

ECOLOGY

An herbivore-induced plant volatile reduces parasitoid attraction by changing the smell of caterpillars

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Herbivore-induced plant volatiles (HIPVs) can mediate tritrophic interactions by attracting natural enemies of insect herbivores such as predators and parasitoids. Whether HIPVs can also mediate tritrophic interactions by influencing the attractiveness of the herbivores themselves remains unknown. We explored this question by studying the role of indole, a common HIPV in the plant kingdom. We found that herbivory-induced indole increases the recruitment of the solitary endoparasitoid *Microplitis rufiventris* to maize plants that are induced by *Spodoptera littoralis* caterpillars. Surprisingly, however, indole reduces parasitoid recruitment when the caterpillars themselves are present on the plants. Further experiments revealed that indole exposure renders *S. littoralis* caterpillars unattractive to *M. rufiventris*, leading to an overall reduction in attractiveness of plant-herbivore complexes. Furthermore, indole increases *S. littoralis* resistance and decreases *M. rufiventris* parasitization success. *S. littoralis* caterpillars are repelled by indole in the absence of *M. rufiventris* but specifically stop avoiding the volatile in the presence of the parasitoid. Our study shows how an HIPV can undermine tritrophic interactions by reducing the suitability and attractiveness of caterpillars to parasitoids.

INTRODUCTION

In response to herbivore attack, plants release distinct blends of herbivore-induced plant volatiles (HIPVs). HIPVs are perceived by plants, herbivores, and natural enemies and, consequently, influence the behavior of all three trophic levels. Plants, for instance, use HIPVs to anticipate herbivore attack and prime their defensive systems (1, 2). Herbivores can use HIPVs to avoid plants that are infested by conspecific or heterospecific competitors (3, 4) or to aggregate and overcome the defenses of their host plants (5). Finally, natural enemies, such as predators and parasitoids, use HIPVs to locate their prey (6, 7). Because of the latter, HIPVs are often viewed as a form of indirect plant defense (8). Although evidence that plants benefit from attracting natural enemies through HIPV release is emerging for some systems (9), whether this is a general phenomenon remains unclear.

Apart from attracting natural enemies, HIPVs may also modulate tritrophic interactions by changing the physiology and potentially the attractiveness of the herbivores. Several HIPVs are known to have direct or indirect negative effects on herbivore performance (10–12). Furthermore, predators and parasitoids use a variety of visual and olfactory stimuli to locate their prey or hosts (7, 13), including odors that directly emanate from their insect prey (14–18). Therefore, it is possible that parasitoids also adjust their behavior to HIPV-mediated changes in herbivore physiology. To date, this type of HIPV effect remains unexplored.

Herbivores are capable not only of responding to plant defenses, such as HIPVs, but also of modulating their responses according to experience and environmental conditions (19, 20). Certain caterpillars may even be able to self-medicate by ingesting higher levels of plant toxins to inhibit endoparasite development (21). Therefore, if HIPVs modulate herbivore resistance and attractiveness to natural enemies, then it is conceivable that the herbivores may adjust their behavioral responses to HIPVs as a function of natural enemy presence. These behavioral changes would represent an additional unexplored route

by which herbivore-mediated effects of HIPVs may change the dynamics of tritrophic interactions.

Here, we studied the influence of indole, a common aromatic HIPV that is emitted by many different plant species (22–27), on tritrophic interactions in maize. Indole is released specifically as a volatile in response to herbivore-derived elicitors (28, 29). It is produced through the shikimic acid pathway from indole-3-glycerol phosphate by the indole-3-glycerol phosphate lyase (IGL) (30). The *Igl* gene is induced by herbivory and treatment with methyl jasmonate or volicitin, an elicitor in the oral secretions of caterpillars (28, 30). Recently, indole was described as a potent priming signal that is required for within-plant priming of systemic terpene release (31). Furthermore, indole was found to slightly increase mortality of the generalist herbivore *Spodoptera littoralis* (Boisduval; Lepidoptera: Noctuidae) (32). We therefore hypothesized that indole exposure may also affect the suitability and attractiveness of *S. littoralis* larvae as hosts for parasitoids. To test this hypothesis, we used wild-type and indole-deficient *igl* maize mutants (33) that were infested with *S. littoralis* without or in combination with synthetic indole. The plants and caterpillars were then used to study the behavioral responses of the solitary endoparasitoid *Microplitis rufiventris* (Kokujev; Hymenoptera: Braconidae). *M. rufiventris* occurs sympatrically with *S. littoralis* (34) and has been described to use HIPVs and host odors as host location cues (35, 36). We also assessed the behavioral response of *S. littoralis* caterpillars in the presence and absence of *M. rufiventris* to test whether the caterpillars adjust their exposure to indole according to the perceived risk of parasitism. Together, our experiments add a novel dimension to HIPV-mediated tritrophic interactions, with implications for the ecology, evolution, and application potential of HIPV-mediated tritrophic interactions.

