Who is my neighbor? Volatile cues in plant interactions

Velemir Ninkovic, Merlin Rensing, Iris Dahlin, and Dimitrije Markovic

Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden; Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden; Faculty of Agriculture, University of Banja Luka, Banja Luka, Bosnia and Herzegovina

ABSTRACT
One of the most important challenges for individual plants is coexistence with their neighbors. To compensate for their sessile lifestyle, plants developed complex and sophisticated chemical systems of communication among each other. Site-specific biotic and abiotic factors constantly alter the physiological activity of plants, which causes them to release various secondary metabolites in their environments. Volatile organic compounds (VOCs) are the most common cues that reflect a plant’s current physiological status. In this sense, the identity of its immediate neighbors may have the greatest impact for a plant, as they share the same available resources. Plants constantly monitor and respond to these cues with great sensitivity and discrimination, resulting in specific changes in their growth pattern and adjusting their physiology, morphology, and phenotype accordingly. Those typical competition responses in receivers may increase their fitness as they can be elicited even before the competition takes place. Plant–plant interactions are dynamic and complex as they can include many different and important surrounding cues. A major challenge for all individual plants is detecting and actively responding only to “true” cues that point to real upcoming threat. Such selective responses to highly specific cues embedded in volatile bouquets are of great ecological importance in understanding plant–plant interactions. We have reviewed recent research on the role of VOCs in complex plant–plant interactions in plant-cross kingdom and highlighted their influence on organisms at higher trophic levels.

Introduction

In nature, plants are members of complex and dynamic communities, where they experience a variety of neighbors of different identity. Coexistence with other plants is a constant challenge for individual plants and characterized by fierce confrontation over available resources. The wide range of interactions between plants in these communities determine species’ coexistence and performance, as well as community organization. Plants perceive their neighbors through different kinds of cues that indicate their proximity, such as light quality, root chemicals, acoustic cues, mechanical stimuli, and airborne volatile organic compounds (VOCs). The constantly present chemical cues that plants sense force them to distinguish between essential one predicting competitive neighbors from cues that are not crucial for their own fitness. Although the mechanisms with which plants can accurately detect and distinguish a variety of cues from their neighbors by relevant gradients remain unknown, the advantage of this perception is self-evident, as it could provide valuable advance information about the presence of future competition. As the occurrence of neighbors can differ over space and time, plants have evolved the ability to detect their presence in a timely manner. In response to chemical cues that point out nearby competitors, a single plant can exhibit a multitude of adaption responses including physiological and morphological changes or resource allocation to optimize their performance. Those plant responses to potential competitor are not fixed due to their dependence on various environmental conditions. In other words, plants can have highly specific responses to the proximity of their neighbor under one set of conditions, but not under another set. In this review, we present the role of VOCs produced by plants in response to various abiotic and biotic factors in interactions between plants taking into consideration the implications of these interactions on some organisms across different trophic levels.

Volatile-mediated chemical interactions

For every individual plant, the production, storage, and release of secondary metabolites are essential components of their phenotype as they influence important ecological functions. Each plant species is capable of synthesizing a unique set of secondary metabolites that depends on a diverse set of environmental conditions under which plants grow. Plants are known to synthesize and emit in significant amounts more than 1700 VOCs, which conveys detailed information about their identity and physiological condition. Fast-growing plants are considered to emit more VOCs due to their high physiological activity. Plants in an early stage of development produce and release more VOCs. VOCs can serve as external signals in plant communication providing an advantage to the producer but also as cues that can induce responses in nearby plants. From the receiver’s perspective, VOCs represent the fastest and most reliable cues in plant neighbor detection since they are constantly present compared to periodical cues such as light, mechanical contact, or acoustic cues. In this case, any other...
cues received may provide additional information or extra confirmation about potential upcoming challenges. Some VOCs with higher volatility such as isoprene, methanol, phytohormone ethylene, and some monoterpenes are limited to plant interactions at shorter distances, while heavier compounds with less volatility, like terpene, methyl jasmonate (MeJA), methyl salicylate (MeSA), or green leaf volatiles, can transfer cues at longer distances. Many of these VOCs are emitted constitutively in bouquets in which the ratio of compounds in that bouquet is often considered to be driven by species taxonomy with an amplitude of differentiation among species. Such fluctuating and species-specific ratios between individual compounds released in a bouquet can determine plant–plant interactions and thus prevent or reduce the risk of eavesdropping by other species.

