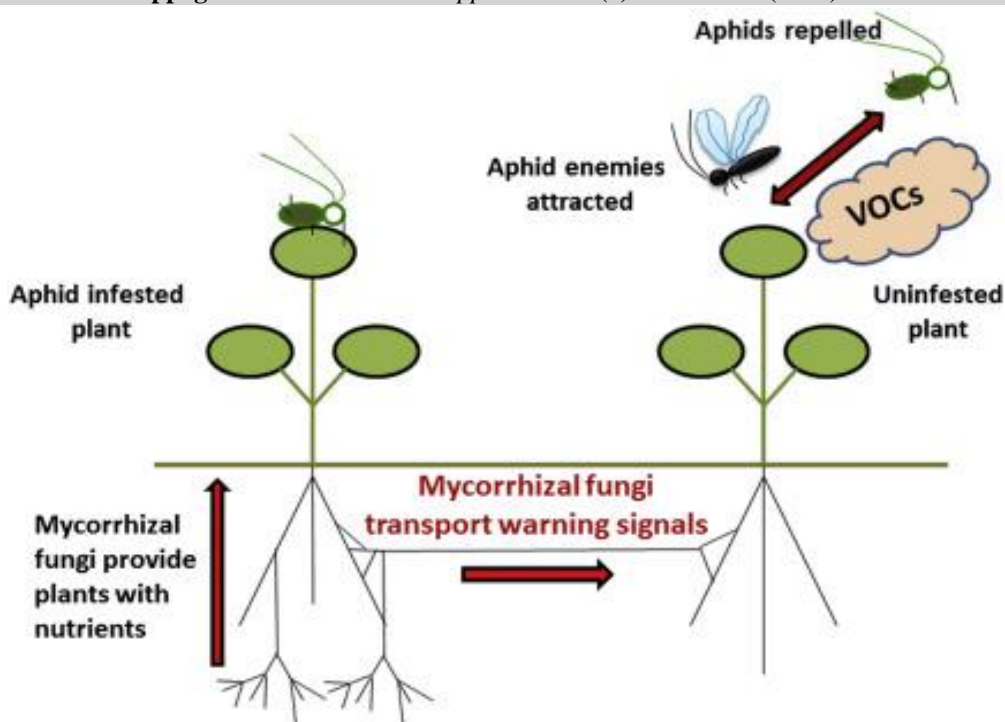


Fig. 1: VOCs mediated Plant–Plant Communication in Response to Herbivore Attack

Aboveground plant communication is mainly mediated through VOCs and belowground, root systems can exchange carbon and defence-related signals through common mycorrhizal networks. Plants also release a wide array of molecules via root exudation in the rhizosphere that play numerous roles, particularly in plant nutrition and biotic interactions between plant roots and soil organisms.

Aboveground communication

VOCs are key elements of aboveground plant communication. VOCs protect plants from stress (biotic and abiotic), attract insects for pollination and seed dispersal, and even send warning signs to neighbor plants and animals that predators are attacking. VOCs essentially mediate relationships between plants and the organisms with which they interact.

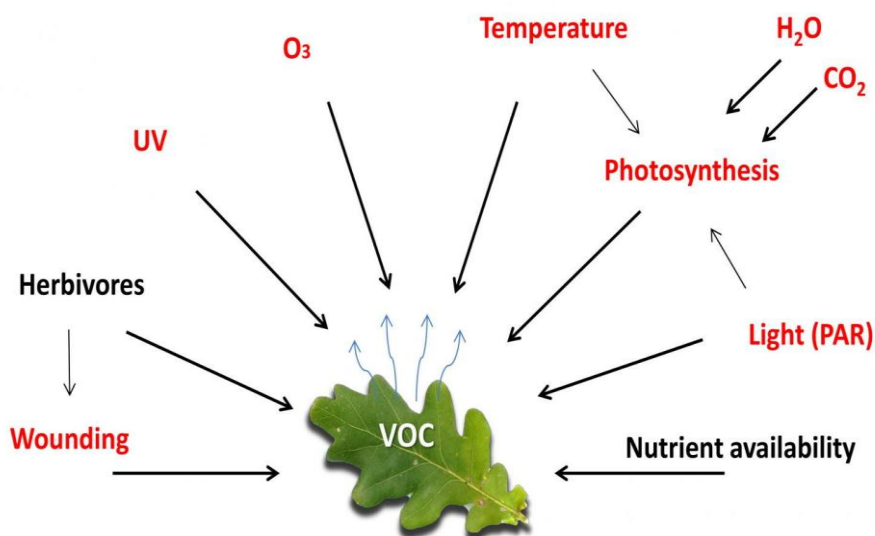


Fig. 2: Roles of VOCs

In addition to having roles in plant defence against biotic stress and communication with other organisms, plant volatiles also protect plants from some abiotic stress factors and the

dynamics of plant emissions are strongly affected by abiotic conditions, such as temperature, humidity, light intensity, drought, ozone, CO₂ and nutrient availability.