RESULTS

Indole decreases the attractiveness of plant-herbivore complexes

When given a choice in an olfactometer, *M. rufiventris* female parasitoids were significantly more attracted to volatiles from wild-type plants induced by wounding and application of *S. littoralis* regurgitant than to those from induced indole-deficient *igl*-mutant plants ($P = 0.023$; Fig. 1A). Indole alone at physiological release rates of 50 ng hour⁻¹ was

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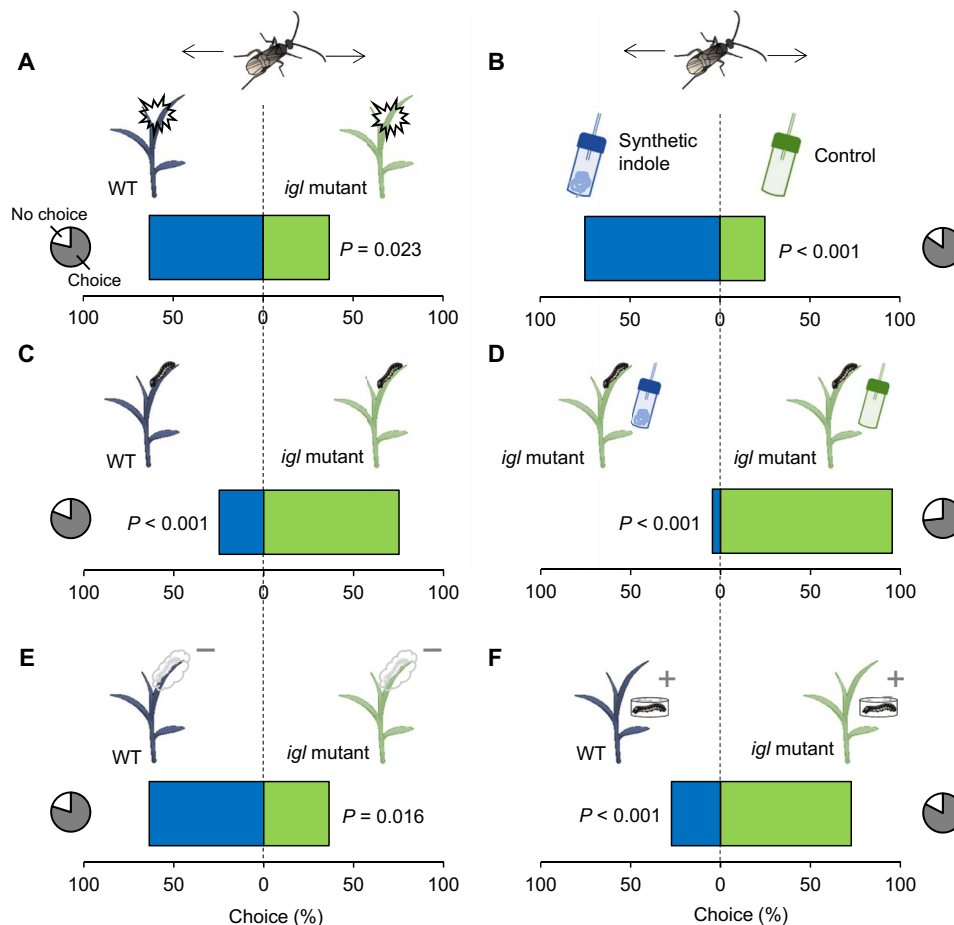


Fig. 1. Effect of indole on parasitoid attraction to plant-herbivore complexes. (A to F) Female *M. rufiventris* parasitoids were allowed to choose between odors from wild-type (WT) and indole-deficient *igl*-mutant plants that were induced by wounding and caterpillar (*S. littoralis*) oral secretions ($n = 6$) (A), synthetic indole dispensers (50 ng hour^{-1}) and empty dispensers (control; $n = 5$) (B), WT and *igl*-mutant plants that were infested by *S. littoralis* caterpillars ($n = 8$) (C), *S. littoralis*-infested *igl*-mutant plants and *S. littoralis*-infested *igl*-mutant plants supplemented with an indole dispenser ($n = 6$) (D), *S. littoralis*-induced WT plants and *S. littoralis*-induced *igl*-mutant plants with the larvae removed from the plants ($n = 8$) (E), and *S. littoralis*-induced WT plants and *S. littoralis*-induced *igl*-mutant plants with the larvae added back into the systems in small-mesh cages ($n = 8$) (F). Bars represent the percentages of parasitoids choosing either of the odor sources. Pie charts indicate the proportion of parasitoids that made a choice. False discovery rate (FDR)-corrected P values are given for treatment comparisons [generalized linear model (family, quasi-Poisson)], followed by least squares means (LSM) pairwise comparisons.