The ecological relevance of VOCs in plant–plant communications is limited and can be effective only at shorter distances due to their rapid dilution in the air to inactive concentrations. The sensitivity of the receiver to specific volatile bouquets or single compounds at different concentrations, coupled with the duration of exposure, makes plant responses much more complex. For instance, periodic exposure during three weeks to trace amounts of (Z)-3-hexenol and (Z)-3-hexenyl acetate emitted by damaged plants can induce defense responses in nearby neighbors (Figure 1(2)). In another study, airborne (Z)-3-hexenol produced by infested tomato plants was involved in the synthesis of (Z)-3-hexenylvicianoside (HexVic) in exposed conspecific plants that protect them against herbivores. The resistance of lima bean to a bacterial pathogen was significantly enhanced after the exposure to nonanal for 6 and over 24 h, whereas this effect was only observed after 24 h when exposed to MeSA. These findings indicate that plant interactions by specific VOCs also involve accumulations of volatiles up to certain quantity in receivers to induce defense response. Apart from active response to VOCs, plants like Betula spp. and broccoli can adsorb ledene, ledol, and palustrol produced by Rhododendron tomentosum and then re-release, making them less attractive to herbivore insects (Figure 1(3)).

The emission of highly specific VOCs allows the identification of, and response to, cues from the same species or even relatives. In that way, nearby plants can exploit volatile cues about the presence of specific neighbors, inducing growth responses that increase their competitiveness.

Roots can also synthesize and release VOCs in the rhizosphere which can play an important role in mediating belowground plant–plant interactions. Plants also use these belowground cues to identify the presence of their neighbors and prepare for competition with a non-self neighbor or avoid competitors’ roots (Figure 1(8)). The presence of a specific neighbor can be an important factor in belowground plant–insect interaction as well. For instance, exposure to root VOCs released from Centaurea stoebe induces changes in Taraxacum officinale and makes it more susceptible to the larvae of Melolontha melolontha. Secondary metabolites released by roots like benzoxazinoids can interfere with root-associated fungal and bacterial communities, reducing plant growth but increasing defenses against herbivores in the next generation of plants. Plant root volatiles are also known to modify soil microbial community and thus have an important feedback that determines growth and defense. Microorganisms also alter the emission of plant volatiles. However, it is still unknown whether these altered variations in root VOCs may have implications on plant–plant interactions and further effects on other trophic levels.

Figure 1. Volatiles from neighboring plants can have informative value for a receiver plant about the presence of (1) plants of the same species, (2) herbivore-infested plants of the same species, (3) plants of another species, (4) herbivore-infested plants of another species, (5) plants exposed to low red:far-red light, (6) highly competitive plants (weeds), (7) mechanically stimulated plants, and (8) root VOCs.
The above-mentioned examples show that individual plant growth strategies in plant communities are not exclusively formed by resource limitations as suggested\textsuperscript{49,50} but also by chemical interactions among plants. Thus, volatile interactions among plants should not be ignored in plant community theory because they have various consequences such as compensatory growth and increased resource uptake.\textsuperscript{12}

**Plant volatiles in allelobiotic interactions**

To describe a wider trophic effect of chemical interactions between plants, the term allelobiosis was introduced.\textsuperscript{51} Allelobiosis is defined as beneficial interactions between undamaged plants, which may affect organisms at other trophic levels, such as herbivores and/or their natural enemies.\textsuperscript{52} Undamaged plants constantly release VOCs that can be exploited by con- or hetero-specific neighbors. For instance, barley cultivar Kara exposed to VOCs from another cultivar Alva (Figure 1(1)) allocated more biomass from shoots to roots than unexposed plants or Kara exposed to VOCs of another Kara.\textsuperscript{16} The aforementioned response enhances the competitive ability of the exposed plants because resource allocation to root biomass may contribute to the fitness by facilitating higher nutrient uptake, especially in habitats characterized by low productivity.\textsuperscript{53} The exposure of one barley cultivar to VOCs from another cultivar in laboratory experiments reduced aphid acceptance, but only in specific emitter and receiver combinations.\textsuperscript{24} Cultivar combinations that affected aphid plant acceptance resulted also in significantly decreased aphid population development in the field, suggesting that volatile interactions also occurred under field conditions and that herbivore response was dependent on the identity of the neighboring cultivar.\textsuperscript{55}