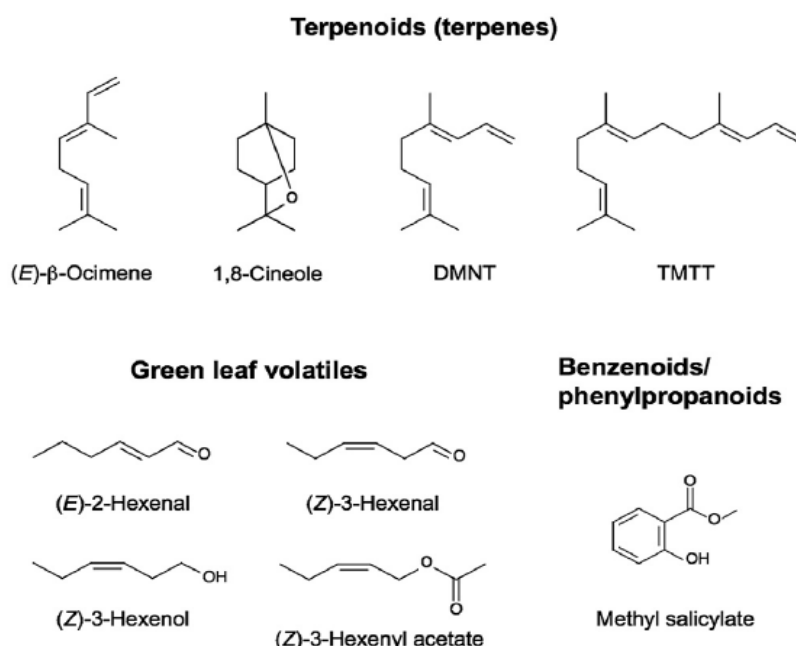


Fig. 3: Volatile organic chemicals serving as signalling cues for plant communication

Majority of plant volatiles are derived from terpenoids, fatty acid catabolites, aromatics, amino acid derived products and alcohols.

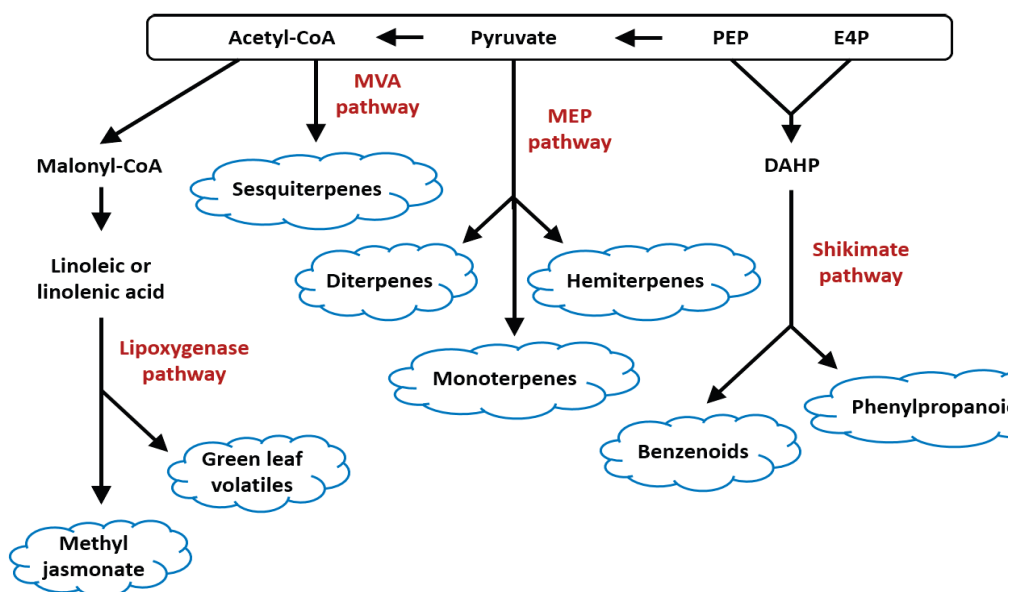


Fig. 4: Overview of biosynthetic pathways of VOCs

VOCs produced by plants aboveground are dominated by four chemical families originating from the following biosynthetic pathways: terpenoids (mevalonic acid [MVA] and methylerythritol phosphate [MEP]

pathways); fatty acid derivatives (lipoxigenase [LOX] pathway); benzenoid and phenylpropanoid compounds (shikimic acid pathway). These compounds are low molecular weight molecules that can be

emitted either constitutively (e.g., floral volatiles attracting pollinators) or in response to biotic or abiotic stress.

