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Supporting Online Material

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

Justin B. Runyon, Mark C. Mescher, Consuelo M. De Moraes*

The importance of plant volatiles in mediating interactions between plant species is much debated. Here, we demonstrate that the parasitic plant *Cuscuta pentagona* (dodder) uses volatile cues for host location. *Cuscuta pentagona* seedlings exhibit directed growth toward nearby tomato plants (*Lycopersicon esculentum*) and toward extracted tomato-plant volatiles presented in the absence of other cues. Impatiens (*Impatiens wallerana*) and wheat plants (*Triticum aestivum*) also elicit directed growth. Moreover, seedlings can distinguish tomato and wheat volatiles and preferentially grow toward the former. Several individual compounds from tomato and wheat elicit directed growth by *C. pentagona*, whereas one compound from wheat is repellent. These findings provide compelling evidence that volatiles mediate important ecological interactions among plant species.

Plant volatiles serve as important foraging cues for both insect herbivores and their natural enemies and can convey complex information regarding plant location, identity, and condition (1–5). It has been suggested that volatiles may have similar importance for interactions among plants, but such claims have remained controversial (6–13) and where plant-plant volatile effects have been demonstrated, their ecological importance remains unclear (6–9). Previous work on volatile-mediated interactions among plant species has dealt with the role of volatiles induced by herbivory or other environmental stressors in initiating defensive responses in neighboring plants (7, 14–19). Parasitic plants, which to survive must rapidly locate and attach to other plants, provide an alternative system in which host-plant volatiles might be expected to play an important role.

Parasitic plants are important components of both natural and agricultural ecosystems and have considerable influence on the structure and dynamics of the communities they inhabit (20, 21). Yet, little is known about the ecology of interactions between parasitic plants and their hosts. Like insect herbivores, para-

sitic plants exhibit various “foraging” patterns (22–25) and are capable of “selecting” among potential hosts (22–25), but the mechanisms involved in host location and discrimination are not well understood.

Flowering plants in the genus *Cuscuta* are obligate parasites with little photosynthetic capability; they obtain nutrients by attaching to aboveground shoots of other plants (26) (Fig. 1). *Cuscuta* spp. are important agricultural pests, included on the U.S. Department

of Agriculture’s *Top Ten Weeds List*, and can be difficult to control without also impacting host plants (27). Seeds of *Cuscuta* spp. contain minimal energy reserves, allowing growth of only several centimeters, and upon germination, the rootless seedlings must locate and attach to a suitable host within a few days (26). In some parasitic plants, contact with chemical cues secreted from host-plant roots is required for germination (28, 29), but *Cuscuta* spp. have no specialized germination requirements and must depend on seedling “foraging” for host-plant location (26) (fig. S1). After germination, *C. pentagona* seedlings exhibit a rotational growth habit (circumnutation) until contacting a host (26) (movie S1). Host secondary metabolites are known to influence the belowground growth of parasitic plants that attach to host roots (28, 29), and host-derived chemicals also induce haustorial development by these parasites (30). However, the role of host-derived compounds in aboveground host location by *Cuscuta* spp. has not previously been determined.

In this study, we explored host finding by seedlings of *C. pentagona*. First, we examined whether *C. pentagona* seedlings exhibit directed growth toward host plants (potted 20-day-old tomato seedlings). The basal end of a *C. pentagona* seedling was inserted into a water vial placed at the center of a dry filter-

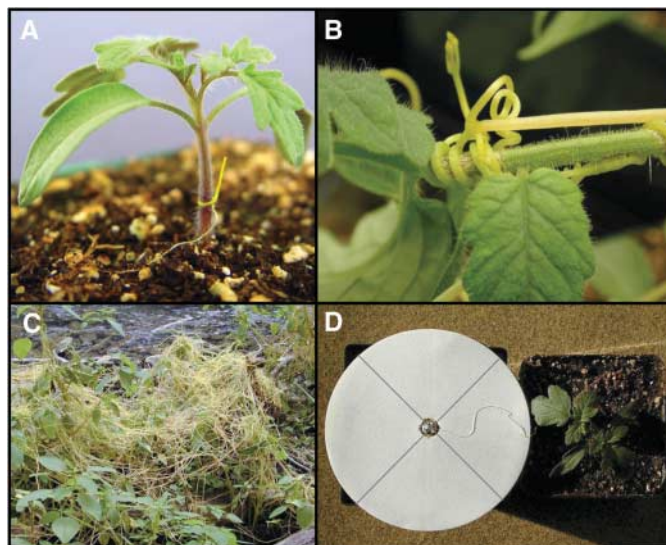


Fig. 1. Parasitic plants in the genus *Cuscuta*. (A) *C. pentagona* seedling attaching to a tomato plant. (B) Vines of *C. pentagona* coiled around the petiole of a tomato leaf. (C) Growth habit of *Cuscuta*. (D) *C. pentagona* seedling growing toward a tomato plant across a filter-paper disc.

