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Talking Plants: Communication and Signaling via Volatiles

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Abstract

There is an urgent need for new sustainable solutions to support plants in facing current environmental challenges. In particular, strengthening of productivity and food security needs sustainable exploitation of natural resources and metabolites. In this review, we fetch the attention to the agronomic potential of volatile organic compounds (VOCs) emitted from plants, as a natural and eco-friendly solution to defend from stresses and to enhance crop production. Plants defense by emitting volatile organic compounds communicate with herbivore-attacked neighbors to activate defenses before being attacked. Many volatile compounds especially, transcriptome and signal cascade analyses of VOC-exposed plants indicates that plants snoop to prime direct and indirect defenses and to hone competitive abilities. A diversity of emission responses have been observed from stressed plants. Although, the similarities have been seen in bearing environmental stress, it is also established fact that an emission of VOCs can be induced at any time from leaves of all plant species following abiotic and abiotic stress.The present challenges regarding changing environment which may hamper the use of VOCs in open field are analyzed by several scientist and solutions for a better exploitation of VOCs in future sustainable agriculture are envisioned.

Keywords: Biotic and Abiotic stress, Plant defense, , Talking plants, VOCs, Signaling,

1. Introduction

Plants eavesdrop on their neighbors through the detection of volatile organic compounds (VOCs). These compounds can, as mentioned, be emitted from the root system, but can also be found airborne and floral as well. The ability to detect and respond to VOCs of most competitive neighbors is an important strategy for individual plants since it enables them to adjust their physiological status and growth pattern accordingly, especially in the early stages of their life (Stephen and Harry 2006).

As it is well established fact that plants produce many volatile metabolites and a small subset of these compounds is identified by animals and humans, and the volatile profiles are defining elements of the distinct flavors of individual foods. Flavor volatiles are derived from an array of nutrients, including amino acids, fatty acids, and carotenoids. In tomato, almost all of the important flavor-related volatiles are derived from essential nutrients (Baldwin, 2010). The predominance of volatiles derived from essential nutrients and health-promoting compounds suggest that these volatiles provide important information about the nutritional makeup of foods (Stephen and Harry 2006).

Contrary to the long-held idea that plants are uncommunicative, recent research has made it clear that many species conduct lively and informative conversations with one another. Scientists have revealed that plants communicate through the air, by releasing odorous chemicals called volatile organic compounds (VOCs), and through the soil, by secreting soluble chemicals into the rhizosphere and transporting them along thread-like networks formed by soil fungi. In addition, this is more than mere gossip: these signals warn neighbors of the many dangers facing plants (Baldwin, 2010).

Volatile organic compounds (VOCs), first theorized by plant scientists Jack Schultz and Ian Baldwin in the early 1980s, are now a well-known form of plant communication. Maple tree (**Acer**) saplings (ramp up their own defenses in the presence of herbivore-damaged neighbors.

In late 1990, however, a drop of more carefully designed experiments began to yield convincing evidence to the contrary. In 2000, Karban showed that wild tobacco plants grown in close proximity to sagebrush plants whose leaves had been clipped became resistant to herbivores, ostensibly in response to VOCs released by the sagebrush. Other researchers soon reported similar VOC-induced defense responses, both intra and interspecies in several other plants, including lima bean, broad bean, barley, and corn. Moreover, in 2006, Karban showed that VOCs released by damaged sagebrush induce herbivore resistance in plants growing at distances of up to 60 cm, well within the range of sagebrush neighbors in nature. By now, the wonder of VOC-based plant communication is well established. Different researches demonstrated that volatile cues increase fitness in receiver plants. In one experiment, lima bean plants exposed to herbivore-induced VOCs lost less leaf mass to herbivores and produced more new leaves than controls (Kost and Heil, 2006). But very little information available that demonstrates volatile signaling between neighboring plants can benefit the emitting plant, prompting some researchers to suggest that "eavesdropping" is a more accurate description of what has been observed than "intentional" communication.

2. Impact of Environment on Volatile Compound Emission

A variety of emission responses are observed from stressed plants. Although all environmental stresses bear similarities, e.g. any stress typically leads to reductions in leaf photosynthesis rates, different stresses differently affect volatile emission rates, and the responses can be different for constitutive and induced emissions. In addition, for any stress, the effects depend on stress severity and duration. Mild stress characteristically first results in physiological responses those are quickly reversible upon a return to non-stressed conditions. Such physiological responses typically result from changes in substrate availability for all stresses and from changes in enzyme activity for temperature stresses. Thus, the effects can be positive, e.g. due to enhanced substrate availability for isoprene emission upon mild drought stress or due to enhanced substrate availability and enzyme activity upon mild heat stress. For other mild stresses, the effects can be negative or occasionally no effects can be observed. Mild stress seldom elicits release of stress volatiles, or if it does, the elicitation is minor. More severe stress typically leads to major reductions in constitutive emissions and release of characteristic stress volatiles. The available evidence demonstrates that the release of stress volatiles is stress dose dependent (Baldwin and Schultz, 1983; Rhoades, 1983; Heil and Silva Bueno, 2007; Heil and Karban 2010).