Role of VOCs

Herbivorous insects often move from one leaf to another, but adjacent leaves are not always directly connected via the plant's vascular system. Therefore, volatile compounds may reach distal parts of the plant faster than vascular signals. Herbivore-induced VOCs can directly repel herbivores such as butterflies and aphids. VOCs can attract natural enemies of herbivores, including predators and parasitic wasps. Plant volatiles especially isoprene have been linked to thermo tolerance Isoprene has been shown to be avoided by foraging *Manduca sexta* larvae¹², which may reduce the

attractiveness of some plants as hosts under high temperature conditions. Isoprene also has the ozone quenching effect.

Disadvantages of VOCs

In nature everything will be having both positive and negatives. In VOCs mediated plant communication there is lot of advantages with regard to defence signalling but few negatives also exists let us know about them.

1. Parasitic plants and herbivorous insects can use VOCs to locate their hosts

Cuscuta pentagona (dodder) uses volatile cues for host location. Dodder plant is smart enough to distinguish tomato and wheat volatiles and preferentially grow toward the tomato (host). Volatiles identified in this case are phellandrene and myrcene¹⁹.



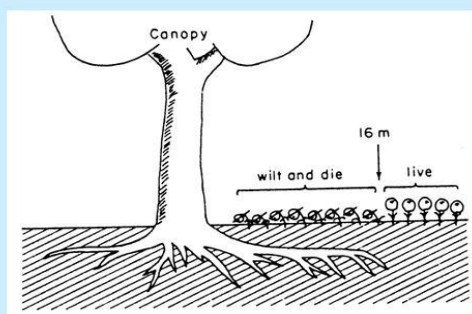
Fig. 5: Dodder Parasites Tomato Plant

1. Allelopathy:

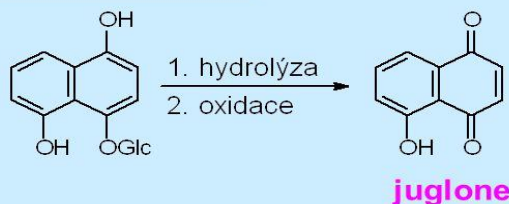
Plants have to compete with their neighbours for resources like water and light. As part of that battle, some release chemicals that harm their rivals. This "allelopathy" is quite common in trees, including acacias, sugarberries, American sycamores and several species of *Eucalyptus*. They release substances that either reduce the chances of

other plants becoming established nearby, or reduce the spread of microbes around their roots. One of the best-studied examples of allelopathy is the American **black walnut tree**. It inhibits the growth of many plants, including staples like potatoes and cucumbers, by releasing a chemical called juglone from its leaves and roots.

Allelopathy



best known example:
Eastern Black walnut
(Juglans nigra)
 and **Common walnut**
(Juglans regia) – plants
 under tree wilt and die
 to the distance of tree
 roots



2

Belowground communication

Belowground, root systems can exchange carbon and defence-related signals through **common mycorrhizal networks (CMN)**. Plants also release a wide array of molecules via root exudation in the rhizosphere that play numerous roles, particularly in plant nutrition and biotic interactions between plant roots and soil organisms. Once released by plant roots into the rhizosphere, some of these molecules can have negative (phytotoxins, autoinhibition, development of associations with parasitic plants) or positive effects (resistance to herbivores and root detection) on neighbouring

plants and can affect plant growth directly (production of phytotoxins) or indirectly (alteration of soil chemistry, microbial populations and nutrient availability). It is now well documented that roots are able to synthesise and release volatile compounds in the rhizosphere and that VOC mediated interactions also occur belowground between plant roots and soil organisms^{22,18}.

Plants Communicates To whom?

Plant communication was first reported in 1983. This includes interspecific communication, intraspecific communication and within plant communication.

