CellPress

Opinion

Do Plants Eavesdrop on Floral Scent Signals?

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Plants emit a diverse array of volatile organic compounds that can function as cues to other plants. Plants can use volatiles emitted by neighbors to gain information about their environment, and respond by adjusting their phenotype. Less is known about whether the many different volatile signals that plants emit are all equally likely to function as cues to other plants. We review evidence for the function of floral volatile signals and conclude that plants are as likely to perceive and respond to floral volatiles as to other, better-studied volatiles. We propose that eavesdropping on floral volatile cues is particularly likely to be adaptive because plants can respond to these cues by adjusting traits that directly affect pollination and mating.

Trends

Plants emit volatile organic compounds that can function as cues to other plants.

Plants may use floral volatiles from their neighbors to sense their mating environment.

Plants could respond by adjusting floral traits that affect pollination and mating.

Plant responses to floral volatiles cues are particularly likely to be adaptive.

Plants Listen to the Airborne Signals of their Neighbors

Plants emit a diverse array of airborne **volatile organic compounds** (see Glossary) [1]. Plant volatiles can function as **signals** to mutualists such as seed dispersers [2], pollinators [3], and predators of herbivores [4]. However, these volatiles can also function as **cues** to other plants [5]. Plants can perceive volatiles emitted by neighbors, and use these volatiles to gain information about their environment, including the presence of herbivores [6] and competitors [7]. In response to this information, plants can adjust their phenotype; for example, in response to volatile cues emitted by herbivore-damaged neighbors, plants can increase their own herbivore defenses [8]. While it is clear that plants can use volatiles to gain information about their environment, less is known about whether the many different volatile signals emitted by plants are all equally likely to function as cues to other plants.

In this opinion article we review the evidence that **floral volatiles**, in the same way as other volatile signals, can function as cues to other plants. First, we describe what is known about how plants perceive and respond to non-floral volatiles emitted by their neighbors. Second, we discuss why plants should also be able to perceive floral volatiles emitted by their neighbors, and use these volatiles to gain information about their **mating environment**. Third, we predict how plants should respond to this information by adjusting their floral traits. Fourth, we hypothesize the ecological conditions under which plants are likely to perceive and respond to floral volatiles emitted by their neighbors. We conclude (i) that floral volatiles are as likely as other, better-studied volatile signals to function as cues to other plants, and (ii) that **eavesdropping** on floral volatile cues is particularly likely to be adaptive because plants can respond to these cues by adjusting traits that directly affect pollination and mating.

The Evidence that Non-Floral Volatiles Function as Cues to Other Plants

The first studies on **plant–plant communication** were controversial, but there are now many examples demonstrating that plants can perceive and respond to volatile cues emitted by their neighbors [5]. Many of these studies have focused on volatiles emitted following herbivore damage (i.e., **herbivore-induced plant volatiles**) [8]. Plants can use these volatiles to gain information about the presence of herbivores, and respond in at least two different ways. First,

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plants can increase their defenses against herbivores. For example, wild tobacco (*Nicotiana attenuata*) growing next to damaged sagebrush (*Artemisia tridentata*) had less leaf herbivory than wild tobacco growing next to undamaged sagebrush [9]. Second, plants can change their physiology to more quickly or vigorously respond to future herbivore attack (i.e., **priming**) [10]. For example, wild tobacco plants growing next to damaged sagebrush plants upregulated the expression of genes that play a role in herbivore defense [11].

Although most studies have focused on volatiles emitted by herbivore-damaged neighbors, plants can also perceive and respond to volatile cues emitted by undamaged neighbors [12]. Plants can use the volatiles from undamaged neighbors to gain information about the presence of conspecifics and heterospecifics, and respond in at least two ways. First, plants can alter their biomass allocation and growth. For example, seedlings of the parasitic species five-angled dodder (*Cuscuta pentagona*) grew towards volatiles produced by their preferred host species, and away from volatiles produced by non-preferred hosts [13]. Second, plants can suppress [14] or change the composition [15] of their own volatile signals. For example, potato (*Solanum tuberosum*) plants exposed to volatiles produced by undamaged onion (*Allium cepa*) plants produced more of two terpenoid compounds [15]. Potato plants that produced more of these terpenoids attracted fewer aphid herbivores [16] and more of the natural enemies of aphids [17]. Overall, these studies suggest that herbivore-induced plant volatiles are not the only plant volatile signals that can function as cues to other plants.

