# CHAPTER 2

# MOLECULAR PLANT VOLATILE COMMUNICATION

Jarmo K. Holopainen* and James D. Blande

*Department of Environmental Science, Kuopio, Campus, University of Eastern Finland, Kuopio, Finland*
**Corresponding Author: Jarmo K. Holopainen—Email: jarmo.holopainen@uef.fi*

**Abstract:** Plants produce a wide array of volatile organic compounds (VOCs) which have multiple functions as internal plant hormones (e.g., ethylene, methyl jasmonate and methyl salicylate), in communication with conspecific and heterospecific plants and in communication with organisms of second (herbivores and pollinators) and third (enemies of herbivores) trophic levels. Species specific VOCs normally repel polyphagous herbivores and those specialised on other plant species, but may attract specialist herbivores and their natural enemies, which use VOCs as host location cues. Attraction of predators and parasitoids by VOCs is considered an evolved indirect defence, whereby plants are able to indirectly reduce biotic stress caused by damaging herbivores. In this chapter we review these interactions where VOCs are known to play a crucial role. We then discuss the importance of volatile communication in self and nonself detection. VOCs are suggested to appear in soil ecosystems where distinction of own roots from neighbours roots is essential to optimise root growth, but limited evidence of above-ground plant self-recognition is available.

## INTRODUCTION

Plants are literally rooted to the ground and therefore unable to change location. Consequently, they are easy targets to organisms that wish to feed on them. Plants have evolved a vast array of defensive features that effectively reduce the number of their enemies.[1] However, defences are rarely flawless, meaning that plants cannot exist as static, non-interactive organisms. Instead they can benefit through exchanging information with other organisms. In order to communicate without physical contact, plants require a ‘language’ and volatile organic compounds (VOCs) are the ‘words’ in the plants ‘vocabulary’. The quantities and relative proportions of VOCs in the bouquet

---

*Sensing in Nature*, edited by Carlos López-Larrea.

emitted by plants allow the plant to send complex signals, which using the linguistic analogy could be described as ‘sentences’.

Plants produce a huge diversity of different chemicals, which include an array of VOCs emitted by flowers, foliage, bark, roots and specialised structures.[2] Many of these chemicals play roles in structuring relationships that plants have with a plethora of arthropods. These relationships can be beneficial or deleterious to the plant. Scientific advances in the field of plant-plant communication have led to VOCs being assigned an important role in transmitting signals from a damaged plant to a healthy neighbour. Moreover, signals from a herbivore-damaged part of a plant can be transmitted to a distant part of the same plant via VOCs.

We currently have a fairly robust knowledge of the processes and metabolic pathways involved in the production of many VOCs,[3,4] but we have an extremely limited understanding of how plants can detect these signals. Even less is known about how plants may differentiate signals from conspecifics representing the same or different genotypes. In this chapter we will provide a short review of plant communication via VOCs, detail current knowledge on the detection of self and nonself in plants and complete the chapter with suggestions of future directions for this fascinating research field.

## ROLES OF VOLATILE ORGANIC COMPOUNDS

Plant secondary chemistry is defined by Schoonhoven et al[1] as ‘plant compounds that are not universally found in higher plants, but are restricted to certain plant taxa at much higher concentrations than in others and have no (apparent) role in primary metabolism’. Plant volatiles represent 1% of known plant secondary metabolites and to date, 1700 plant volatiles from over 90 plant families have been isolated.[3] Plants emit volatiles constitutively; it is known that constitutive isoprene and monoterpene production in chloroplasts is related to protection against heat stress,[5] and some constitutive VOCs can directly affect the physiology and behaviour of herbivores through their toxic, repellent and deterrent properties.[5-7] For generalist herbivores VOCs can be repellent signals, but species specific volatile signals released by a plant individual reveal the plant identity and if perceived by specialist herbivore species will increase feeding damage and reduce the plant’s fitness.[6]

A number of different stresses induce plants to emit a broad range of volatiles in a temporally, qualitatively and quantitatively complex pattern.[7] Such stresses include abiotic factors including drought, heat stress and ozone,[5] and biotic stressors such as pathogens,[8] and herbivore feeding.[9,10] Feeding by herbivorous invertebrates is known to have profound and variable effects on the volatile bouquets emitted by a multitude of plant species in a range of taxa. It is these induced volatiles that are most active in mediating the numerous signalling processes involving plants.

When herbivores begin to feed, plants have two types of volatile response. The first response is the rapid emission of stored compounds, which are released when plant tissue is damaged. The second response is the de novo synthesis of compounds, which are not stored, but emitted as they are produced.[11] The compounds released by these two mechanisms may have some overlap with constitutively emitted volatiles, amounts of which are often increased by herbivore feeding.[7] Other compounds are completely exclusive to herbivore damaged plants. For instance, *Phaseolus lunatus* only emit the monoterpenes $\alpha$-pinene and limonene when intact, but after 48 hours of feeding by spider

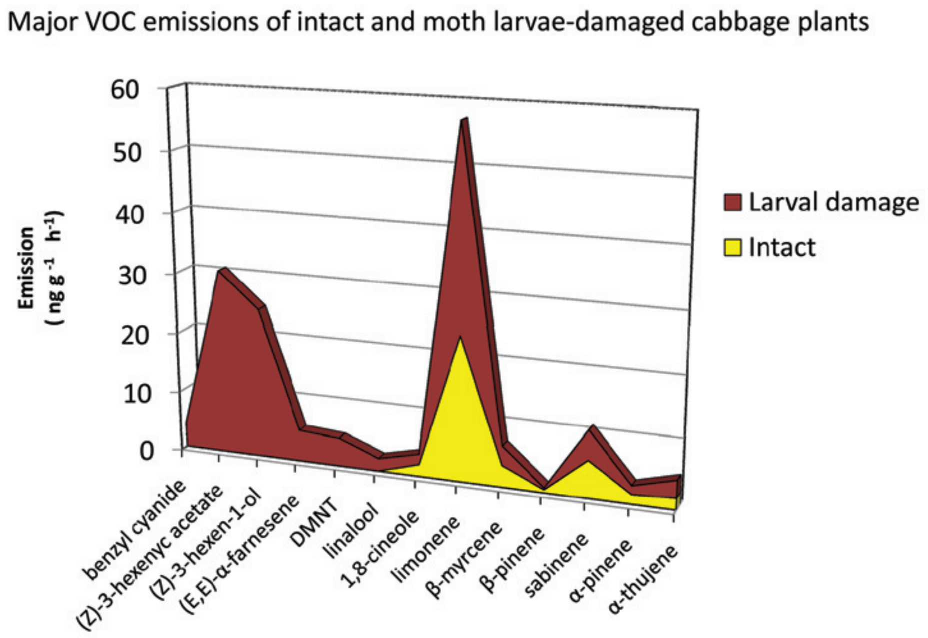

**Figure 1.** Example of VOC emission profiles of healthy intact cabbage plants and Diamond Back Moth (*Plutella xylostella*) larvae-damaged cabbage plants.

mites seven other VOCs are emitted.[12] Intact *Brassica oleracea* plants constitutively emit at least seven monoterpenes, but after 48 hours of feeding by diamond back moth larvae three more terpenes and three other compounds are emitted (Fig. 1).