attractive to *M. rufiventris* ($P < 0.001$; Fig. 1B). Surprisingly, when actual *S. littoralis* caterpillars were feeding on the plants, this choice was reversed: Suddenly, *M. rufiventris* preferred *igl*-mutant plants over wild-type plants ($P < 0.001$; Fig. 1C). Similarly, more than 90% of wasps preferred *S. littoralis*-infested *igl*-mutant plants over infested *igl*-mutant plants supplemented with an indole dispenser ($P < 0.001$; Fig. 1D). On the basis of these results, we hypothesized that *M. rufiventris* may avoid volatiles from indole-exposed *S. littoralis* caterpillars, resulting in reduced attractiveness of herbivore-plant complexes. To test this hypothesis, we first let *S. littoralis* caterpillars feed on wild-type and *igl*-mutant plants. Then we removed the caterpillars and tested the attractiveness of the plants alone and of the plants to which the caterpillars were added back to the small-mesh cages. Without the caterpillars, induced wild-type plants were more attractive to *M. rufiventris* ($P = 0.016$; Fig. 1E). As soon as the caterpillars were added back to their respective plants, this preference was again reversed ($P < 0.001$; Fig. 1F). These results imply that *igl*-dependent changes in *S. littoralis* physiology reduce the attractiveness of plant-herbivore complexes to *M. rufiventris*.

Indole renders caterpillars less attractive by changing their body odor

To further explore the impact of indole on *S. littoralis* attractiveness, we conducted a series of additional olfactometer experiments. *S. littoralis* caterpillars that had been feeding on wild-type plants overnight were significantly less attractive for *M. rufiventris* than caterpillars from *igl*-mutant plants ($P < 0.031$; Fig. 2A). Pre-exposing caterpillars to synthetic indole yielded similar effects ($P < 0.001$; Fig. 2B). Moreover, volatiles released by pentane surface extracts of indole-exposed *S. littoralis* larvae were less attractive than those released by surface extracts of control caterpillars ($P = 0.002$; Fig. 2C). These results show that indole exposure directly decreases the attractiveness of *S. littoralis* larvae to *M. rufiventris* through changes in caterpillar body odors. To test whether caterpillars re-release indole from their body, we conducted a series of gas chromatography-mass spectrometry (GC-MS) volatile profiling experiments using (i) solid-phase microextraction (SPME) and (ii) direct injection of pentane extracts. No indole release from indole-exposed *S. littoralis* caterpillars was detected (fig. S1). To gain first insights into the change in body odor that is responsible for the differential