3. Impact on Biotic and Abiotic stress

Emission of VOCs can be induced at any time from leaves of all plant species following abiotic (Loreto *et al.,* 2006; Loreto and Schnitzler, 2010) or biotic stresses (Dicke and Baldwin, 2010). Results from many studies have demonstrated that emission of isoprenoids, the most abundant group of VOCs (Guenther *et al.,* 2006), is stimulated by abiotic stresses and improves plant resistance either by direct quenching of reactive oxygen species (ROS) (Loreto and Velikova, 2001), or indirectly by stabilizing cell membranes (Velikova *et al.,* 2011). However, protection of cell membranes to avoid toxic accumulation of ROS is only one among the many roles of VOCs that may be exploited in agriculture.

Grapevines are generally well-adapted to arid and semi-arid climates, and they appear to primarily rely on drought avoidance mechanisms in water stress situations. In terms of the response of the grapevine to drought conditions, rootstock can have an impact on the gas exchange and water status. The mechanism of drought tolerance, rootstock anatomy, stomatal regulation, physical and chemical responses are the main contributing factors during grapevine drought stress responses (Tsegay*et al.,* 2014; Lovisolo*et al.,* 2016).

Plant volatiles are the metabolites that plants release into the air. Plants are champion synthetic chemists; they take advantage of their anabolic ability to produce volatiles, which they use to defend themselves against biotic and abiotic stresses and to deliver information- and potentially disinformation- to mutualists and competitors alike. Volatiles have provided plants with solutions to the challenges associated with being rooted in the ground and immobile (Baldwin *et al.,* 2006; Baldwin, 2010; Dudareva *et al.,* 2006; Kessler *et al.,* 2008; Kostand Heil, 2006).

Plant volatile blends are dominated by four biosynthetic classes: terpenoids, compounds with aromatic rings, the fatty acid derivatives and volatiles derived from amino acids. Terpenoids play a central role in generating the chemical diversity of plant volatiles and appear to have been under strong diversifying selection. Methanol and ethylene are two the most commonly emitted plant volatiles (Baldwin, 2010; Maffei, 2010; Blande*et al.,* 2007).

Most plant volatiles help in communication to the outside world, providing information to other organisms about a plant's physiology (e.g., its sexual receptivity, fruit maturity, insect damage, oviposition, and competitive status). They can also transmit information within a plant and potentially between plants. Green leaf volatiles, ethylene and perhaps other plant volatiles transmit information within plants, affecting transcript abundance or directly activating defense responses in distal branches that are not well connected by the private communication channels of the vascular system. Plants are known to change their metabolism in response to other long-distance signals. This change in resource allocation priorities likely reflects the more severe consequences of resource competition than of attack from herbivores and pathogens for a plant's fitness (Baldwin, 2010; Dudareva*et al.,* 2006; Lovisolo*et al.,* 2016; Choudhary*et al.,* 2008).

When plants are attacked, they attract predators and parasitoids of the attacking herbivores with volatile blends that provide information about the location, activity and perhaps even developmental stage of the attacking herbivore. The more information about attacking herbivores a plant can encode into its volatile emissions, the more effectively a carnivore will be able to respond to a plant's 'cry for help' and the more likely the carnivore will benefit the plant by disposing of its attackers (Baldwin *et al.,* 2006; Baldwin, 2010; Dicke and Baldwin 2010; Engelberth*et al.,* 2014).

The floral bouquets also contain potent repellants to the unbidden guests of flowers: nectar robbers and florivores. These repellants likely signal the presence of high concentrations of less volatile toxins and other deterrents in the flower. The blends released from ripe fruits are highly attractive to potential seed dispersers, and since many fruit volatiles are derived from amino and fatty-acids, the blend likely represents the true nutritional value of the fruit to a potential disperser (Baldwin *et al.,* 2006; Baldwin, 2010).

4. Impact on Agriculture

Plants can detect their neighbors by stimuli sensed either through their leaves or by root exudates. The researcher also found that a brief and light touch to the leaf has an impact on above and below ground communication, affecting the pattern of biomass allocation and reducing their attractiveness for herbivore insects. The chemical composition of the soil is a key factor in the lifespan of any plant as conveys signals not only about the presence of surrounding neighbours but also their physiological status. Intriguingly, some reports demonstrated that brief touch stimuli perceived by the leaves can affect belowground plant interactions. The recent study demonstrated the extraordinary capacity of maize roots to discriminate between belowground signals and then to respond differentially according to the stress status of their neighbours (Rhoades, 1983).