These herbivore-inducible compounds or their relative ratios in the scent released by damaged plants are used by the natural enemies of plant feeding insects to locate their host and this has been shown in laboratory,[13] semi-natural[14] and natural conditions.[15] The quantity of VOCs released by damaged plants is much larger than the amount of VOCs released by the actual herbivores, for example herbivorous mites and insects[1] or by their faeces (Fig. 2).[16] It can be concluded that the specific VOC signals released by plants after damage by a herbivore are important signals that improve the fitness of the plant by eliciting behavioural responses in herbivore natural enemies and thus increasing the predation rate leading to reduced plant damage. This plant response has often been referred to as a 'cry for help', due to natural enemies of herbivores using these volatile signals as cues in the process of prey or host foraging. However, it could be suggested that the receiver of the signal, may interpret it as a 'cry',[17] while the complex nature of the signal could be deemed a far more eloquent monologue. Certain compounds seem to provide particularly reliable indication of herbivore feeding, such as the acyclic homoterpenes (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and 4,8,12-trimethyl-1,3(*E*),7(*E*),11-tridecatetraene (TMTT). These compounds are emitted by plants in different quantities and ratios depending on the herbivore, which determines the attractiveness of the emitted volatile blend to different species of foraging predators.[18] The composition of emissions is often plant specific and herbivore specific to the species level—and even to the level of larval feeding stage.[19]

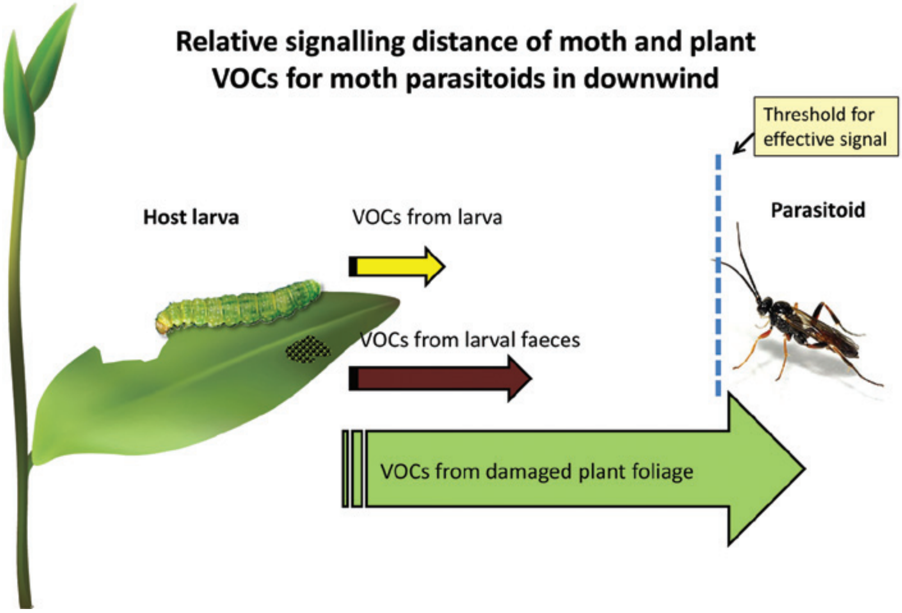

**Figure 2.** Schematic illustration of interactions between herbivores and their natural enemies (parasitoids) communicated via plant volatile molecules. Plant volatiles induced by herbivore feeding are emitted in higher quantities and have better communication value than direct emissions from herbivorous larvae or larvae faeces. It has been shown that parasitoids can learn to detect plant emissions related to herbivore damage.

## PLANT-PLANT SIGNALLING

### Above-Ground

*The Ecology of Plant-Plant Signalling*

As herbivore-induced volatiles are reliable indicators of herbivore presence, plants stand to gain a benefit if they can detect these volatiles and modify their defences accordingly. Plant-plant communication was first reported in 1983,[20] and has since been a topic of considerable debate. Much of the debate has centred on the ecological relevance of a process that had been demonstrated to occur in the laboratory,[20,21] but not observed in nature. However, in more recent years a body of evidence has accumulated to suggest plant-plant communication in field conditions. This evidence includes interspecific communication,[22-24] intraspecific communication [25-27] and within plant communication.[28]

Sagebrush, *Artemisia tridentata*, has been the subject of numerous studies conducted under field conditions. Interspecific communication was observed,[22-24] with wild tobacco plants shown to experience less foliar damage when exposed to clipped sagebrush neighbours than plants exposed to unclipped sagebrush. This communication was also shown to occur with sagebrush damaged by herbivores.[23] In both cases the distance over which this communication occurred was 10 cm.[23] Intraspecific communication has also been demonstrated in sagebrush,[25,23] whereby undamaged sagebrush with clipped sagebrush neighbours received significantly less damage than sagebrush with unclipped neighbours. This communication occurred at distances of up to 60 cm from the clipped plants.[25] Methyl jasmonate is constitutively emitted by sagebrush, but upon damage the isomeric composition of emissions is altered, with overall emissions increased and emissions of the cis isomer proportionally increased.[29] Consequently, methyl jasmonate was predicted to be an important signal mediating interplant communication.[29] However, application of methyl jasmonate in concentrations representing the amounts naturally released by sagebrush did not elicit nicotine responses in open-grown plants.[30] Herbivore resistance in tobacco plants was recently shown to be primed,[31] see below.

### *The Chemistry of Plant-Plant Signalling*

A large number of chemical compounds have been implicated in signalling to herbivores, predators and parasitoids, but we will focus on reviewing the compounds involved in signalling between and within plants. Typically many of the volatiles effective in plant to plant signalling are the compounds synthesised de novo upon herbivore attack.