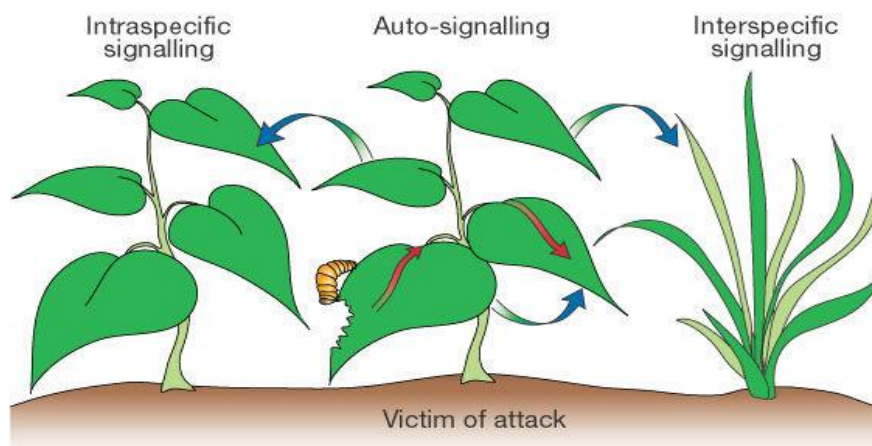


Fig. 6: Plant –Plant Communication

When there is stress or herbivory attack plants communicate to

1. Other parts/tissues of the same plant (Auto-signalling): Plants use within-plant signaling via volatiles to overcome vascular constraints and/or synergize vascular signaling.
2. Neighbouring plant of same species (intra specific signalling): helps the neighbour plants to get ready to overcome the upcoming threats.
3. Neighbouring plant of other species (inter specific signalling): plants are super co-operators they are so good enough to inform other species of plants about the upcoming danger.

Why plants communicate?

1. **Defence:** There are two types of defence strategy, direct defence i.e., through the repulsion of pests and indirect defence i.e., through the attraction of predatory and parasitic insects that prey on the

herbivores

2. **Reproduction benefits:** Plants produce VOCs to attract pollinators and seed dispersal agents which will help for successful reproduction.
3. Plant-plant communication may benefit the remitters by evoking over dispersal of herbivores within the plant population.

Ecological communication networks via herbivory induced plant volatiles (HIPVs).

HIPVs are also transmitted systemically from damaged parts to undamaged parts within an individual plant. Systemic induction allows leaves distant from a current herbivore attack to elicit defence response before the aggregation of the pests from damaged area. Plants sense the existence of herbivores and initiate changes in a battery of signalling pathways, including Ca^{2+} influxes, membrane depolarization, kinase activation, and jasmonate accumulation.

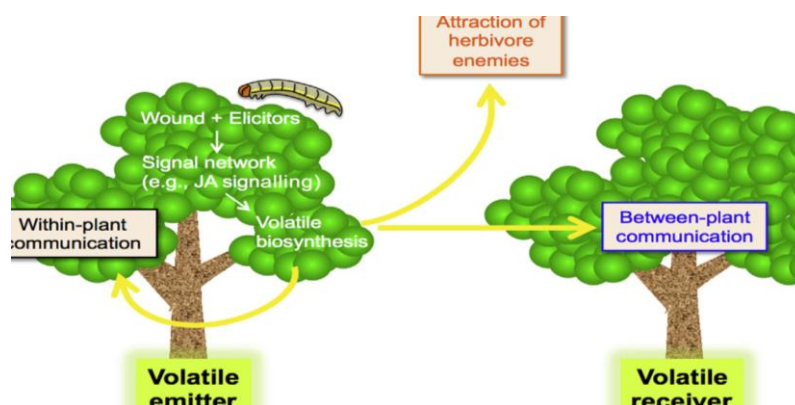


Fig. 7: HIPVs mediated plant communication

ELICITORS

Factors in insect saliva are now recognized as having a critical role to play in herbivore-induced blends of volatiles. **Elicitors in the oral secretions** of Lepidoptera larvae were found to play a critical role in the differences observed between volatiles induced by a mechanical wound and volatiles induced by insect feeding. **b-glucosidase** isolated from *Pieris brassicae* oral secretions¹⁵ and the compound N-(17-hydroxylinolenoyl)-L-glutamine, known as volicitin, isolated from the oral secretion of beet armyworm

(*Spodoptera exigua*) are two well documented elicitors²¹.

Supressors of Plant Defense

Factors in oral secretions can also suppress plant responses to damage, an example being glucose oxidase which was the first insect salivary enzyme shown to suppress wound-inducible plant defences¹⁷. These examples of salivary constituents are among a number of factors derived from herbivores e often gathered under the term herbivore-associated molecular patterns that fine-tune the information content of a volatile blend.

Perception

There is an expanding body of work on the identification of the elicitors and effectors derived from herbivores, but our knowledge on plant receptors that perceive these herbivore specific cues is still limited¹. It is essential to better understand how plants can perceive specific herbivores and activate responses that are tuned to a specific threat. Glycosidation is one of the mechanism involved in reception but **no specific receptors identified**.

Response to HIVs

Jasmonic acid (JA)-responsive genes will be activated in response to perception of HIVs. **protein dephosphorylation** is involved in the induction of the defense related genes by the volatile compounds.

