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Addendum

Plant Host Finding by Parasitic Plants

A New Perspective on Plant to Plant Communication

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Volatile Chemical Cues Guide Host Location and Host Selection by Parasitic Plants

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ABSTRACT

Plants release airborne chemicals that can convey ecologically relevant information to other organisms. These plant volatiles are known to mediate a large array of, often complex, interactions between plants and insects. It has been suggested that plant volatiles may have similar importance in mediating interactions among plant species, but there are few well-documented examples of plant-to-plant communication via volatiles, and the ecological significance of such interactions has been much debated. To date, nearly all studies of volatile-mediated interactions among plant species have focused on the reception of herbivore-induced volatiles by neighboring plants. We recently documented volatile effects in another system, demonstrating that the parasitic plant *Cuscuta pentagona* uses volatile cues to locate its hosts. This finding may broaden the discussion regarding plant-to-plant communication, and suggests that new classes of volatile-meditated interactions among plant species await discovery.

For nearly 25 years, the ecological importance of plant-to-plant communication through volatiles has remained an open and much debated question. Plants exchange gases with the atmosphere and, in so doing, release plumes of volatile chemicals that can convey ecologically important information to other organisms. The potential ecological significance of these volatile cues is demonstrated by the large and growing array of interactions between plants and arthropods known to be mediated by plant volatiles. Volatiles serve as foraging cues both for insects that are beneficial to plants, such as pollinators,[1] and those that are harmful such as herbivores.[2,3] Because the volatile blends released by plants exhibit variation in response to environmental stimuli, volatiles can convey detailed information about the status of the emitting plant. Predatory and parasitic insects that feed on herbivorous insects respond preferentially to plant volatiles that are induced by insect feeding,[4] while female herbivores use such cues to avoid laying their eggs on already-infested plants.[3,5] Moreover, the volatile blends released in response to herbivory can differ between individual herbivore species, providing highly specific cues to specialist parasitoids.[6] Thus, plant volatiles are known to mediate complex interactions among plants and insects across multiple trophic levels.

It has long been speculated that plant volatiles might have similar significance for interactions among plant species, yet there are few well-documented examples of communication between plants by way of volatile signals. Essentially all previous work on plant-to-plant communication has focused on the reception of herbivore-induced volatile signals by neighboring plants, which may use them as early warning signals to initiate their own direct and indirect defense responses. The first studies claiming to document such effects were published almost 25 years ago.[7,8] But issues with the experimental design of these early experiments and the availability of alternative explanations for their results led many ecologists to disregard the phenomenon.[9-11] Later, a number of studies demonstrated that direct and indirect plant defenses could be elicited by exposure to certain induced plant volatiles.[12-15] But many of these effects were demonstrated in airtight chambers with volatile concentrations far higher than those likely experienced in natural settings, again raising doubts about the ecological significance of plant-plant communication.[16-18] Still more recently, some researchers have provided evidence that more realistic volatile concentrations likely induce priming of the defenses of receiving plants, rather than the initiation of full scale responses,[15] while others have documented volatile effects under natural conditions.[19-21] Thus, despite continuing caution about the interpretation of experiments in this area,[17,18] there is mounting evidence that plant herbivore-induced volatiles can serve as early warning signals to neighboring plants.

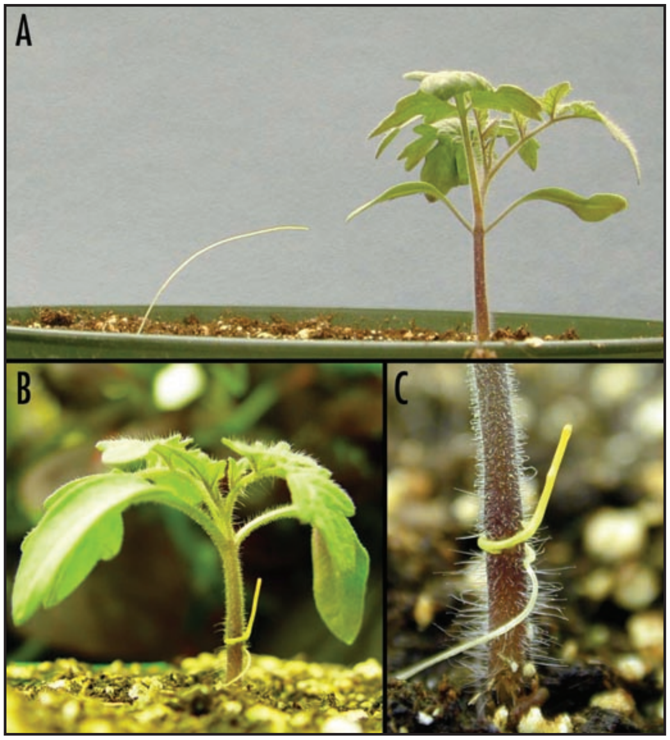

Figure 1. Seedling of *Cuscuta pentagona* (A) foraging toward a 20-day-old tomato plant, (B) attaching to and beginning to grow from stems of tomato seedlings and (C) close up of *C. pentagona* attachment.