Department of Entomology, Pennsylvania State University, University Park, PA 16802, USA.

*To whom correspondence should be addressed. E-mail: czd10@psu.edu

paper disc. A host plant was placed near the edge of the disc (Fig. 1D), and the seedling was allowed to “forage” for 4 days. Seedlings’ growth across the discs was recorded by tracing their position on the filter paper (Figs. 1D and 2A). Our initial assay determined whether plants grew into the semicircle (disc half) adjacent to the target plant or into the semicircle opposite the target. This assay yielded statistically significant results (80%

grew toward the host plant) (Table 1), indicating that directed growth does occur. Visual observation of the recorded growth patterns further suggested that a large proportion of plants grew more or less directly toward the target plant. To quantify this impression, we divided the disc into four quadrants (Fig. 2A) and used chi-square analysis to compare expected and observed numbers of plants growing into each. More seedlings than expected

by chance grew into the quadrant nearest the target, whereas significantly fewer grew into the quadrant directly opposite the target (Table 1).

These results provide strong evidence for directed growth by *C. pentagona* seedlings toward host plants but do not establish the cues responsible for eliciting this growth. Because we suspected a role for host-plant volatiles, we used the experimental design described above to test seedling growth responses to control targets designed to mimic possible alternative cues. Targets included pots of moist soil without plants, artificial tomato seedlings, and vials of green- or red-colored water. None of these control targets elicited a growth response from *C. pentagona* seedlings (Table 1). However, these controls provided at best a crude representation of the cues available from actual host plants, and the lack of response to these targets does not conclusively eliminate a possible role for shading or other light cues in host location. The moist soil control does indicate that the cues involved in host location, volatile or otherwise, are derived from the host plants themselves (Fig. 2A and Table 1).

To demonstrate more firmly a role for volatile cues in host location, we placed *C. pentagona* seedlings, arranged on filter-paper discs as before, in a small open-air enclosure linked to two enclosed target chambers by short lengths of black polyvinyl chloride pipe, each with an intervening 90° bend (Fig. 2B). Four potted 20-day-old tomato seedlings were placed in one of the target chambers and four artificial tomato plants in pots of moist soil in the other. This configuration was designed to permit volatile transmission while blocking most light cues. Previous studies testing plant response to volatiles have been criticized for using airtight chambers that produce elevated volatile concentrations and may influence the physiological status of plants (6–8, 13). Our open system avoided such problems. Multiple plants were used to increase volatile concentrations, because the design of this experiment necessitated placing host plants unrealistically far away from the *C. pentagona* seedlings (i.e.,