Example: **basic pathogenesis related protein 2 (PR-2), basic PR-3, lipoxygenase (LOX), phenylalanine ammonia-lyase (PAL) and farnesyl pyrophosphate synthetase (FRS)** was induced in uninfested lima bean leaves in response to HIPVs from conspecific leaves infested by **two-spotted spider mites**²³.

Specific messages of plants by blending their ratio

Plants constitutively emit volatile organic compounds into the atmosphere, but when they are **damaged** they **alter** the composition and quantity of the chemical blend; compounds within this induced blend may defend plants by intoxicating herbivores or signal to a multitude of other organisms in the plant's community. Insect **saliva components** are having a **critical** role to play in **herbivore-induced blends of volatiles**. When plants are damaged they **alter** the **composition and quantity of the chemical blend**¹¹.

Specific Functions of Specific volatiles

Heil *et al.* reported **(Z)-3-hexenyl acetate**, a substance naturally released from damaged lima bean induces **EFN (extra floral nectar)** secretion which attracts the pollinators. Floral volatiles, **(Z)-3-hexenyl acetate** and **b-ocimene**, attract pollinators⁴. **In corn plants**, **(Z)-3-hexenal**, **(Z)-3-hexenol** and **(Z)-3-hexenyl acetate** have **priming** activity⁸. Volatiles involved in **antimicrobial defense**

are often produced in pistils and/or nectaries, as was shown for **linalool and linalool oxide** in flowers of *Clarkia* species⁶.

Emitters Fitness Benefit

In a recent study, the effects of *Silene littoralis* feeding on *Silene latifolia* floral volatiles and pollination success were investigated⁴. More fruit production was observed and floral volatiles involved in this plants are **(Z)-3-hexenyl acetate and b-ocimene**, This results suggest that the presence of a herbivore can potentially make a plant more attractive to pollinators and increase reproductive fitness.

Defense

In response to herbivore attack, plants activate a wide array of defences that can reduce herbivore damage, including blends of volatile organic compounds (VOCs) that can be used as foraging cues by natural enemies of the herbivores. Herbivore induced plant volatiles (HIPVs) have also been implicated in plant-plant communication, as they can be perceived by neighbouring plants and prime them for an enhanced response upon subsequent insect attack. By targeting jasmonic acid (JA)-inducible genes, HIPVs have been shown to enhance both direct and indirect defence responses which can benefit the receiver by decreasing herbivore damage.

When there is herbivore attack plant produce HIVs at the site of herbivore damage as a defense response. These volatiles are powerful signals involved in both plant-plant and plant-insect communication. Direct defense is the herbivore-induced production of repellent or toxic compounds at the site of herbivore damage. Indirect defense is the herbivore-induced emission of a particular subset of VOCs which attracts natural enemies of the pest.

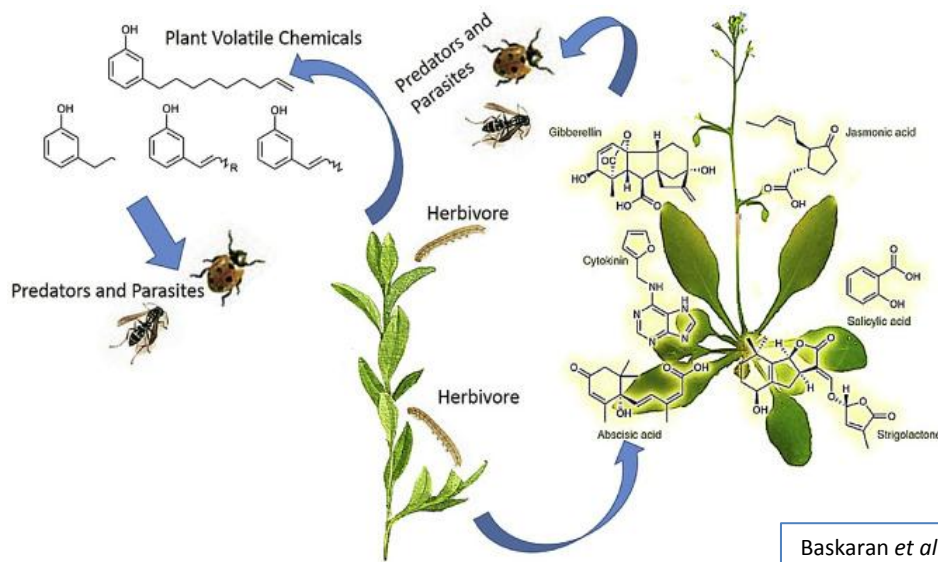
Cry for Help/ Call for Body Guard

The simultaneous damage of plants by herbivores and pathogens can influence plant defense. Receivers of herbivore induced volatile organic compounds (HI-VOCs) comprise distant parts of the same plant (within-plant signaling), neighbouring plants (plant-plant signaling), herbivores, and multiple carnivores that respond to the plant's

cry for help, such as parasitoids and hyperparasitoids, entomopathogenic nematodes, and predatory mites, beetles, bugs and birds.