Could Floral Volatiles Function as Cues to Other Plants?

Floral volatiles have been shown to function as signals to pollinators and herbivores [18,19], and researchers in disparate fields have speculated that floral volatiles could function as cues to other plants (Box 1). However, only one study [20] that we are aware of has explored whether floral volatiles function as cues to other plants. This study found that floral volatiles produced by snapdragon (*Antirrhinum majus*) inhibited root growth of *Arabidopsis*. The response of *Arabidopsis* to floral volatiles was specific: of the three primary VOCs produced by snapdragon flowers, only methyl benzoate affected root growth, and root growth was not affected by

Box 1. Past Speculation that Plants Can Sense Floral Volatiles

With one exception [20], the hypothesis that floral volatiles function as cues to other plants has not been tested using the methods described in Box 2. However, this hypothesis has been invoked by researchers in two disparate fields: chemical ecology and reproductive biology.

Chemical ecologists who study communication between undamaged plants have speculated that floral volatiles could function as cues to other plants for two reasons [12]. First, floral volatiles are emitted in a wide range of ecological conditions, including in the absence of herbivore damage and abiotic stress. Consequently, floral volatiles could function as cues to plants growing in a wide range of ecological conditions. Second, floral volatiles and herbivore-induced plant volatiles are chemically similar. This similarity suggests that if plants can perceive herbivore-induced plant volatiles emitted by their neighbors, then they should also be able to perceive floral volatiles emitted by their neighbors.

Reproductive biologists who study gynodioecious species have speculated that plants could use floral volatiles emitted by their neighbors as a cue to the mating environment [45]. In gynodioecious species, plants are either female or hermaphroditic, and females cannot produce seeds without receiving pollen from hermaphrodites. Consequently, there should be selection on females to perceive the frequency of hermaphroditic neighbors and respond by adjusting their floral traits. Consistent with this hypothesis, females in the gynodioecious species great blue lobelia (*Lobelia siphilitica*) adjust their rate of flower opening in response to the frequency of hermaphroditic neighbors; females open more flowers per unit time when they are rare relative to hermaphrodites than when they are common relative to hermaphrodites. Female great blue lobelia plants adjust their rate of flower opening even when hand-pollinated and grown in individual pots, suggesting that they do not use pollen receipt or soil chemicals as cues to the frequency of hermaphroditic neighbors. However, in some gynodioecious species, female and hermaphroditic flowers emit different volatile compounds [46], suggesting that female plants could use floral volatiles as a cue to hermaphroditic neighbors.

Glossary

Adaptive plasticity: phenotypic plasticity that increases fitness (i.e., survival or reproduction). Plasticity is adaptive when genotypes that adjust their phenotype in response to the environment have higher fitness than genotypes that do not adjust their phenotype.
Cue: a trait used by a receiver that is not intentionally displayed for that purpose. For example, if herbivores use floral volatiles to find host plants, then floral volatiles are functioning as a cue.
Eavesdropping: using a signal intended for other receivers to gain information about the surrounding environment. For example, plants that detect floral volatiles emitted to attract pollinators are eavesdropping.
Fine-grained environmental variation: when an individual experiences more than one environment within its lifetime.
Floral volatiles: low molecular weight organic molecules emitted by flowers. These compounds are the constituents of floral scent, which can range from simple blends with few compounds to complex bouquets of >50 compounds.
Herbivore-induced plant volatiles (HIPVs): low molecular weight organic molecules emitted by plants following consumption by an animal. Green leaf volatiles are common components of HIPVs.
Mating environment: environmental factors that affect plant reproduction. The mating environment of a plant can include conspecific plants that act as mates, pollinators that transfer gametes between conspecifics, and heterospecific plants that compete for or facilitate pollination.
Phenotypic plasticity: when a genotype produces a different phenotype in response to different environmental conditions.
Plant–plant communication: when a plant signal is perceived by another plant. Plant–plant communication can occur via soil or airborne cues, and is often used synonymously with eavesdropping.
Priming: a physiological response that prepares a plant to more quickly or vigorously respond to a stressful biotic or abiotic environment in the future. For example, plants exposed to herbivore-induced plant volatiles can upregulate the expression of herbivore defense genes.