To date several compounds (Fig. 3) have been reported to function as between and within plant signals, these include the green leaf volatiles (*E*)-2-hexenal,[32-34]

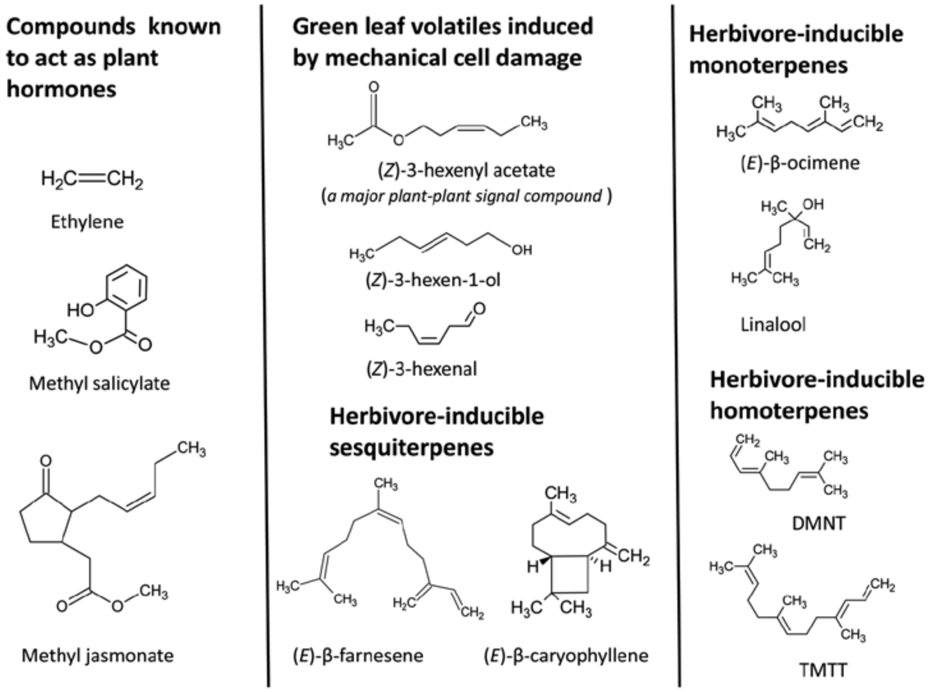

**Figure 3.** Chemical structures of selected plant volatile compounds, which are known to have function in intraplant, intraspecies and interspecies communication. Emissions of most of these compounds are induced by herbivore damage. (*E*)-β-caryophyllene (shadowed) is the only inducible volatile compound which is shown to be active in inter specific below ground communication. DMNT = (*E*)-4,8-dimethyl-1,3,7-nonatriene, TMTT = (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene.

(*Z*)-3-hexen-1-ol[35] and cis-3-hexenyl acetate,[36-38] the terpenes myrcene and blended ocimene volatiles ((*E*)-β-ocimene, (*Z*)-β-ocimene and allo-ocimene)[39] and the phytohormones methyl jasmonate,[21] methyl salicylate[40] and ethylene.[41]

Green-leaf volatiles include a range of C6 compounds including aldehydes, alcohols and esters. Formed via the lipoxygenase pathway, these compounds are emitted rapidly upon disturbance of the plant, by mechanical damage as well as herbivore feeding.[42] These compounds are therefore indicative of any mechanical damage and could provide early signals to receiving plants. However, they do not have the same reliability as emissions such as DMNT and TMTT, emissions of which are highly correlated with herbivore damage.[18]

Terpenoids are the largest group of secondary compounds, consisting of approximately 40,000 compounds,[43] including at least 1,000 monoterpenes and 6,500 sesquiterpenes.[1] All terpenoids originate from isopentenyl diphosphate (IPP) and its allylic isomer dimethylallyl diphosphate (DMAPP), which are derived via two alternative pathways. In the cytosol, IPP is synthesised via the mevalonic acid (MVA) pathway, while in plastids it is synthesised via the 2-C-methyl-D-erythritol 4-phosphate (MEP) pathway, see Arimura et al[44] and Dudareva et al[3] for reviews. Some terpenoids are constituents of essential oils and resins and are constitutively produced and stored in specialised structures, such as glandular trichomes or resin ducts. Upon damage by herbivores these structures are broken and the compounds are released. The de novo biosynthesis of terpenoids can be induced locally and systemically by herbivore feeding. Terpenoids as a group are therefore, able to provide rapid, but also herbivore-damage related signals to receiving plants.

Methyl jasmonate is a volatile derivative of jasmonic acid, which is an integral component of plant defence responses to insect feeding. Application of methyl jasmonate to tomato plant leaves has been shown to increase production of proteinase inhibitors under laboratory conditions.[21]

Methyl salicylate is synthesised from salicylic acid, it is a phenolic compound and plays an important role in plant defence. It is released in significant amounts from plants in response to aphid feeding damage and is emitted by tobacco in response to tobacco mosaic virus infection. Tobacco plants exposed to methyl salicylate have been shown to have increased resistance to tobacco mosaic virus.[40]

Plant-plant signalling in maize was shown to be mediated by the green leaf volatile (*Z*)-3-hexen-1-ol, with ethylene synergising the effect. Plants exposed to (*Z*)-3-hexen-1-ol increased emission of several compounds associated with herbivore feeding by 2.5-fold. Treating plants with ethylene increased the effect to 5.1- to 6.6-fold.[35] Ethylene also plays an important role in shade avoidance in tobacco.[45,46] Wild-type tobacco leaves normally stop growing as they get close to neighbouring plants; however, a mutant variety of tobacco that does not produce ethylene does not reduce growth and results in overlapping leaves, reduced shade avoidance and possible loss of energy. This indicates that plant to plant communication mediated by ethylene occurs under laboratory conditions.[47]

The fate of VOCs in the atmosphere is particularly relevant to plant to plant signalling. Plants cannot move great distances towards an odour source and therefore rely on sufficient quantities of any signalling cues being transported through the atmosphere and to the plant. The atmospheric life times of VOCs are therefore relevant in determining how effective they will be in mediating communication. Many of the inducible VOCs including, monoterpenes, GLVs and sesquiterpenes have atmospheric life times of only a few minutes, a few hours or less than 24 hours.[48,49] Other VOCs, which are considered less reactive with atmospheric oxidants, have extended atmospheric life times of longer than 24 hours.[48] High reactivity and short atmospheric life times significantly reduce the signalling distance of most reactive compounds.