In tritrophic communication plants attract herbivore enemies i.e. calls for

“bodyguards” to localize their hosts. Such indirect defence provides plants a top-down control of herbivore populations that was for the first time observed within spider mite-infested Lima beans calling carnivorous mites for help⁵.



Baskaran et al., 2017

Fig. 8: VOCs attracting natural enemies of herbivore

Ex: Corn (*Zea mays* L.) under attack of armyworm larvae (*Spodoptera exigua* Hübner) released volatiles that were attractive for the wasp parasitoid *Cotesia marginiventis* Cresson²¹.

Priming and Induced resistance

Herbivore-induced volatile organic compounds prime non-attacked plant tissues to respond more strongly to subsequent attacks is called priming defense response.

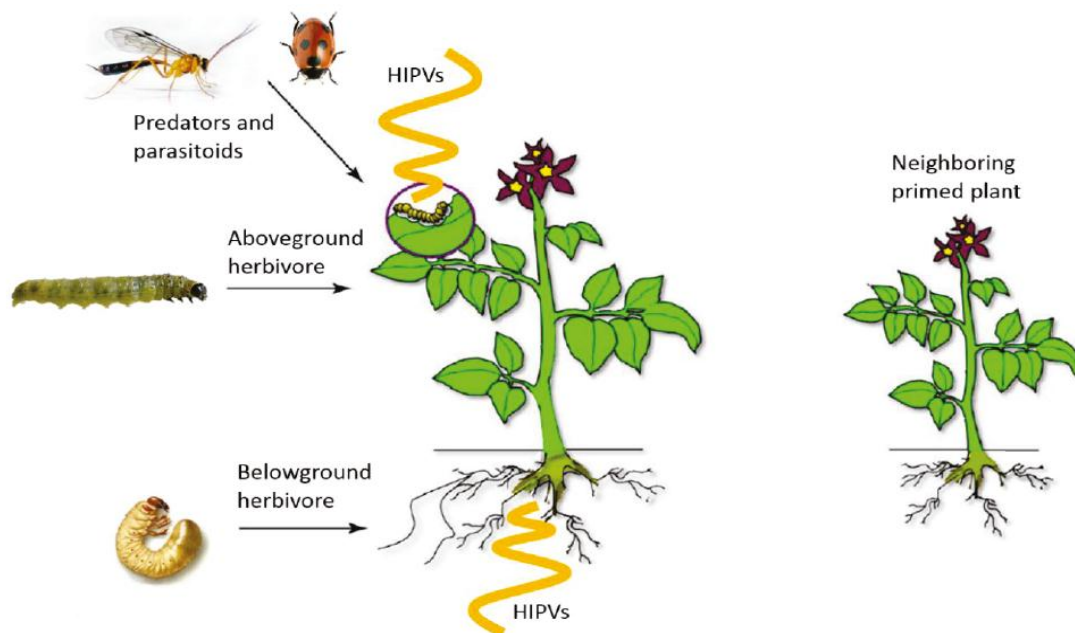


Fig. 9: Priming and Induced resistance stimulated by VOCs

Examples for priming in plants

Resistance-related genes in maize were expressed faster after caterpillar feeding when the plants previously had been exposed to VOCs released from caterpillar-infested plants²⁰. Hybrid poplar, the expression of

genes for PdnKTI (Kunitz trypsin inhibitor) and PdnIFRL1 (an isoflavone reductase-like) involved in direct defense was strongly induced once herbivores (gypsy moth larvae) began to feed¹⁰.