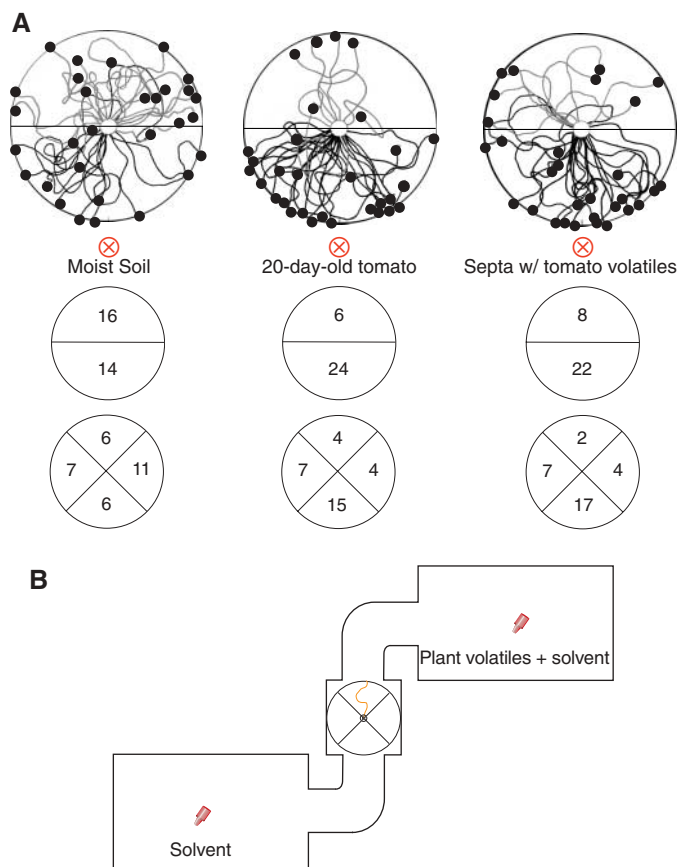


Fig. 2. Foraging by *Cuscuta pentagona* seedlings. **(A)** Summary of *C. pentagona* seedling growth responses to a pot containing moist soil, a nearby 20-day-old tomato plant, and tomato volatiles released from rubber septa. The position of the target is indicated by a circled X. The final position of the apex of each seedling is highlighted with a solid black circle. The numbers of seedlings growing into each disc half and quadrant are summarized in the smaller circles below each disc. **(B)** Experimental setup for the release of plant volatiles while blocking light cues.

Table 1. Foraging of *Cuscuta pentagona* seedlings on filter paper discs to various targets.

Exp	Target	Seedlings choosing disc half with or without targets				χ^2 (P value)	Seedlings choosing quadrants (direction relative to target)				χ^2 (P value)
		No. with target	No. without target	% with target	% without target		A (away)	B (side)	C (side)	D (toward)	
1	10-day-old plants	23	7	77	23	8.53 (0.004)	4	5	4	17	16.1 (0.001)
2	20-day-old plants	24	6	80	20	10.8 (0.001)	4	4	7	15	10.8 (0.013)
3	Red glass	14	16	47	53	0.13 (0.715)	11	8	6	5	2.80 (0.423)
4	Green glass	12	18	40	60	1.20 (0.273)	13	9	3	5	7.87 (0.052)
5	Artificial plant	12	18	40	60	1.20 (0.273)	8	8	9	5	1.20 (0.753)
6	Moist soil	14	16	47	53	0.13 (0.715)	6	7	11	6	2.27 (0.519)
7	20-day-old plants*	23	7	77	23	8.53 (0.004)	4	6	4	16	13.2 (0.004)
8	Volatile extracts*	22	8	73	27	6.53 (0.011)	2	7	4	17	17.7 (< 0.001)

*Target tested in experimental enclosure.

Table 2. Pair-wise test using logistic regression to contrast different target treatments. χ^2 (*P* value).

Exp.	1	2	3	4	5	6	7	8
1	–	0.098 (0.754)*	5.47 (0.019)‡	7.82 (0.005)‡	7.82 (0.005)‡	5.47 (0.019)‡	0.0 (1.0)*	0.089 (0.766)*
2			6.75 (0.009)‡	9.25 (0.002)‡	9.25 (0.002)‡	6.75 (0.009)‡	0.098 (0.754)*	0.371 (0.543)*
3				0.271 (0.603)†	0.271 (0.603)†	0.0 (1.0)†	5.47 (0.019)‡	4.31 (0.038)‡
4					0.0 (1.0)†	0.271 (0.603)†	7.82 (0.005)‡	6.49 (0.011)‡
5						0.271 (0.603)†	7.82 (0.005)‡	6.49 (0.011)‡
6							5.47 (0.019)‡	4.31 (0.038)‡
7								0.089 (0.766)*
8								–

*Group A (Exps. 1, 2, 7, and 8) †Group B (Exps. 3, 4, 5, and 6) ‡Contrast tests between groups A and B

Table 3. Average volatiles released by 20-day-old tomato plants and by rubber septa treated with tomato volatiles.

Compound	Volatiles released (ng/24hours ± SEM)	
	Four 20-day-old tomato plants	Rubber septum treated with tomato volatiles
α-Pinene	83.8 ± 13.9	10.8 ± 3.9
β-Myrcene	93.5 ± 6.2	44.5 ± 8.8
2-Carene	1131.6 ± 173.4	448.3 ± 89.6
p-Cymene	53.6 ± 13.1	50.4 ± 13.9
β-Phellandrene	2843.9 ± 395.8	1457.6 ± 367.7
Limonene	602.7 ± 64.6	346.2 ± 85.4
(E,E)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene	376.9 ± 141.8	176.5 ± 35.8
Unidentified monoterpene	138.9 ± 18.2	52.9 ± 14.2

farther than a seedling could grow before exhausting its energy reserves). We observed a directed growth response similar to that in our first experiment. Significantly more *C. pentagona* seedlings grew toward the target chamber containing host seedlings than toward the chamber containing artificial plants (77% grew toward host plants) (Table 1). This response was statistically indistinguishable from that to a single tomato plant in a completely open system (Table 2). Dividing the discs into quadrants again revealed more seedlings than would be expected by chance growing more or less directly toward the target and fewer growing directly away from the target (Table 1).