### *Priming*

Priming in terms of plant defence is where plants ready their defences in response to a signal or previous challenge so that they can respond with increased rigour should they be subsequently challenged by herbivores or pathogens. The priming of plants as a product of plant-plant communication via volatile organic compounds is a recent discovery, but work in this field has already gathered enough momentum to yield at least two reviews.[37,50] Although, research of priming in plant-plant interactions is still in the early stages, the phenomenon of priming in plant-pathogen interactions was recognised many years ago, with understanding of this phenomenon progressing substantially in recent years.[51-53]

The first study to clearly demonstrate priming via airborne signals from a herbivore-damaged plant to an undamaged neighbour was conducted by Engelberth et al[54] with corn plants. The authors showed that exposing plants to three different green leaf volatiles primed plants to emit inducible terpenoids and accumulate jasmonic acid with increased rigour following challenge with a wound and added caterpillar regurgitant extract. This is a protocol used for mimicking herbivory, whereby enzymes present in the regurgitant are responsible for causing significant differences in volatile emissions caused by caterpillar feeding and mechanical damage alone.[13] Interestingly, jasmonic acid accumulation was not primed to increase in response to mechanical damage alone. Other plant defence responses have also been shown to be primed. In Lima bean, the production of extra-floral nectar is increased by exposure to VOCs emitted by mechanically damaged conspecifics.[55] This exposure also primes receiver plants to increase extrafloral nectar more rapidly in response to both mechanical damage[55] and spider-mite feeding.[56] Therefore, it would seem that this priming is more general than the example of jasmonic acid in corn, which is not increased by mechanical damage alone. Other primed defence responses include accelerated production of trypsin-proteinase inhibitors in tobacco exposed to volatiles from damaged sagebrush.[31]

Analyses of gene expression have complemented these records of primed defence. Changes in transcription patterns of defence-related genes following exposure to volatile compounds have been described in several studies.[37,57-60] This suggests that signals have been detected by receiver plants, even though changes in phenotype are not observed.

In the future it is possible that we could purposefully prime crop plants to increase their resistance to herbivores or pathogens. The use of transgenic ‘beacon’ plants that are engineered to continually produce and release quantities of priming compounds has been suggested as a potential mechanism for increasing resistance.[61]

### *Within Plant Signalling*

Within-plant signalling by VOCs is a potentially relevant discovery with regards to furthering our understanding of self and nonself recognition in plants. Heil and Silva Bueno[28] showed that herbivore-damaged Lima bean tendrils release a VOC signal that results in an undamaged tendril of the same plant increasing extrafloral nectar secretion. We know from previous studies that undamaged neighbouring plants increase their EFN secretion in response to a VOC signal, but the knowledge that damage induced VOCs function to transmit a signal within the same plant suggests that this could be the main or the primary function. This lends credence to the expression ‘eavesdropping plants’[62] with regard to plant-plant signalling. This term was first coined to describe plants that receive a VOC signal intended for a different recipient, with the intended recipient suggested to be the natural enemies of herbivores. However, the accumulating evidence for within-plant communication in different plant species suggests that the ‘intended recipient’ is likely to be the emitting plant itself. As well as in Lima bean, within-plant communication has been demonstrated in a tree, hybrid poplar,[63] and two woody shrubs, sagebrush[25] and blueberry.[64] In all these species, branches have either reduced or absent vascular connections, which means that regulation of a systemic response to herbivore attack is not possible via internal signals. Therefore, external volatile cues provide a means to negate these constraints.

Interestingly, in both Lima bean and hybrid poplar[37] the green-leaf volatile cis-3-hexenyl acetate has been shown to play a vital role in within-plant communication. This compound is also released by blueberry[64] and sagebrush[31] and is emitted within five minutes of the start of herbivore-feeding[44] and therefore a good candidate for providing a fast signal from damaged to undamaged parts of a plant. However, the commonness of cis-3-hexenyl acetate and the fact that it is released in response to mechanical damage as well as herbivore feeding, suggest that it is rather a general signal, detectable by multiple species and inducible by multiple stimuli.

### *Below-Ground Signalling*

Roots of non-aquatic plants usually spend their lives below ground, but they are the site of synthesis of plant secondary metabolites such as alkaloids, which have been shown to be produced in the roots and transported via the xylem and into the leaves.[48] In the rhizosphere, free air and aerial communication is limited to soil pores as most of the root surfaces and soil particles are covered by a water film. Therefore, below-ground chemical communication is strongly based on nonvolatile hydrophilic plant root exudates, which are used to compete with invading root systems of neighbouring plants for space, water and mineral nutrients, but also with other soil-borne organisms, including herbivorous animals, bacteria and fungi.[65] Particularly in wet soils allelopathic effects between plant roots are mediated predominantly by phenolic compounds,[66] including e.g., catechins and various phenolic acids.[65] There is also evidence that these root exudates could be responsible for internal root communication by self-inhibition. Falik et al[67] were able to show that development of lateral roots of *Pisum sativum* towards an obstacle were reduced, when the lateral root first faced an obstacle, other lateral roots then withered. However, this avoidance growth pattern was suppressed in the presence of potassium permanganate or activated carbon which adsorbs active compounds of root exudates. The result indicates a significant role of root exudates in plant self-signalling to promote obstacle avoidance by other lateral roots of the same plant. External self-inhibition of root growth towards obstacles could increase plant performance by directing resource allocation in the root system to more profitable directions in the rhizosphere.[67]

Our knowledge of volatile communication in the rhizosphere is limited. Potential and reported volatile interactions above and below ground are summarised in Figure 4. Some volatile compounds such as the sesquiterpene (*E*)-β-caryophyllene are induced in plant roots by abiotic stresses like heat stress[68] and by biotic stress caused by insect feeding damage.[69] In sesquiterpene-rich plant species such as *Copaifera officinalis* several sesquiterpenes were found from roots, but two-thirds of the amount was (*E*)-β-caryophyllene,[70] which indicates a