Use of VOCs in agriculture

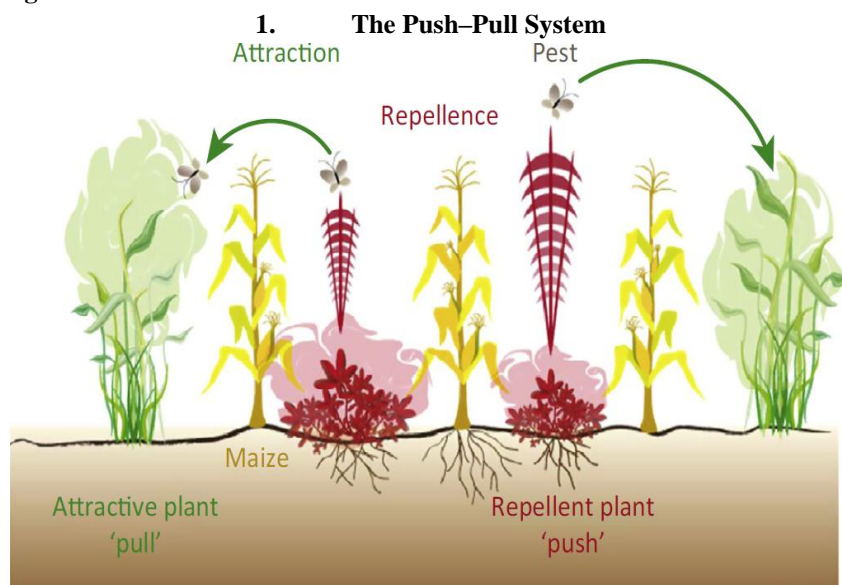


Fig. 10: Pull and push of herbivores by VOCs

The push–pull system mainly consists of intercropping the crop of interest (here maize) with a plant species that emits volatile organic compounds (VOCs) that repel the major pest. Planting an attractive (pull) plant around the field further enhances directional movements

of the pest insect out of the field. Ideally, the pull plant does not allow the pest to reproduce, and both push and pull plants also serve other functions, for example, as ornamental plants, vegetables, spices, or as food for livestock.

1. Susceptible plants within the main crop

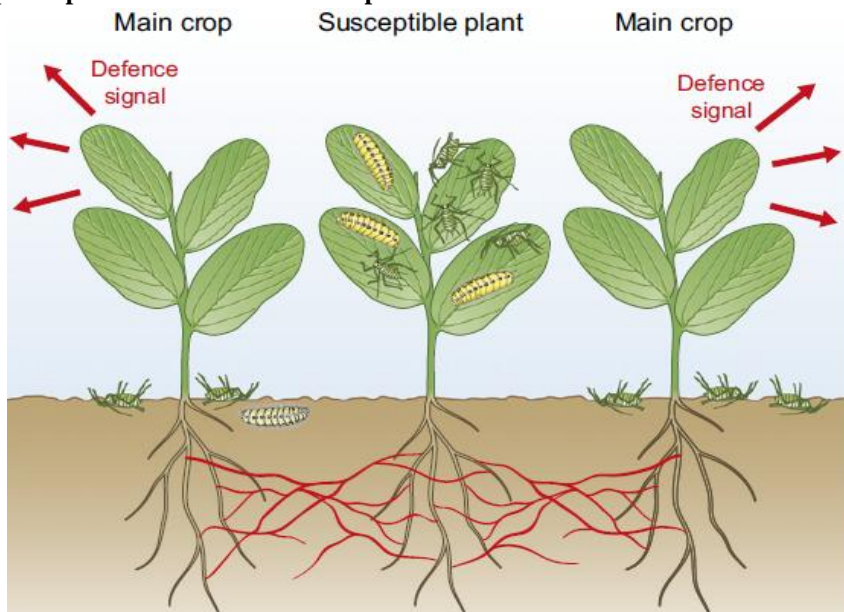


Fig. 11: defence signal transfer via CMN

Stress-related signals from damaged plants, for example elicited by herbivore attack, can pass through soil within the plant rhizosphere and, more effectively, via shared arbuscular mycorrhizal fungal networks (see rhizosphere connections in red) to intact plants. These cause induction of volatile defence signals repelling herbivores and attracting parasitoids to attack the herbivores. This opens up the possibility of using susceptible plants within the main crop so that, when attacked, susceptible plants signal via mycorrhizal rhizosphere connections to the main crop. This would then mount defence when needed, rather than suffering the metabolic cost of constitutive defence normally provided by resistant crop plants.

Plant volatiles and smart agriculture

Modern biological and chemical techniques (e.g. natural chemical stimulants, such as jasmonates) can be used to optimize the volatile patterns to prime the plants and to trigger plant–plant or plant–insect communications for biological pest and weed control. There is desired to be developed optimal cultivars for different agricultural systems and climates, plant phenotyping tools that include volatile emission analysis. Volatile formation in plants via metabolic

engineering to improve scent and aroma quality of flowers and fruits or to enhance crop protection through direct and indirect plant defense.

The bioengineering of volatiles can be achieved either through the modification of existing pathways or by the introduction of new gene (s) normally not found in the host plant. Improvement of volatile-based direct plant defense was accomplished by over expressing a dual linalool/nerolidol synthase (FaNES1) from strawberry in Arabidopsis chloroplasts. Linalool and its derivatives produced by the transgenic plants significantly **repelled** an agricultural pest, the aphid *Mysus persicae*, in dual-choice assays².