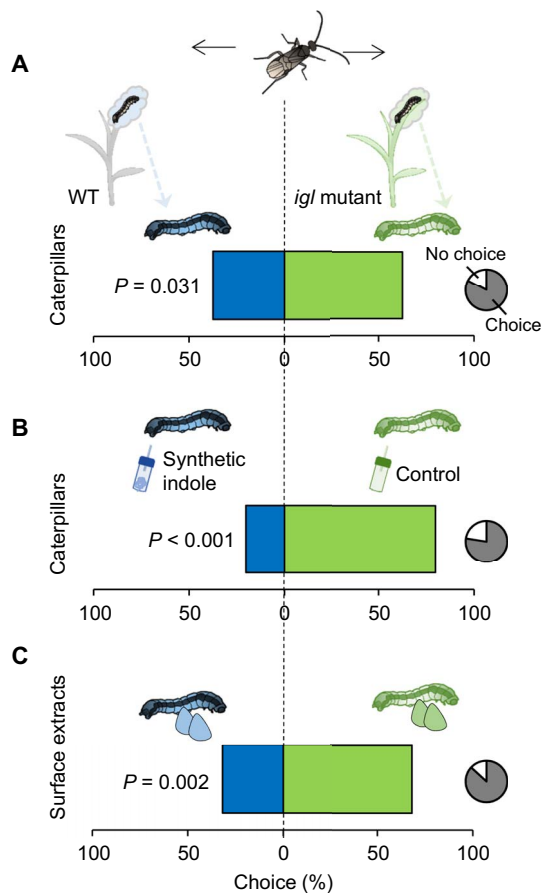


Fig. 2. Indole renders caterpillars unattractive to parasitoids. (A to C) Female *M. rufiventris* parasitoids were allowed to choose between odors from *S. littoralis* caterpillars that had been feeding on WT or indole-deficient *igl*-mutant plants ($n = 8$) (A), *S. littoralis* caterpillars that had been feeding on artificial diet in the presence of an indole-releasing dispenser (50 ng hour^{-1}) or control dispenser ($n = 5$) (B), and surface extracts of *S. littoralis* caterpillars that had been feeding on artificial diet in the presence of an indole-releasing or control dispenser ($n = 6$) (C). Bars represent the percentages of parasitoids choosing either of the odor sources. Pie charts indicate the proportion of parasitoids that made a choice or not. FDR-corrected P values are given for treatment comparisons [generalized linear model (family, quasi-Poisson)], followed by pairwise comparisons of LSM.

M. rufiventris attraction, we screened the chemical profiles of indole-exposed and control larvae for differences. The obtained chromatograms did not differ significantly (fig. S1), which suggests that volatiles outside of the detection range of our GC-MS system are responsible for the change in *M. rufiventris* behavior. Previous studies in maize have shown that major parasitoid attractants are likely to be present in very low concentrations and/or may be hard to detect by current MS techniques (37).

Indole increases caterpillar resistance against parasitoids

To determine whether indole exposure protects *S. littoralis* caterpillars against parasitism, we allowed *M. rufiventris* parasitoids to parasitize control or indole-exposed *S. littoralis* larvae, as well as larvae that fed on wild-type or *igl*-mutant plants. In the absence of *M. rufiventris*, the survival of *S. littoralis* larvae exposed to volatile indole was reduced by 10% ($P = 0.05$; Fig. 3A). Exposure to a parasitizing *M. rufiventris* female reduced the survival of *S. littoralis* larvae from 90% to less than 40%. This *M. rufiventris*-caused caterpillar mortality was significantly re-

duced by exposure to synthetic indole ($P < 0.001$; Fig. 3A) and by feeding on wild-type instead of *igl*-mutant plants ($P < 0.001$; Fig. 3B). In the presence of *M. rufiventris*, indole exposure increased the chance of larval survival from 40% to more than 60%. Conversely, *M. rufiventris* parasitoids were significantly more likely to develop on control larvae compared to indole-exposed larvae ($P = 0.007$; Fig. 3C) and on larvae feeding on *igl* mutants compared to those feeding on wild-type plants ($P < 0.001$; Fig. 3D). In no-choice experiments, *M. rufiventris* females attacked *S. littoralis* larvae with the same frequency, irrespective of the food source of the caterpillars ($P = 0.44$; Fig. 3E). Thus, indole exposure increases *S. littoralis* resistance toward *M. rufiventris* and reduces the reproductive success of *M. rufiventris*.

Parasitoid exposure suppresses the repellent effect of indole in caterpillars

S. littoralis caterpillars are repelled by indole (31). To determine whether the presence of parasitoid modulates this response, we performed choice tests with naïve and parasitoid-exposed caterpillars. Naïve caterpillars strongly avoided indole ($P < 0.001$; Fig. 4A). In contrast, caterpillars that had been in close proximity, but without physical contact with *M. rufiventris* females for 30 min, no longer avoided volatile indole ($P = 0.75$; Fig. 4B). To test whether this loss of indole aversion represents a specific response or a general loss of volatile-mediated choice behavior, we tested the response of *S. littoralis* larvae toward the attractive volatile 1-hexanol. *S. littoralis* caterpillars were attracted to 1-hexanol regardless of previous parasitoid exposure (fig. S2).

DISCUSSION

HIPVs have been extensively studied as tritrophic signals that attract natural enemies (7, 38). The present study reveals that certain HIPVs modulate tritrophic interactions indirectly via physiological changes in the herbivores. This finding adds a new dimension to the role of HIPVs as mediators of tritrophic interactions.