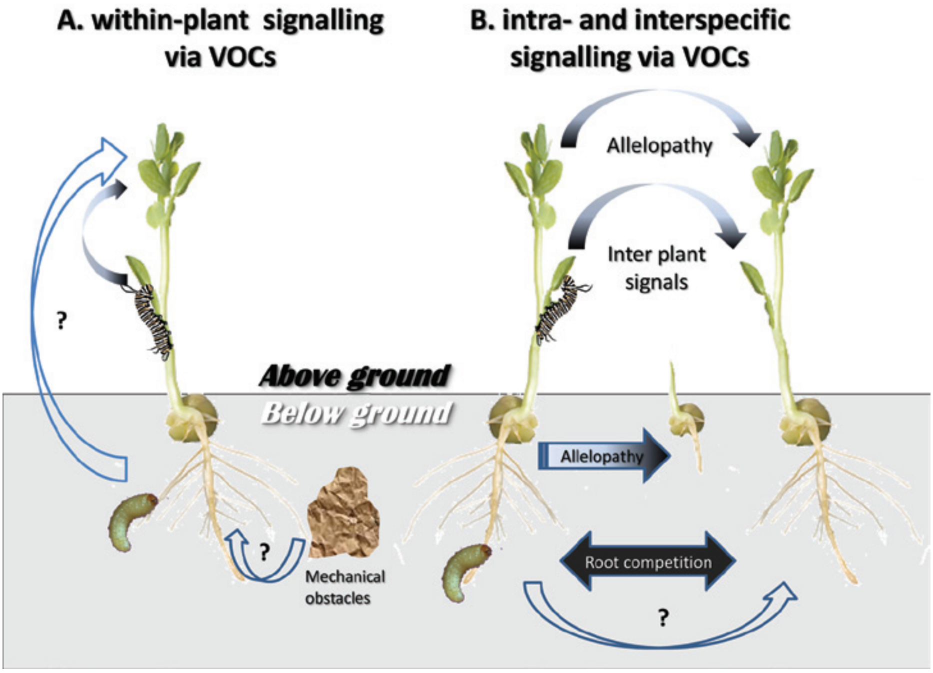

**Figure 4.** Example of participation of volatile compounds in above ground and below ground plant to plant signalling. A) Within-plant signalling via VOCs and (B) intra- and interspecific signalling via VOCs. Curved arrows with gradient colour describe reported signalling and nonfilled curved arrows indicate putative signalling routes.

root-specific role for this volatile compound. Maize root worm larvae (*Diabrotica virgifera virgifera*) feeding on maize roots induced (*E*)-β-caryophyllene production in the roots and attracted entomoparasitic soil nematodes to orientate toward damaged plant roots in tests with a sand-filled olfactometer.[69] It was shown that (*E*)-β-caryophyllene evaporated and moved in moist sandy soil rapidly, 90% of experimentally released compound was recovered through a 5 cm thick sand layer.[69] This is an indication that volatile signal compounds released from root systems can rapidly reach neighbouring roots and has the potential to transmit information between self and nonself root systems in soil. Interestingly, root exudates from aphid infested broad bean plants have been shown to make non-infested conspecific neighbouring plants more attractive to foraging parasitoids.[71] This interesting demonstration of positive plant-plant communication through the rhizosphere is in contrast with the many allelopathic effects of root exudates.

## SELF AND NONSELF RECOGNITION IN PLANTS

Vascular plants can be unitary organisms appearing in individual units such as humans or other animals. Many plants, however, are modular organisms which look-like separate individuals, but are somehow connected like e.g., grasses which are often connected through their root system and represent the same genotype.[72] In perennial and woody plants the situation may become more complicated. European aspen (*Populus tremula*) grows root extensions which develop new shoots, asexually produced modules, which are called ramets or clones. Clones can physically remain connected through roots to their sexually reproduced parent tree, called a genet. They could also become disconnected from parent trees and start to function independently, which means that "a tree" could have three phenotypes: The parent tree, physically connected clones and physically disconnected clones. In a forest ecosystem these genetically identical individuals compete for light, water and nutrients with half-siblings i.e., sexually reproduced seedlings of the parent tree and clones and seedlings of other conspecific and heterospecific trees and other plants.

### *Self and Nonself Recognition Belowground*

Self and nonself recognition in plants has mainly been studied belowground, with focus on interactions between roots of plants competing for resources. To date, information to confirm self and nonself recognition involves comparing the root growth of plants grown in proximity to plants of differing levels of relatedness. Several studies have shown that when roots encounter nonself root growth there is a different growth response to encountering its own roots.[73] Root growth experiments with the clonal perennial grass *Buchloe dactyloides* showed that individuals have shorter root growth when confronted with self than nonself competing roots.[74] Gruntman and Novoplansky[74] conducted experiments with 'twin' plants originating from the same plant node and showed that while plants were able to recognise self and modify their root growth reflectively, they did not recognise separated plants as self after a prolonged period of separation. The authors concluded that in this circumstance self and nonself discrimination is mediated by physiological co-ordination among roots that develop on the same plant rather than allogenetic recognition. Falik et al[75] used a similar method to study discrimination between self and nonself in *Pisum sativum*, they also observed greater root growth when plants were grown in the same pot as nonself plants than when grown in the same pots as separated twins. Although the authors could not rule out allogenetic recognition, they also hypothesised that a physiological co-ordination among roots was the most likely reason for their results. These studies give firm support to the idea that recognition of nonself competing plants results in an increase in root production. However, there are some methodological issues that have complicated this field, with Hess and de Kroon[76] providing an enlightening account of the need to consider resource competition aspects in future experiments. They showed that in most previous studies the over-production of roots correlated with increased soil volume and nutrient availability for plants growing in competition than for plants growing alone.

Interestingly, in the annual plant *Cakile edentula*[77] individuals sharing a pot with a group of 'strangers' allocated more resources to root growth than plants sharing a pot with siblings. This indicated that kin recognition may occur as a result of root based communication. This shows that whereas some plants lose the ability to recognise genetically identical twin plants following a period of separation, effectively no longer recognising self, others are able to recognise kin. The authors suggested a different mechanism to that used in self/nonself recognition due to genetically identical individuals sometimes being determined as nonself.[74,75]

### *Self and Nonself Recognition Aboveground*

The only study to have satisfactorily addressed the phenomenon of self and nonself recognition in plants above ground was recently conducted by Karban and Shiojiri[78] using sagebrush as a model plant system. The ecological relevance of plant-plant communication in sagebrush has been documented in a series of elegant experiments by Karban and colleagues carried out over a number of years. The sensitivity of different plants to signals released by sagebrush is variable, for example tobacco growing at up to 10 cm[22,23] from sagebrush neighbours receives a tangible benefit by responding to cues from the damaged intraspecific neighbour, whereas undamaged sagebrush plants are able to gain a benefit at distances up to 60 cm from a damaged conspecific neighbour.[25] The recent study has gone further and produced genetically identical sagebrush clonal cuttings to demonstrate that when a sagebrush plant is defoliated by clipping, a genetically identical neighbour will receive 42% less damage than genetically different neighbours. This is a landmark discovery in understanding to what extent and via what mechanism plants are able to distinguish self from nonself.