This result strongly suggests a role for host-plant volatiles in host location by *C. pentagona* seedlings; however, we cannot rule out the possibility that this experimental design still allows the transmission of some alternative cues. To establish conclusively a role for volatile cues, we used the same experimental design to test seedling growth responses to extracted host volatiles experimentally released from rubber septa in the absence of any other plant-derived cues. Volatiles were collected from four 20-day-old tomato plants onto SuperQ (Alltech Associates, Deerfield, IL) adsorbent filters. Extracts from these filters were then released from a rubber septum placed in one of the target chambers (Fig. 2B). A septum containing solvent alone was placed in the other chamber. Gas chromatographic analysis revealed that undamaged tomato seedlings re-

leased eight major volatile compounds [α -pinene, β -myrcene, 2-carene, p-cymene, β -phellandrene, limonene, (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, and one unidentified monoterpene] and that rubber septa treated with tomato volatile extracts released the same compounds in about the same proportions as intact plants but in lesser amounts (Table 3). We observed a growth response to extracted volatiles similar to that observed in response to whole plants: Significantly more *C. pentagona* seedlings grew toward the target chamber containing the septum with extracted host volatiles than toward the chamber containing the septum with solvent alone (73% grew toward host-plant volatiles) (Table 1 and Fig. 2). Once again, dividing the discs into quadrants revealed an excess of seedlings growing more or less directly toward the target and fewer than would be expected by chance growing directly away from the target (Table 1 and Fig. 2A).

A pairwise comparison using logistic regression showed no significant difference in seedling responses to the three tomato volatile treatments (a single tomato plant, four tomato plants in the experimental enclosure, or extracted volatiles) but did show significant differences between the tomato volatile treatments and all other targets (Table 2), providing further confirmation of a role for host-plant volatiles in foraging by *C. pentagona* seedlings. These results demonstrate decisively that *C. pentagona* seedlings exhibit directed growth toward volatile compounds derived from

tomato plants and strongly suggest that this is an adaptive mechanism for host location.

In a subsequent experiment, we found that *C. pentagona* seedlings also exhibited directed growth toward nearby cultivated *Impatiens wallerana* ‘Dazzler’ (disc half: $\chi^2 = 6.53$, $P = 0.01$; quadrant: $\chi^2 = 10.27$, $P = 0.01$, $n = 30$). Wheat plants (*Triticum aestivum* ‘McNeal’), an unsuitable host on which *C. pentagona* does not survive (26), elicited a growth response that was statistically marginal ($\chi^2 = 3.33$, $P = 0.06$, $n = 30$); however, a small increase in sample size yielded a significant result (disc half: $\chi^2 = 5.57$, $P = 0.01$; quadrant: $\chi^2 = 8.09$, $P = 0.04$, $n = 34$). These results suggest that *C. pentagona*’s host-location mechanism operates across a wide range of plant species.

Having established the role of volatiles in host-plant location by *C. pentagona*, we examined whether *C. pentagona* seedlings were also able to distinguish between potential hosts of differing quality. When *C. pentagona* seedlings were planted between tomato (host) and wheat (nonhost) seedlings and equidistant from each, they exhibited a strong and consistent growth bias toward tomato ($\chi^2 = 12.57$, $P < 0.001$, $n = 23$). This result cannot be explained by contact cues, because there were no cases in which *C. pentagona* seedlings contacted one host before attaching to the other. To confirm that this host preference was mediated by plant volatiles, we gave seedlings a choice between rubber septa treated with extracted tomato and wheat volatiles (using the setup described above for extracted tomato volatiles) (Fig. 2B). *Cuscuta pentagona* seedlings exhibited a clear preference for extracted tomato volatiles ($\chi^2 = 6.53$, $P = 0.011$, $n = 30$). This result suggests that, although *C. pentagona* may respond to a variety of plant odors, it is capable of preferentially responding to volatiles produced by its preferred hosts.