Our initial experiments seemed to show that indole follows the classical HIPV paradigm because it attracted *M. rufiventris* and increased the attractiveness of induced maize plants. However, surprisingly, the influence of indole on plant attractiveness was inverted as soon as *S. littoralis* caterpillars were present in the system. Reduced attractiveness of plant-herbivore complexes in the presence of indole by both naïve and experienced *M. rufiventris* females was also documented in a previous study within the same system (39). We devised two hypotheses to explain this choice pattern: First, we suspected that indole may suppress plant consumption by *S. littoralis* and thereby reduce HIPV emission and the attractiveness of the plant. However, this hypothesis was rejected because wild-type plants were more attractive than *igl*-mutants even after real *S. littoralis* attack as soon as the larvae were removed. As an alternative explanation, we hypothesized that indole may render the *S. littoralis* caterpillars unattractive. Indole exposure rendered the body odors of the caterpillars significantly less attractive, an effect that persisted even in the presence of more attractive host plants.

Natural enemies can be assumed to use foraging cues to maximize their own fitness (40–42). Many predators avoid toxic prey, including, for instance, herbivores that sequester plant secondary metabolites (41–43). Here, we show that HIPVs can also alter the quality of herbivores as hosts to parasitoids and thereby change reproductive success. Indole-exposed caterpillars were significantly more likely to survive parasitoid attack, and parasitoids were less likely to develop

