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Natural Enemy Attraction to Plant Volatiles

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Without Abstract

Leaves normally release low levels of volatile chemicals. However, when a plant is damaged by herbivorous insects, the emission of volatile organic compounds increases. The chemical composition varies with the herbivorous insect species as well as the plant species. Volatile phytochemicals can serve as airborne semiochemicals, deterring or promoting interactions between plants and insect herbivores. For example, moths (*Heliothis virescens*) are repelled by herbivore induced volatiles released from tobacco plants at night; such odor cues may allow females to avoid oviposition on previously damaged plants. For swallowtail butterflies, volatiles from host plants enhance the effect of contact stimulants, increasing landing rates and oviposition relative to non-host plants. Volatile plant signals may also induce defense responses in neighboring plants. Such semiochemicals that function in communication between and among species are emitted from a diverse group of plants and mediate key processes in the behavior of specific insects.

Plant Volatiles Signal of Beneficial Insects

In addition to the bouquet of compounds that render leaves attractive or disagreeable to herbivores, volatile terpenoids and other compounds emitted from leaves in response to insect damage allow insect parasitoids (such as parasitic wasps) and predators to distinguish between infested and non-infested plants, and thus aid in locating hosts or prey. These phytodistress signals, which result in an active interaction between herbivore-damaged plants and a third trophic level, have been described for several agricultural systems. Examples include lima bean and apple plants, which produce volatiles that attract predatory mites when damaged by spider mites, and corn and cotton plants, which release volatiles that attract hymenopterous parasitoids that attack larvae of several Lepidoptera species. In the case of endoparasitoids, the female injects her eggs when she stings and immature parasitoids develop within the body of the herbivore as it continues to feed on the plant. Once a caterpillar has been stung, its own reproductive cycle is terminated and a new generation of wasps is produced.

Several experiments have shown that natural enemies such as parasitoids make effective use of plant volatile organic compounds to locate the microhabitat of their host. Wind tunnel flight experiments indicate that herbivore odors alone do not provide the required chemical information to allure parasitoids. In contrast, the odors released from herbivore-damaged plants appear to contain critical information that draws parasitoids to air streams spiked with these plant odors in the laboratory and to damaged plants placed among a group of undamaged neighbors in the field. To examine whether systemically released chemicals alone provide sufficient chemical cues to attract parasitic wasps, herbivore-damaged leaves have been removed immediately before flight tests. Wind tunnel experiments showed that systemically released components were detectable at levels sufficient to direct parasitoids to their hosts. In cotton and tobacco field trials using female wasps (*Cardiochiles nigriceps*), the ratio of landings on host (tobacco budworm) damaged versus undamaged plants was high: approximately 95% to 5%, respectively, in systemic or whole-plant volatile emissions. To examine the role of volatile organic compounds in a natural plant system, volatile emissions have been quantified from *Nicotiana attenuata* grown in natural populations during the attack by three species of leaf-feeding herbivores. When volatiles emitted with herbivore damage to the plant were exogenously applied to undamaged plants, three compounds (*cis*-3-hexen-1-ol, linalool, and *cis*-alpha-bergamotene) increased egg predation rates by a generalist predator while linalool and the complete blend decreased Lepidopteran oviposition rates. As a consequence, plants reduced local herbivore populations by more than 90% by releasing volatiles.

Parasitoids Learn the Rewards of Host Odor Cues

Although the volatile organic compounds released by insect herbivore damage are similar among the several plant species studied thus far, the specific blends are quite distinct, varying in both the number of compounds and the actual structures produced. Thus, the task of finding a host is more complicated for the parasitoid when the host feeds on several different plant species. The wasp have overcome this obstacle by developing the ability to learn chemical cues associated with the presence of a host. The odors to which a female wasp is exposed during interactions with her host, familiarize her to particular host location cues. A successful host experience increases the wasp's responsiveness to host-associated chemicals. For example, an oviposition experience on the plant-host complex significantly increase the oriented flight and landing responses of females of the aphid parasitoid *Aphidius ervi* relative to those that are not allowed to sting, but that are exposed to undamaged or host-damaged plants. This points to the importance of the oviposition experience in combination with host-damage plant cues. Interestingly, female wasps can also learn volatile odors associated with food sources and use them to locate necessary food.

Adaptive Advantages of Volatile Emissions for Plants

Parasitoids can and do use plant generated volatile organic compounds in the location of the micro-environment of their host, however the selective pressure for plants to produce these volatile organic compounds is less certain. If increased parasitism results in higher fitness for herbivore-attacked plants, plants that signal parasitoids by the emissions of volatile organic compounds are at a selective advantage. During certain stages of a larva's life cycle, parasitization can result in elevated leaf consumption compared to non-parasitized cohorts, however there are recent examples where parasitism of herbivores provides a clear selective advantage for the plant. In maize seedlings under attack by *Spodoptera littoralis* larvae, parasitization by the endoparasitoid *Cotesia marginiventris* significantly reduced feeding and weight gain in the host larvae. In fact, plants attacked by parasitized larvae suffered less feeding damage and at maturity produced 30% more seed than plants that were attacked by an unparasitized larva. For a member of the mustard family, *Arabidopsis thaliana*, herbivory by unparasitized *Pieris rapae* caterpillars resulted in a decrease in seed production compared to damage by *P. rapae* caterpillars that have been parasitized by a solitary endoparasitoid *Cotesia rubecula*. Interestingly, plants damaged by parasitized larvae did not result in a significant reduction in seed production compared to undamaged plants.

Exploitation of Plant Volatiles in Agriculture

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For members of the agricultural community to exploit the release of volatiles from plants as a non-toxic form of pest control will require more research in the area of chemistry genetics and ecology. A simple approach might be to spray plant volatiles directly onto crops or to induce their production using an elicitor such as methyl jasmonate; in fact, tomato fields that have been sprayed with jasmonate have a twofold higher level of parasitism for *Spodoptera exigua* caterpillars by the parasitic wasp *Hyposoter exiguae*. However, if parasitoids are lured to plants that do not contain their host, the learned association between the volatiles released from plants and the availability of host species on plants will be broken and plant volatile organic compounds may lose their attractant powers. Another option is to look for plant varieties that respond more strongly to attack by pests in terms of the speed and/or level of volatiles that are released. Since some of the enzymes involved in volatile biosynthesis are known, plants could be screened and selected for enzymatic activity. Such traits could then be introduced into crops by conventional plant breeding. DNA microarrays are also being employed to determine patterns of gene expression in plants responding to herbivore attack. Such studies may suggest ways of genetically engineering plants to boost their production of volatile chemicals in response to herbivore attack. Studies are also needed to understand how parasitoids and predators interpret the complex cocktail of volatiles; perhaps particular components are more potent than others in their attraction of parasitoids. Even though there are many unanswered questions that need to be addressed before plant volatiles are widely used as an agricultural strategy to protect crops against herbivore pests, this research area has already provided many fascinating new examples championing the adage "the enemy of my enemy is my friend."

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