To explore the contribution of individual compounds to the attractiveness of host volatiles, we used the same assay previously described for whole plants (Fig. 1D) to examine the growth responses of *C. pentagona* seedlings to synthetic standards released from rubber septa. When we tested seven identified compounds from the tomato blend, a significant positive response was observed to

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Table 4. Foraging of *Cuscuta pentagona* seedlings on filter paper discs to individual tomato (top) and wheat (bottom) volatiles released from rubber septa.

Volatile compound	Seedlings choosing disc half with or without volatile					Seedlings choosing quadrants (direction relative to volatile)				
	No. with volatile	No. without volatile	% with volatile	% without volatile	χ^2 (<i>P</i> value)	A (away)	B (side)	C (side)	D (toward)	χ^2 (<i>P</i> value)
α -Pinene	23	11	68	32	4.23 (0.039)	6	8	9	11	1.53 (0.676)
β -Myrcene	21	9	70	30	4.80 (0.029)	6	6	4	14	7.87 (0.049)
2-Carene	14	20	41	59	1.06 (0.304)	11	9	8	6	1.53 (0.676)
<i>p</i> -Cymene	17	13	57	43	0.53 (0.465)	5	7	9	9	1.47 (0.690)
β -Phellandrene	21	9	70	30	4.80 (0.029)	5	6	6	13	5.47 (0.141)
Limonene	16	14	53	47	0.13 (0.715)	9	6	5	10	2.27 (0.519)
TMTT*	14	16	47	53	0.13 (0.715)	8	8	5	9	1.20 (0.753)
(<i>Z</i>)-3-Hexenyl acetate	11	23	32	68	4.23 (0.039)	13	5	9	7	4.12 (0.249)
(<i>Z</i>)-3-Hexen-1-ol	15	19	44	56	0.47 (0.493)	13	6	6	9	3.88 (0.275)
(<i>E</i>)- β -Ocimene	16	14	53	47	0.13 (0.715)	3	7	10	10	4.40 (0.221)
Linalool	14	16	47	53	0.13 (0.715)	9	8	9	4	2.27 (0.519)
Decanal	22	12	65	35	2.94 (0.086)	8	7	9	10	0.59 (0.899)
Nonanal	17	17	50	50	0.00 (1.000)	6	15	6	7	6.71 (0.082)

*(*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene

β -phellandrene, β -myrcene, and, after a small increase in sample size, α -pinene (Table 4). Notably, β -myrcene is also released by wheat seedlings. Six other compounds released by 20-day-old wheat seedlings did not show a significant positive growth response (Table 4). Unexpectedly, one wheat compound, (*Z*)-3-hexenyl acetate, appeared to have a repellent effect—although this result initially was not significant ($\chi^2 = 3.33$, $P = 0.06$, $n = 30$), a small increase in sample size yielded statistical significance (Table 4). This finding suggests a possible mechanism for the observed preference for the volatile blend produced by the preferred host tomato over that produced by the nonhost wheat.

The positive growth response observed to individual compounds suggests that these compounds may be important for host location and discrimination. However, complex qualitative features of the blend may play an important role (31). Until the detailed mechanisms by which *C. pentagona* perceives and responds to host-plant volatiles are elucidated, it will be difficult to determine exactly how the information content of the signal is encoded in the volatile blend, because cross talk may occur between components of the blend or their effects on the receiver (6). Because of its parasitic life-style and the concomitant reduction in physiological complexity (e.g., the almost complete absence of photosynthesis and leaves), *C. pentagona* may provide an excellent model system for further investigation of the mechanisms by which plants perceive and respond to volatile signals.

Aboveground plant structures have previously been shown to exhibit directed growth in response to light, gravity, humidity, and physical contact (32). Our results demonstrate that directed growth can also be elicited by airborne chemical cues. In addition, our find-

ings provide insight into the host-location and host-selection mechanisms used by parasitic plants, showing that host-plant volatiles play a role in this system similar to that previously described for foraging insect herbivores (1) and thus revealing unexpected convergence in the host-location strategies used by disparate natural enemies of plants. Finally, our results provide an example of chemical communication between plant species that plays an important role in mediating interspecific ecological interactions. We expect these findings to have broad implications for research in a variety of fields, including chemical ecology, parasite-host interactions, and plant biology. Moreover, these results provide knowledge that may be useful in developing new tactics for controlling parasitic plants that attack agricultural crops.

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Supporting Online Material

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References

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