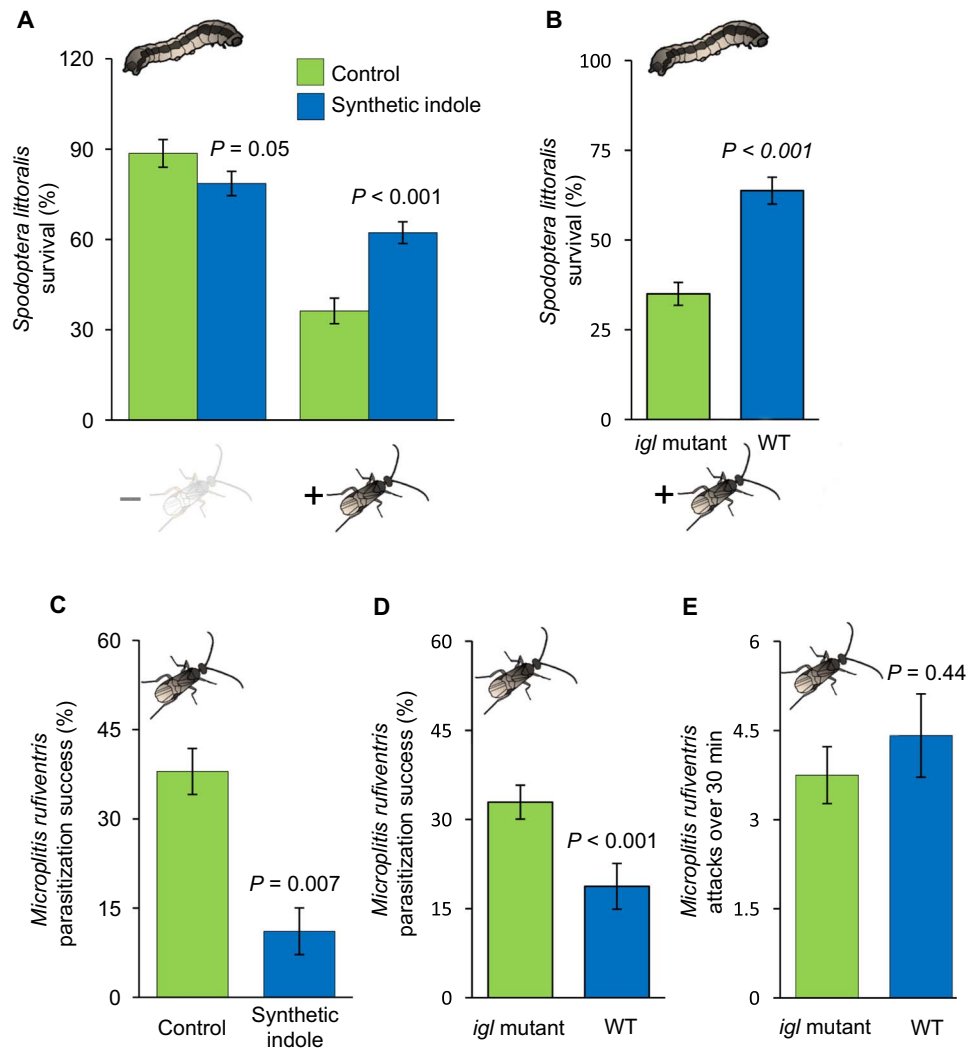


Fig. 3. Indole increases caterpillar resistance toward parasitoids. (A) Survival of *S. littoralis* larvae (\pm SE, $n = 7$) under control conditions (–) and after parasitism by *M. rufiventris* (+). Caterpillars were exposed to empty control dispensers (green bars) or indole-releasing dispensers (50 ng hour^{-1} ; blue bars). (B) Survival of *S. littoralis* larvae (\pm SE, $n = 12$) that fed on WT and indole-deficient *igl*-mutant plants after parasitism by *M. rufiventris*. (C) Number of *M. rufiventris* parasitoids (\pm SE, $n = 7$) developing successfully within *S. littoralis* caterpillars in the presence of indole or control dispensers. (D) Number of *M. rufiventris* parasitoids (\pm SE, $n = 12$) developing successfully within *S. littoralis* caterpillars that reared on WT and *igl*-mutant plants. (E) *M. rufiventris* attack rates (\pm SE, $n = 12$) of *S. littoralis* larvae that fed on WT or *igl*-mutant plants. *P* values are given for treatment comparisons (Student's *t* tests).

in indole-exposed hosts. Parasitoid attack rates were not different between caterpillars feeding on wild-type and *igl*-mutant plants, suggesting that the observed reduction in emerging parasitoids was due to lower parasitoid survival inside the indole-exposed caterpillars or due to reduced egg laying by the attacking parasitoid females. The lower parasitism success rate may explain why *M. rufiventris* avoids indole-exposed caterpillars and opens up the possibility that *M. rufiventris* specifically evolved the capacity to use differences in host body odors to locate the best-quality hosts.

S. littoralis survival was slightly reduced by indole exposure in the absence of *M. rufiventris* but significantly increased in its presence. This selective benefit of indole exposure was also mirrored by the behavior of the caterpillars: Although they avoided indole under normal conditions, they lost this aversion after perceiving the presence of *M. rufiventris*. In contrast, caterpillars that had detected the presence of parasitoids maintained a preference for 1-hexenol, demonstrating that the loss of

aversion upon parasitoid detection is not due to a general inhibition of volatile-mediated behavior. It is therefore conceivable that *S. littoralis* caterpillars allow for indole exposure in the presence of natural enemies to reduce the risk of parasitism and increase their resistance toward the latter. Self-medication through selective ingestion of plant secondary metabolites has been described repeatedly in vertebrates (43). Furthermore, *Grammia incorrupta* caterpillars increase the ingestion of pyrrolizidine alkaloids (PAs) when parasitized by tachinid flies at specific egg densities, and PA ingestion resulted in increased caterpillar survival (21). Similarly, *Arctia virginialis* caterpillars change their feeding preference from lupine to poison hemlock when parasitized by non-lethal tachinid flies, which results in increased caterpillar survival and possibly also increased fly performance (44). Our study shows that the mere perception of a lethal, solitary endoparasitoid is sufficient to trigger the loss of an aversion response in an invertebrate herbivore.

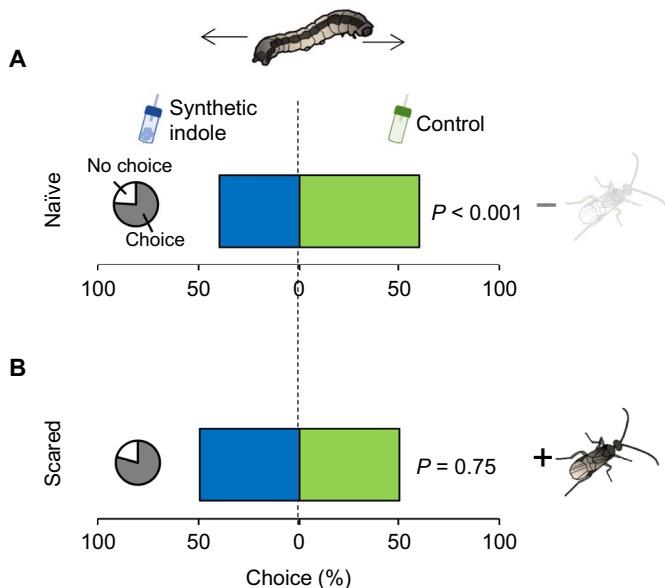


Fig. 4. Parasitoid exposure suppresses the repellent effect of indole toward caterpillars. *S. littoralis* larvae were allowed to choose between odors from synthetic indole dispensers (50 ng hour^{-1}) and empty dispensers (control). (A and B) Naïve caterpillars (A) and scared caterpillars that were in proximity to *M. rufiventris* females for 30 min without direct contact (B) were tested separately ($n > 4$). Bars represent the percentages of caterpillars choosing either of the odor sources. Pie charts indicate the proportion of parasitoids that made a choice or not. FDR-corrected P values are given for treatment comparisons [generalized linear model (family, Poisson)], followed by pairwise comparisons of LSM.