It has been shown that within-plant signalling in woody plants between different branches or adjacent leaves with little or no vascular connection can be based on volatile signals released from wounded leaves to prime the defence in receiving foliage.[63,37] These observations suggests that plants would benefit by recognising signals representing their own genotype.

### *Nonself Recognition by Parasitic Plants*

One particularly interesting example of plants responding to nonself volatiles has been reported in the parasitic plant *Cuscuta pentagona*[79] or dodder. *C. pentagona*, an obligate parasite with little photosynthetic capacity, was shown to use volatile compounds to orientate toward host plants.[79] *C. pentagona* oriented toward its preferred host plant tomato (*Lycopersicon esculentum*) with significantly greater frequency than to wheat (*Triticum aestivum*) a nonhost. Three volatile compounds emitted by tomato, the terpenes β-phellandrene, β-myrcene and α-pinene, were significantly oriented toward when tested in isolation, while (*Z*)-3-hexenyl acetate emitted by wheat had a repellent effect. In order to respond to these volatile compounds the host-foraging parasitic plant needs to in some way detect or perceive them. The mechanism for this is still unknown and should be the focus of further research in this field.

## CONCLUSION AND FUTURE DIRECTIONS

At the moment the most intriguing question in plant to plant communication by volatile compounds regards the mechanism; how plants perceive the signal molecules and how the potential VOC receptors function in plants. Moderate ozone concentrations (80ppb) have recently been shown to significantly reduce the distance over which plant-to-plant communication occurs, with oxidation of the signalling compounds indicated as the mechanism. Obviously the receiver plants are not able to sense the reduced concentrations of signalling compounds.[80]

In antennal sensilla of an insect there are general odour binding proteins and more compound-specific receptor molecules.[81] In plants, several salicylic acid (SA) binding proteins have been described e.g. from tobacco.[82] SA-binding proteins have methyl salicylate (MeSA) esterase activity, which is required to release the active defense phytohormone SA from MeSA.[83] Recently, several members of the AtMES gene family, which is functionally homologous to SA binding proteins, have been described in Arabidopsis.[83] Proteins produced by this gene family have potential for MeSA hydrolysis, which is essential to activate SA when MeSA serves as a long-distance signal for systemic acquired resistance (SAR) in Arabidopsis and tobacco.

After detection of volatile signal molecules by receiver cells, a signalling cascade will be activated in that plant part. Receiver cells could be located in another organ or another module of the emitter plant or in longer distance signalling receiver cells could be in conspecific or heterospecific neighbouring plants. According to our current understanding, compounds known to transmit information between plants are rather common in the plant kingdom and are released by many plant species. Thus the recognition may be based on the ratio of specific signalling compounds perceived concomitantly, as reported for insect antennae,[6] where different type sensors can be found. Thus, receiver plants should have different mechanisms or sensors for sensing e.g., GLVs and monoterpenes than the SA binding proteins used for MeSA sensing. Recently we have found[84] that plants are able to adsorb volatiles from neighbouring plants and re-release these molecules back to the atmosphere. This suggests that the plant epidermis may have importance in storing VOC molecules for signal perception and possibly enrich the concentration of received compounds for more accurate identification by potential sensor molecules. Furthermore, our observation could also suggest that plants can possibly use VOCs from neighbouring plants to camouflage themselves from their specialist herbivores by letting VOC molecules condensate on their leaf epidermis and then releasing misleading compounds for detection by the antennae of their herbivores. When the mechanism of signal perception for specific volatile compounds has been elucidated, hypersensitive genetically engineered crop plant varieties can be developed. VOCs released from plants first attacked by pest insects can probably elicit better pest protection in neighbouring plants by long-distance systemic acquired resistance. With this type of "primed" crop plant cultivar, defence can be elicited by a farmer as a part of a plant protection strategy. It requires the artificial release of the volatile compounds needed for the plant to be primed as a part of other plant protection actions in the field. To conclude, our knowledge of phytogenic organic compounds is still limited and their role in intraspecific communication between plant individuals and in interspecific communication is not fully elucidated. Better understanding of the VOC receptors and their functions in plants will improve our possibilities to assess the ecological significance of above-ground and below-ground molecular communication in plant communities.

## REFERENCES

1. Schoonhoven LM, van Loon JJA, Dicke M. Insect-plant biology, 2nd edition Oxford: Oxford University Press, 2005.
2. Kesselmeier J, Staudt M. Biogenic volatile organic compounds (VOC): an overview on emission, physiology and ecology. J Atmos Chem 1999; 33:23-88.
3. Dudareva N, Negre F, Nagegowda DA et al. Plant volatiles: recent advances and future perspectives. Crit Rev Plant Sci 2006; 25:417-440.