Plant allelobiotic responses were observed in the volatile interaction between plants of different species (Figure 1(3)). Potato exposed to onion released significantly higher quantities of (E)-nerolidol and (3E,7E)-4,8,12-Trimethyltrideca-1,3,7,11-tetraene (TMTT) repelling aphids in laboratory experiments and resulting also in significantly reduced aphid abundance in the field.\textsuperscript{54} This type of VOC-mediated plant interactions is specific and depends on the plant species involved. For instance, volatile chemical interactions between different weed species and barley (Figure 1(6)) only affected aphid plant acceptance after exposure of the two weed species Cirsium arvense and Cirsium vulgare and not when exposed to 16 other weed species.\textsuperscript{37,58}

Volatile interactions between undamaged plants have also been shown to affect herbivores’ natural enemies. The odour of potato previously exposed to onion VOCs became more attractive to ladybirds than unexposed potato, indicating that volatile communication between plants may contribute to increased abundance of natural enemies in complex plant habitats.\textsuperscript{59} This is in line with the study of Ninkovic and Pettersson,\textsuperscript{60} who found a higher frequency of ladybirds in barley plots containing high densities of weeds such as thistle (Cirsium arvense) and couch grass (Elytrigia repens) than in control plots only with barley. This was supported by laboratory studies in which barley plants exposed to VOCs released by thistles were more attractive to ladybirds in olfactory experiments than unexposed barley plants but not after exposure with couch grass.\textsuperscript{60} Ladybirds preferred specific cultivar combinations over others used in the field, which occurred even before aphids arrived in the field and again when aphids were emigrating.\textsuperscript{61} Higher olfactory attractiveness of ladybirds to specific cultivar combinations in the field and laboratory suggests that plant–plant volatile interaction is an underlying mechanism of ladybird’s habitat preference.\textsuperscript{61} These studies show that volatile communication between undamaged plants affects not only the plants themselves but can have wider trophic effects on herbivore insects and their natural enemies. However, these interactions seem to occur only in specific combinations of emitter and receiver both within and between species.

**Stress-induced plant volatiles**

Both abiotic and biotic stress factors, such as high temperatures, high light intensity, or herbivore attack, may have increased VOC emissions as a consequence\textsuperscript{62} and alter emission patterns, which can also be species specific. Alternation in the VOC bouquet is frequently associated with stimulating or suppressing the emissions that can be induced in a systemic way\textsuperscript{63} by wounding, herbivore feeding, or after environmental stresses.\textsuperscript{64–67} These herbivore-induced plant volatiles (HIPVs) can stimulate neighbors to adjust their defenses at the right time, which subsequently reduces herbivore feeding damage\textsuperscript{68–70} (Figure 1(2) and (4)) and increases their attractiveness to carnivores by providing them with biologically relevant information about the presence of their prey.\textsuperscript{71,72} The presence of a neighbor plant with a specific identity can drastically increase the emission of HIPVs of a focal species.\textsuperscript{73}

The emission of induced VOCs from plants is known to increase at high temperatures, which has been observed for different terpenes, including isoprene,\textsuperscript{74} monoterpenes, and sesquiterpenes.\textsuperscript{75} Increased temperatures due to climate change might accumulate VOCs such as sesquiterpenes and MeSA because of their low volatility, which could serve as a new mode of defense against herbivores or pathogens.\textsuperscript{62} For example, the high light intensity increased the emission rates of β-caryophyllene.\textsuperscript{76} Salt-induced VOC emissions include terpenes such as isoprene, mono- and sesquiterpenes, lipooxygenase (LOX) products, and methanol from Arabidopsis plants, which are relevant in priming stress tolerance and triggering induction of high salt resistance in neighboring plants.\textsuperscript{77} Relative growth rate, stomatal conductance, and photosynthetic rate were significantly higher in exposed plants, making them better prepared for upcoming salt stress.\textsuperscript{78}