Interplant communication play a key role in the resistance of plants. Cotton aphids and corn borer are important insects in cotton and maize, respectively. The resistance of healthy cotton and maize plants is induced by their neighbour damaged plants. Phenylalanine ammonia-lyase (PAL) is a chemical marker of induced resistance in many plants. Inductions of PAL enzymatic activity and gene expression in the damaged and undamaged seedlings suggest inter-species communication between cotton and maize¹⁴.

RECENT REPORTS

Year	Species	Life form	Local damage	Systemic response	Environment	Refs
2006	Sagebrush (<i>Artemisia tridentata</i>)	Woody	Clipping	Reduced leaf damage	Field	10
2007	Lima bean (<i>Phaseolus lunatus</i>)	Herbaceous	Wounding+JA; <i>Gynandrobrotica guerreroensis</i>	Induced and primed EFN secretion	Field	12
2007	Hybrid poplar (<i>Populus deltoides x nigra</i>)	Woody	<i>Lymantria dispar</i>	Primed volatile release	Laboratory	13
2009	Blueberry (<i>Vaccinium corymbosum</i>)	Woody	<i>Lymantria dispar</i>	Reduced leaf damage; Induced JA synthesis; Primed volatile release	Greenhouse	14
2011	Tea (<i>Camellia sinensis</i>)	Woody	Wounding+JA	Induced production of unidentified metabolites	Laboratory	15
2014	Silver birch (<i>Betula pendula</i>)	Woody	<i>Epirrita autumnata</i>	Primed volatile release	Greenhouse	16
2015	Maize (<i>Zea mays</i>)	Herbaceous	Wounding+ <i>Spodoptera littoralis</i> regurgitant	Primed volatile release	Laboratory	17
2017	Hybrid aspen (<i>Populus tremula x tremuloides</i>)	Woody	<i>Phratora laticollis</i>	Induced volatile release	Field; Laboratory; Greenhouse	18

Li et al., 2017

SUMMARY

Overview of volatile-mediated plant interactions with the surrounding environment

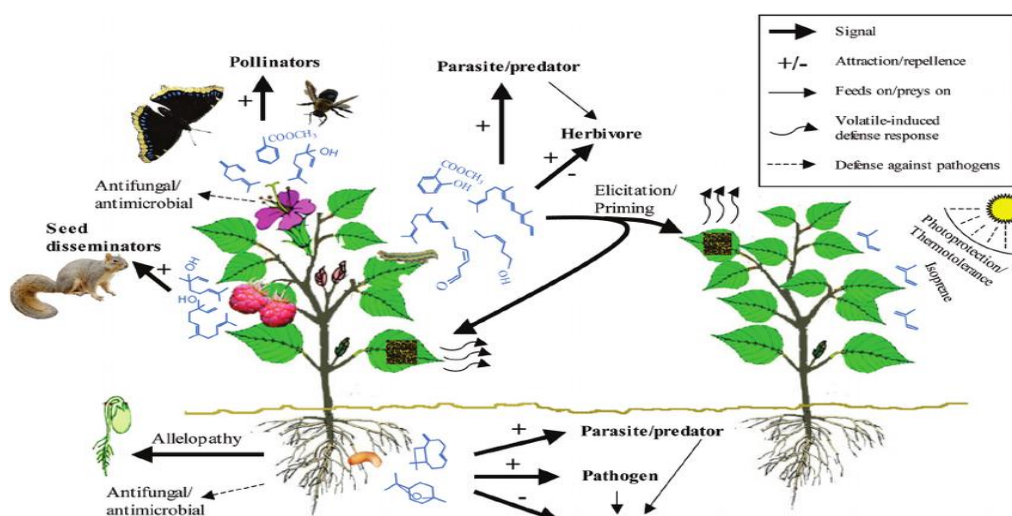


Fig. 12: Summary of plant communication via VOCs

Plant-animal interactions include the attraction of pollinators and seed disseminators by floral and fruit volatiles, attraction/repellence of herbivores, and attraction of natural enemies of attacking herbivores both in atmosphere and rhizosphere. Aboveground plant-plant interactions comprise elicitation or priming of defense responses in healthy undamaged leaves of the same plant or in the neighboring unattacked plants. Belowground, these interactions include allelopathic activity on the germination and growth of competitive neighboring plants. Volatiles released from reproductive organs and roots also have antimicrobial activity thus protecting the plants from pathogen attack. In addition, isoprene, a leaf volatile confers photoprotection and thermotolerance.

CONCLUSION

Air borne signalling is a widespread phenomenon in nature which improve plant performance and fitness in the times of stress. It is very much important to study and understand the plant communication in detail. The receptors of VOCs in plants are still remain elusive, if we identifies them then we can create best plants with higher productivity and stress resistant. The knowledge of plant communication could be used to develop crop plants with desired/improved agronomic traits

such as pest and disease resistance, weed control and pollination of seed crops.

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