4. Dudareva N, Pichersky E, Gershenzon J. Biochemistry of plant volatiles. Plant Physiol 2004; 135:1893-1902.
5. Laothawornkitkul J, Taylor JE, Paul ND et al. Biogenic volatile organic compounds in the Earth system. New Phytol 2009; 183:27-51.
6. Bruce TJA, Wadhams LJ, Woodcock CM. Insect host location: a volatile situation. Trends Plant Sci 2005; 10:269-274.
7. Holopainen JK. Multiple functions of inducible plant volatiles. Trends Plant Sci 2004; 9:529-533.
8. Cardoza YJ, Alborn HT, Tumlinson JH. In vivo volatile emissions from peanut plants induced by simultaneous fungal infection and insect damage. J Chem Ecol 2002; 28:161-174.
9. Walling LL. The myriad plant responses to herbivores. J Plant Growth Regul 2000; 19:195-216.
10. Baldwin IT, Preston CA. The eco-physiological complexity of plant responses to insect herbivores. Planta 1999; 208:137-145.
11. Paré PW, Tumlinson JH. De novo biosynthesis of volatiles induced by insect herbivory in cotton plants. Plant Physiol 1997; 114:1161-1167.
12. Pinto D, Blande JD, Nykänen R et al. Ozone degrades common herbivore-induced plant volatiles: does this affect herbivore prey location by predators and parasitoids? J Chem Ecol 2007; 33:683-694.
13. Turlings TCJ, Tumlinson JH, Lewis WJ. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science 1990; 250:1251-1253.
14. Kappers IF, Aharoni A, van Herpen T et al. Genetic engineering of terpenoid metabolism attracts, bodyguards to Arabidopsis. Science 2005; 309:2070-2072.
15. Kessler A, Baldwin IT. Defensive function of herbivore-induced plant volatile emissions in nature. Science 2001; 291:2141-2144.
16. Steidle JLM, Steppuhn A, Reinhard J. Volatile cues from different host complexes used for host location by the generalist parasitoid Lariophagus distinguendus (Hymenoptera: Pteromalidae). Basic Appl Ecol 2001; 2:45-51.
17. Dicke M. Behavioural and community ecology of plants that cry for help. Plant Cell Environ 2009; 32:654-665.
18. Dicke M. Local and systemic production of volatile herbivore-induced terpenoids: their role in plant-carnivore mutualism. J Plant Physiol 1994; 143:465-472.
19. Gouinguene S, Alborn H, Turlings TCJ. Induction of volatile emissions in maize by different larval instars of Spodoptera littoralis. J Chem Ecol 2003; 29:145-162.
20. Baldwin IT, Schultz JC. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. Science 1983; 221:277-279.
21. Farmer EE, Ryan CA. Interplant communication—airborne methyl jasmonate induces synthesis of proteinase-inhibitors in plant leaves. Proc Nat Acad Sci USA 1990; 87:7713-7716.
22. Karban R, Maron J. The fitness consequences of interspecific eavesdropping between plants. Ecology 2002; 83:1209-1213.
23. Karban R, Maron J, Felton GW et al. Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants. Oikos 2003; 100:325-332.
24. Karban R. Communication between sagebrush and wild tobacco in the field. Biochem Syst Ecol 2001; 29:995-1005.
25. Karban R, Shiojiri K, Huntzinger M et al. Damage-induced resistance in sagebrush: volatiles are key to intra- and interplant communication. Ecology 2006; 87:922-930.
26. Karban R, Huntzinger M, McCall AC. The specificity of eavesdropping on sagebrush by other plants. Ecology 2004; 85:1846-1852.
27. Tscharntke T, Thiessen S, Dolch R et al. Herbivory, induced resistance and interplant signal transfer in Alnus glutinosa. Biochem Syst Ecol 2001; 29:1025-1047.
28. Heil M, Silva Bueno JC. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. PNAS 2007; 104:5467-5472.
29. Preston CA, Laue G, Baldwin IT. Methyl jasmonate is blowing in the wind, but can it act as a plant-plant airborne signal? Biochem Syst Ecol 2001; 29:1007-1023.
30. Preston CA, Laue G, Baldwin IT. Plant-plant signaling: application of trans- or cis-methyl jasmonate does not elicit direct defenses in native tobacco. J Chem Ecol 2004; 30:2193-2214.
31. Kessler A, Halitschke R, Diezel C et al. Priming of plant defense responses in nature by airborne signaling between Artemisia tridentate and Nicotiana attenuata. Oecologia 2006; 148:280-292.
32. Arimura G, Ozawa R, Horiuchi J et al. Plant-plant interactions mediated by volatiles emitted from plants infested by spider mites. Biochem System Ecol 2001; 29:1049-1061.
33. Farag MA, Paré PW. C-6-green leaf volatiles trigger local and systemic VOC emissions in tomato. Phytochemistry 2002; 61:545-554.
34. Mirabella R, Rauwerda H, Struys EA et al. The Arabidopsis her1 mutant implicates GABA in (E)-2-hexenal responsiveness. Plant J 2008; 53:197-213.
35. Ruther J, Kleier S. Plant-plant signalling: ethylene synergizes volatile emission in Zea mays induced by exposure to (Z)-3-hexen-1-ol. J Chem Ecol 2005; 31:2217-2222.