**VOC as cues in indication of complex interaction between neighboring plants**

Volatile cues in a plant’s environment can initiate physiological changes, altering their own volatile profile, which in turn carry information for other proximate plants that can respond to it, reflecting the complexity of plant–plant–plant interactions. Thus, receivers can respond to these cues in completely different ways and adapt to neighbors’ presence depending on their response to nearby plants. For instance, it has been shown
that barley Kara plants allocate more biomass to root when exposed to the Alva variety. However, when emitter Alva plants were exposed to low red:far red light, they significantly reduced the emission of (E)-β-caryophyllene, α-humulene, and caryophyllene oxide\(^1\) (Figure 1(5)). Such modified volatile emission of Alva induced a typical shade avoidance response in exposed Kara plants grown in normal light, which allocated more resources into aboveground biomass than to roots.

Mechanical stimuli are one of the most common cues by which plants can rapidly detect the presence of neighbors and respond by adjusting their growth; these include inhibition of inflorescence elongation which makes them stronger and more resistant to damage. Touch between plants can induce changes in their volatile emissions\(^2\) that can have further impact on neighbors in their proximity. A recent study demonstrated that within minutes in response to brief and light contact, maize plants trigger transcripts of touch- and defense-related genes and consequently rapidly change emission of isoprene fragment, C4 aldehydes fragment, and (E)-3-hexenal and terpene fragments.\(^3\) One-minute treatment per day over a period of 6 d triggered a slower but longer increase in emission of methanol, isoprene fragment, isoprene, alkyl fragment, and terpene fragment. The complex series of coordinated defense responses expressed in neighbors exposed to these volatiles leads to the activation of the same touch- and defense-related genes (transcriptional mirroring effect), making these plants less suitable hosts for aphids\(^4\) (Figure 1(7)). Surprisingly, aboveground touch stimuli can also modify belowground plant–plant communication, revealing a new dimension to the functional role of touch induce cues in plant interactions at the community level.\(^5\) This point out on a new level of complexity in belowground plant–plant interactions, showing that the direction and extent of plant root responses to neighbors can be affected by the aboveground touch interaction to which neighbors are exposed. The extraordinary specific response pattern made by the exposed plant could be difficult to explain if we consider the variety, quantity, and quality of competing cues perceived (VOCs, root exudates, brief mechanical contact), taking into account their interactions with the complex mixture of biotic and abiotic factors.

The aforementioned examples indicate that plant volatiles have important informative value about the physiological status of the emitters that are exposed to complex interactions with their neighbors (Figure 2). Thus, volatiles can differentially modulate plant growth responses of the same neighbor depending on their response to different biotic stresses or interference mechanisms. The exposed plant can use such VOCs carrying specific cues in the detection of forthcoming competitive neighbors, as reflected in their mirroring response that occurred even before the competition took place.

**Conclusions and future perspectives**

Recent studies on plant responses to the diversity of volatile cues received from neighbors have demonstrated their capacity to rapidly modify growth strategies to meet various ecological challenges. Possible forthcoming threats converted into volatile cues showed to have important ecological role preparing responding plants for future stressors that also influence interactions at higher trophic levels. The fact that volatile cues can initiate physiological changes in receivers, altering their own volatile profile, which in turn carry information for other proximate plants, reflects the complexity of cascading plant–plant interactions (Figure 2). Effective chemical interaction among plants is an important functional component in nature but also in agricultural systems where it could be widely exploited. Highly specific volatile cues that activate adaption responses and induce defense in exposed plants represent an important scientific research area in the future and should be considered when studying plant responses either to biotic or abiotic stresses.

**Author Contributions**

All authors contributed to the review through the development of ideas, drafting of the initial text, and providing feedback for revisions. DM prepared the figures.

**Disclosure of Potential Conflicts of Interest**

No potential conflicts of interest were disclosed.

**Funding**

This work was supported by the European Union’s Horizon 2020 research and innovation programme, under grant agreement no. 773554 (EcoStack) (to FP).

**ORCID**

Velemir Ninkovic http://orcid.org/0000-0001-9276-7169
Merlin Rensing http://orcid.org/0000-0003-1749-0061
Iris Dahlin http://orcid.org/0000-0003-0295-6826
Dimitrije Markovic http://orcid.org/0000-0003-3030-4155

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