Whether they are studying volatiles drifting on the breeze or phytochemicals zipping through subterranean fungi, researchers are now bent on elucidating the relevant receptors and deciphering the molecular lingua franca of plant communication. They could then begin to clarify the ecological significance of the phenomenon and, potentially, help farmers grow hardier crops (Kost and Heil 2006).

Understanding how plants perceive airborne volatile signals, for instance, could inform the genetic engineering of crops that are hypersensitive to cues from sacrificial "beacon" plants that are deliberately damaged to emit signals that trigger neighboring plants to activate their antipredator and/or antipathogen defenses. And if researchers could pinpoint the compounds that act as vectors for stress cues passed between roots, they could potentially "train" crop seedlings to better cope with drought and other stresses. Plants maintain memory of any stress event they have experienced (Crisp *et al.,* 2016; Hilker *et al.,* 2016), and this memory is able to influence the response to forthcoming stressful situations. Factors able to shape the plant's stress memory are referred to as "priming stimuli", among which plant VOCs play a crucial role because, due to their volatility, they can quickly reach distant plant parts (Heil and Kost, 2006; Mauch-Mani *et al.*, 2017). A "primed" plant shows an earlier, stronger, and faster response upon further stress occurrence, thereby resulting in increased resistance and/or tolerance (Conrath *et al.*, 2015; Mauch-Mani *et al.,* 2017). VOCs have been extensively demonstrated to prime defenses against herbivorous insects (Kim and Felton, 2013), pathogens (Ameye *et al.,* 2015), and environmental stresses (Cofer *et al.,* 2018). Defense priming against pathogens has also been considered as a sort of "green vaccination" (Luna-Diez, 2016). Green leaf volatiles (GLVs) such as Z-3-hexenyl acetate, ubiquitously and rapidly released after mechanical damage of leaf tissues (Brilli *et al.,* 2011), have been reported to prime resistance of wheat plants to the fungal pathogen *F. graminearum* (Ameye *et al.,* 2015) and to reduce the damage occurring to maize plants during cold stress (Cofer *et al.,* 2018). Other VOCs such as methyl salicylate (MeSA) and monoterpenes (i.e., camphene and pinene) (Riedlmeier *et al.,* 2017) have been found to actively participate in the mechanisms leading to systemic acquired resistance (SAR) (Dempsey and Klessig, 2012). Low concentrations of methyl jasmonate (MeJA) have been demonstrated to prime plant defenses by modifying the epigenetic status of wound-inducible genes in rice, thereby enhancing responsiveness to wounding (Bertini *et al.,* 2018). Even methanol, ubiquitously emitted from plant leaves during cell division and cell wall expansion (Nemecek-Marshall *et al.,* 1995), seems to act as a priming stimulus when released from damaged tobacco leaves by enhancing resistance to the pathogenic bacterium *Ralstoniasolanacearum* (Dorokhov *et al.*, 2012). In addition, antibacterial defenses have also been reported to be primed by VOCs such as nonanal in lima bean plants treated with benzothiadiazole (BTH), a synthetic salicylic acid analog (Yi *et al.,* 2009). Compared to the direct induction of defenses in plants, priming does not incur in an energetically costly activation of metabolic pathways (van Hulten *et al.,* 2006; Martinez-Medina *et al.,* 2016) and therefore represents a sustainable method to develop novel crop protection strategies.

It can be a successful strategy but for that more research should be carried out in this area. Nowadays, the availability of new analytical technologies such as high-resolution Proton Transfer Reaction "Time-of-Flight', mass spectrometry (PTR-TOF-MS) make possible instantaneous and highly sensitive detection of the whole spectra of VOCs with high resolving power (Graus *et al.*, 2010). This can provide *in vivo* a complete and high-throughput measurement of the entire blend of VOCs (the “volatome”) emitted from plant leaves. Phenotyping the volatome could allow non-invasive screening of plant VOC profiles, assisting breeders in the selection of cultivars that successfully perform under changing environmental conditions and associated biotic stressors (Araus and Cairns, 2014). PTR-TOF-MS analysis could also enable a real-time diagnosis of the crop health status (Niederbacher *et al.,* 2015), by monitoring in air the occurrence of specific VOC emissions (i.e., MeSA, sesquiterpenes) as stress biomarkers triggered by abiotic and biotic constraints (Karl *et al.,* 2008; Chalal *et al.,* 2015). Moreover, variations of VOC emission patterns over time can be used for precision agriculture purposes to monitor plant growth and development in the field. Likewise genomics and high throughput platforms for imaging and remote-sensing, real-time highly resolved VOC detection generate massive amount of data (Gandomi and Haider, 2015). This production of ‘big data’ requires computational analysis to extract patters and identify features useful for phenotyping (Singh *et al.,* 2016). Implementation of machine learning tools to process information on VOC emissions along with environmental parameters collected in the field by multiple sensors will allow exploration of big data in order to measure plant performance and recognize early symptoms of stress.

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