36. Yan ZG, Wang CZ. Wound-induced green leaf volatiles cause the release of acetylated derivatives and a terpenoid in maize. Phytochemistry 2006; 67:34-42.
37. Frost CJ, Mescher MC, Dervinis C et al. Priming defense genes and metabolites in hybrid poplar by the green volatile cis-3-hexenyl acetate. New Phytol 2008; 180:722-734.
38. Kost C, Heil M. Herbivore-induced plant volatiles induce an indirect defence in neighbouring plants. J Ecol 2006; 94:619-628.
39. Godard KA, White R, Bohlmann J. Monoterpene-induced molecular responses in Arabidopsis thaliana. Phytochemistry 2008; 69:1838-1849.
40. Shulaev V, Silverman P, Raskin I. Airborne signalling by methyl salicylate in plant pathogen resistance. Nature 1997; 385:718-721.
41. O'Donnell PJ, Calvert C, Atzorn R et al. Ethylene as a signal mediating the wound response of tomato plants. Science 1996; 274:1914-1917.
42. Fall R, Karl T, Hansel A et al. Volatile organic compounds emitted after leaf wounding: on-line analysis by proton-transfer-reaction mass spectrometry. J Geophys Res Atmos 1999; 104:15963-15974.
43. Yu F, Utsumi R. Diversity, regulation and genetic manipulation of plant mono- and sesquiterpenoid biosynthesis. Cell Mol Life Sci 2009; 66:3043-3052.
44. Arimura G-I, Matsui K, Takabayashi J. Chemical and molecular ecology of herbivore-induced plant volatiles: proximate factors and their ultimate functions. Plant Cell Physiol 2009; 50:911-923.
45. Pierik R, Visser EJW, de Kroon H et al. Ethylene is required in tobacco to successfully compete with proximate neighbours. Plant Cell Environ 2003; 26:1229-1234.
46. Knoester M, van Loon LC, van den Heuvel J et al. Ethylene-insensitive tobacco lacks nonhost resistance against soil-borne fungi. Proc Natl Acad Sci USA 1998; 95:1933-1937.
47. Farmer EE. Surface-to-air signals. Nature 2001; 411:854-856.
48. Yuan JS, Himanen SJ, Holopainen JK et al. Smelling global climate change: mitigation of function for plant volatile organic compounds. Trends Ecol Evol 2009; 24:323-331.
49. Erb M, Lenk C, Degenhardt J et al. The underestimated role of roots in defense against leaf attackers. Trends Plant Sci 2010: (in press) doi:10.1016/j.tplants.2009.08.006.
50. Choudhary DK, Johri BN, Prakash A. Volatiles as priming agents that initiate plant growth and defence responses. Curr Sci 2008; 94:595-604.
51. Conrath U, Pieterse CMJ, Mauch-Mani B. Priming in plant-pathogen interactions. Trends Plant Sci 2002; 7:210-216.
52. Newman M-A, Dow JM, Molinaro A et al. Priming, induction and modulation of plant defence responses by bacterial lipopolysaccharides. J Endotoxin Res 2007; 13:69-84.
53. Beckers GJM, Conrath U. Priming for stress resistance: from the lab to the field. Curr Opin Plant Biol 2007; 10:425-431.
54. Engelberth J, Alborn HT, Schmelz EA et al. Airborne signals prime plants against insect herbivore attack. Proc Natl Acad Sci USA 2004; 101:1781-1785.
55. Heil M, Kost C. Priming of indirect defences. Ecol Lett 2006; 9:813-817.
56. Choh Y, Takabayashi J. Herbivore-induced extra-floral nectar production in Lima bean plants enhanced by previous exposure to volatiles from infested conspecifics. J Chem Ecol 2006; 32:2073-2077.
57. Bate NJ, Rothstein SJ. $C_6$-volatiles derived from the lipoxygenase pathway induce a subset of defense-related genes. Plant J 1998; 16:561-569.
58. Farag MA, Fokar M, Zhang HA et al. (Z)-3-hexenol induces defense genes and downstream metabolites in maize. Planta 2005; 220:900-909.
59. Paschold A, Halitschke R, Baldwin IT. Using 'mute' plants to translate volatile signals. Plant J 2006; 45:275-291.
60. Arimura G-i, Ozawa R, Shimoda T et al. Herbivory-induced volatiles elicit defence genes in Lima bean leaves. Nature 2000; 406:512-515.
61. Dudareva N, Pichersky E. Metabolic engineering of plant volatiles. Curr Opin Biotechnol 2008; 19:181-189.
62. Baldwin IT, Kessler A, Halitschke R. Volatile signaling in plant-plant-herbivore interactions: what is real? Curr Opin Plant Biol 2002; 5:351-354.
63. Frost CJ, Appel HM, Carlson JE et al. Within-plant signaling via volatiles overcomes vascular constraints on systemic signaling and primes responses against herbivores. Ecol Lett 2007; 10:490-498.
64. Rodriguez-Saona CR, Rodriguez-Saona LE, Frost CJ. Herbivore-induced volatiles in the perennial shrub, Vaccinium corymbosum and their role in inter-branch signaling. J Chem Ecol 2009; 35:163-175.
65. Bais HP, Park SW, Weir TL et al. How plants communicate using the underground information superhighway. Trends Plant Sci 2004; 9:26-32.
66. Jarchow ME, Cook BJ. Allelopathy as a mechanism for the invasion of Typha angustifolia. Plant Ecology 2009; 204(1):113-124.
67. Falik O, Reides P, Gersani M et al. Root navigation by self inhibition. Plant Cell Environ 2005; 28:562-569.

68. Ibrahim MA, Nissinen A, Prozherina N et al. The influence of exogenous monoterpene treatment and elevated temperature on growth, physiology, chemical content and headspace volatiles of two carrot cultivars (Daucus carota L.). Environ Exp Bot 2006; 56:95-107.
69. Rasmann S, Kollner TG, Degenhardt J et al. Recruitment of entomopathogenic nematodes by insect- damaged maize roots. Nature 2005; 434:732-737.
70. Chen F, Al-Ahmad H, Joyce B et al. Within-plant distribution and emission of sesquiterpenes from Copaifera officinalis. Plant Physiol Biochem 2009; 47:1017-1023.
71. Guerrieri E, Poppy GM, Powell W et al. Plant-to-plant communication mediating in-flight orientation of Aphidius ervi. J Chem Ecol 2002; 28:1703-1715.
72. Smith TM, Smith RL. Elements of Ecology. 7th edition. San Francisco: Benjamin Cummings, 2009.
73. Mahall BE, Callaway RM. Root communication among desert shrubs. Proc Natl Acad Sci USA 1991; 88:874-876.
74. Gruntman M, Novoplansky A. Physiologically mediated self/nonself discrimination in roots. PNAS 2004; 101:3863-3867.
75. Falik O, Reides P, Gersani M et al. Self/nonself discrimination in roots. J Ecol 2003; 91:525-531.
76. Hess L, de Kroon H. Effects of rooting volume and nutrient availability as an alternative explanation for root self/nonself discrimination. J Ecol 2007; 95:241-251.
77. Dudley SA, File AL. Kin recognition in an annual plant. Biol Lett 2007; 3:435-438.
78. Karban R, Shiojiri K. Self-recognition affects plant communication and defense. Ecol Lett 2009; 12:502-506.
79. Runyon JB, Mescher MC, De Moraes CM. Volatile chemical cues guide host location and host selection by parasitic plants. Science 2006; 313:1964-1967.
80. Blande JD, Holopainen JK, Li T. Air pollution impedes plant-to-plant communication by volatiles. Ecol Lett. 2010; 13(9):1172-81.
81. Chapman RF. The insects: Structure and function. Cambridge: Cambridge University Press, 1998.
82. Slaymaker DH, Navarre DA, Clark D et al. The tobacco salicylic acid-binding protein 3 (SABP3) is the chloroplast carbonic anhydrase, which exhibits antioxidant activity and plays a role in the hypersensitive defense response. Proc Natl Acad Sci USA 2002; 99:11640-11645.
83. Vlot AC, Liu PP, Cameron RK et al. Identification of likely orthologs of tobacco salicylic acid-binding protein 2 and their role in systemic acquired resistance in Arabidopsis thaliana. Plant J. 2008; 56:445-456.
84. Himanen SJ, Blande JD, Klemola et al. Birch (Betula spp.) leaves adsorb and re-release volatiles specific to neighbouring plants- a mechanism for associational herbivore resistance? New Phytologist 2010; 186: 722-732.