We recently documented an entirely new class of volatile mediated interactions among plants: the role of plant volatiles in host location by parasitic plants that attach to above ground shoots of other plants. Plant parasites are important components of natural and agricultural ecosystems and play important roles in determining community structure and dynamics.[22,23] We are exploring the mechanisms of host-location and other interactions between parasitic plants in the genus *Cuscuta* (dodder) and their host plants. Dodder vines germinate from seeds containing limited energy reserves and, as the parasites have no roots and little photosynthetic ability, must quickly locate and attach to suitable hosts in order to survive (Fig. 1). Thus, there is presumably significant selection pressure for dodder vines to employ efficient strategies for host location, and host plant volatiles may be expected to provide relevant directional cues. Dodder seedlings exhibit a rotational growth habit (circumnutation) following germination and previous researchers have suggested that host-finding might involve random growth[24] or the exploitation of light cues.[25]

Using a very simple experimental design, we explored the possibility that host-plant volatiles might mediate host-location by seedlings of *C. pentagona*. We placed a germinated seedling in a vial of water located at the center of a dry filter paper disk. A host plant (a 20-day old tomato seedling) was placed near the edge of the disk and the dodder seedling was allowed to forage for four days. By the end of the experiment the seedling would lay horizontally on the disk and we traced its position on the filter paper in order to assess the directionality of growth relative to the host plant. This experiment was replicated 30 times and our results clearly indicated directional growth toward the tomato plant (80% of the tested seedlings grew into the disk half nearest the host) demonstrating that *C. pentagona* seedlings were perceiving some host-derived cue.

We did not observe directed growth when we tested dodder seedling response to alternative targets including pots of moist soil, artificial plants, and vials of colored water intended to mimic possible light cues. In order to confirm a role for plant volatiles in host location by *C. pentagona*, we tested seedling response to host plant volatiles extracted from filtered air in a volatile collection system and then released from rubber septa in the absence of any other host-derived cues. Here we observed a directed growth response similar to that exhibited toward an intact tomato seedling, confirming that host plant volatiles do provide a cue used for host location by *C. pentagona*. In subsequent experiments we found directed growth toward impatiens and alfalfa plants, which are attractive hosts for *C. pentagona* and also toward wheat plants which are poor hosts, suggesting that the host-location mechanisms operate over a wide range of host species.

Since discriminating between more and less desirable host species is likely to be important in natural settings, we next explored whether dodder seedlings could distinguish volatile signals from host and nonhost plants. *Cuscuta pentagona* seedlings exhibited directional growth toward tomato plants in preference to wheat plants and also to extracted volatiles from tomato in preference to those from wheat, demonstrating an ability to distinguish and choose among volatiles from more and less preferred hosts.

When we tested seedling responses to individual compounds from the wheat and tomato blends, we found that three compounds from tomato, α-pinene, β-myrcene, and β-phellandrene elicited directed growth. β-myrcene was also present in the wheat blend. Unexpectedly, we also found that one compound present in the wheat blend, (*Z*)-3-hexenyl acetate, was repellent, providing a plausible explanation for the lower attractiveness of the wheat blend. It is interesting to note that (*Z*)-3-hexenyl acetate is also released by tomato in response to feeding by herbivores, and we have some data suggesting that *C. pentagona* seedlings may find tomato seedlings infested by *Heliothis virescens* caterpillars less attractive than un-attacked plants (unpublished data).

The discovery that some parasitic plants exploit host plant volatiles for host location provides a new perspective on volatile mediated interactions among plant species, demonstrating that plant volatiles play a role in mediating ecologically significant interactions in at least one system other than the transfer of herbivore-induced warning signals. We think it is quite likely that plant volatiles will be found to play a role in host location by other parasitic plants and perhaps even by vining plants generally. Moreover, we think it is more likely than not that more classes of volatile mediated interactions among plants remain to be discovered given the potential availability of volatile cues and the fitness benefits to be derived by plants using such cues to gather information about the identity and condition of their neighbors.

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