Since the initial discovery that HIPVs attract predators and parasitoids (45, 46), a wealth of studies has investigated this phenomenon in detail, also in the context of possible exploitation for pest control (47, 48). However, to what extent HIPV-mediated tritrophic interactions actually benefit plants is still subject to debate, and our findings introduce a new aspect to the discussion. Although evidence that certain HIPVs can improve plant performance by attracting natural enemies is emerging (9), a number of studies also highlight additional roles of HIPVs, which may modulate their net fitness effects for plants, including within-plant priming (49), direct herbivore intoxication (32), herbivore repellence (3, 12), herbivore attraction (4, 50), and hyper-parasitoid attraction (6). Our study reveals that certain HIPVs may modulate parasitism by affecting the attractiveness and quality of herbivores as host of parasitoids. More specifically, it is shown that the emission of indole interferes with the potential benefits that plants derive from HIPV-mediated tritrophic interactions because it reduces overall parasitoid attraction and host suitability. However, as previously demonstrated, indole production has advantages in the absence of natural enemies because it can act as a within-plant priming signal (31), toxin, and repellent for herbivores (32). Together, this leads to a paradoxical situation where the production of a HIPV is likely to be beneficial for the plant in the absence but not necessarily in the presence of natural enemies. Exploring whether high natural enemy abundance has led to the attenuation of these HIPVs in natural plant populations is an exciting prospect of this work.

This work shows that the HIPV indole modulates tritrophic interactions by changing the physiology and odor of caterpillars. Various HIPVs are known to have a negative impact on insect herbivores. For instance, volatile aldoximes and diterpenes affect larval performance

(11, 12). Green leaf volatiles not only have similar direct negative effects (51) but also serve as precursors of toxic glycosides (10). In addition, many volatiles can modulate herbivore behavior (4, 52–54). Thus, we expect HIPV modulation of tritrophic interactions via changes in caterpillar physiology and behavior to be widespread in nature. Further experiments should focus on understanding the physiological mechanism and the prevalence and impact of this phenomenon in the field. Herbivore-mediated effects of HIPVs should be taken into account to better understand the evolution and ecological complexity of tritrophic interactions in nature and to optimize the use of HIPVs in biological control.

MATERIALS AND METHODS

Plants and insects

Different mutant maize lines, including the *igl* mutants 22 (*igl.bx1*) and 32R (*igl.bx1*), which do not emit indole, and their respective wild-type lines 7 (*IGL.bx1*) and 16R (*IGL.bx1*) were obtained as previously described (33). For a detailed characterization of these genotypes, see the studies of Erb *et al.* (31) and Veyrat *et al.* (32). All maize lines were grown individually in plastic pots (10 cm high and 4 cm in diameter) with commercial potting soil (Aussaaterde, Ricoter) and placed in a climate chamber ($23^\circ \pm 2^\circ\text{C}$, 60% relative humidity, 16:8-hour light/dark cycle, $50,000 \text{ lm/m}^2$). Maize plants were 10 to 12 days old and had three fully developed leaves. The evening before the experiments, plants were transferred and kept under laboratory conditions with supplemented light ($25^\circ \pm 2^\circ\text{C}$, $40 \pm 10\%$ relative humidity, 16:8-hour light/dark cycle, and 8000 lm/m^2). *S. littoralis* (Boisduval; Lepidoptera: Noctuidae) caterpillars were reared from eggs provided by Syngenta. The eggs were kept in an incubator at $30.0^\circ \pm 0.5^\circ\text{C}$ until emergence. Subsequently, the larvae were transferred on artificial diet at room temperature ($24^\circ \pm 4^\circ\text{C}$). All experiments were conducted with second-instar larvae. Adult *M. rufiventris* (Kokujev; Hymenoptera: Braconidae) were reared as previously described (55). Twenty-five *S. littoralis* larvae were kept in a plastic box with two mated females for 24 hours. The parasitized caterpillars were reared at room temperature until cocoon formation. Cocoons were kept in petri dishes in an incubator at 30°C until adult emergence. Emerging adults were kept in cages at a sex ratio of 1:2 (male/female) and placed in an incubator (25°C , 16:8-hour light/dark cycle). The cages were provided with moist cotton wool and honey as a food source. For all bioassays, 2- to 3-day-old naïve females were used. Cages were transferred to the laboratory 30 min before the experiments.

Parasitoid attraction experiments

To test the effect of indole on *M. rufiventris* and *S. littoralis* behavior, we used a four-arm olfactometer, as previously described (56). The olfactometer consisted of a central glass choice arena [6 cm in internal diameter (ID) and 5 cm in length] with four arms (15 mm in ID, 5 cm in length), each with a glass elbow (5 cm in length) and an upward connection for a glass bulb (50 ml). Purified and humidified air entered each odor source vessel at 0.6 liter/min (adjusted by a manifold with four flow meters; Analytical Research System) via Teflon tubing and carried the volatile organic compounds through the connector tube to the elbows of the olfactometer. Ten neon tubes were attached to a metal frame above the olfactometer and provided approximately 7000 lm/m^2 at the height of the odor source vessels. To avoid visual distraction of the parasitoid wasps, a white curtain was placed around the olfactometer. Two opposite bottles contained an odor source, and the other two bottles remained empty. The positions of the odor sources

were randomly chosen for different replications of the experiments. The system was left connected for half an hour before releasing wasps in the center of the choice arena. The wasps that were released in groups of six and entered in an arm reached the elbow, where a stainless steel screen blocked their path. They walked up in the direction of the light source above the olfactometer and into a trapping bulb, where they were counted and removed. The wasps that did not make the choice after 30 min were considered as having made “no choice,” and at this time, all wasps were removed from the olfactometer. Three such releases were performed for each replicate and pooled for analysis. Using this system, we first tested the influence of indole on parasitoid attraction using indole-deficient mutant plants. Indole-deficient and wild-type plants were induced through wounding and the application of *S. littoralis* regurgitant, and parasitoids were given a choice between the two genotypes ($n = 6$). Elicitation treatments were performed as previously described (57): by scratching two leaves over an area of approximately 1 cm² on both sides of the central vein with anatomical forceps (stainless steel, 14.5 cm). Ten microliters of *S. littoralis* regurgitant was applied over the scratched leaf areas. Regurgitant was previously collected from fourth-instar *S. littoralis* that fed on maize leaves for 24 hours and was stored at -80°C until use. Second, we tested the effect of indole alone by giving the parasitoids a choice between empty control arms and indole-releasing dispensers ($n = 5$). The dispensers were built from 2-ml amber glass vials (11.6 × 32 mm; Sigma-Aldrich) containing 20 mg of synthetic indole (GC, >98%; Sigma-Aldrich). The vials were sealed with a polytetrafluoroethylene/rubber septum (Sigma-Aldrich) and pierced with a 2- μl micropipette (Drummond). The length of the pipette was calibrated to release a controlled amount of indole corresponding to typical indole release rates of infested maize plants (50 ng hour⁻¹) following a described procedure (56). Third, parasitoids were given a choice between *S. littoralis*-infested wild-type and indole-mutant plants ($n = 8$). To infest maize plants, 15 second-instar *S. littoralis* larvae were placed on the plants and left feeding for 12 hours. Fourth, parasitoids were given a choice between *S. littoralis*-infested mutant plants with or without an indole-releasing dispenser added to the system for 12 hours before the experiment ($n = 6$).

Using the same olfactometer setup, several additional experiments were conducted to test whether *M. rufiventris* are repelled by volatiles from indole-exposed *S. littoralis* larvae. First, 15 second-instar *S. littoralis* caterpillars were left to feed on wild-type and *igl*-mutant plants for 12 hours. The larvae were removed from the infested plants, and the attractiveness of *M. rufiventris* to the infested plants was assessed ($n = 8$). The caterpillars were then placed in plastic cages (5 cm in diameter and 2 cm in height) covered with nylon mesh and added back to the systems together with the plants ($n = 8$). Finally, these caterpillars were tested for attractiveness in the absence of the plants ($n = 8$).

To investigate the direct impact of indole on *S. littoralis* attractiveness, groups of 15 *S. littoralis* larvae feeding on artificial diet were exposed to empty or indole-releasing dispensers for 12 hours. The larvae were then transferred to the olfactometer, and *M. rufiventris* choice for indole-exposed and control larvae was assessed ($n = 5$). Finally, the surface extracts from indole-exposed and control-treated larvae were placed on a filter paper and tested in the olfactometer for attractiveness to *M. rufiventris* ($n = 6$). To obtain these surface extracts, caterpillars were exposed to empty or indole-releasing dispensers for 24 hours and then frozen at -20°C . The larval cadavers were extracted with 150 μl of pentane for 30 min, and the supernatant was collected. Aliquots (2 μl) of the extracts were placed on filter paper disks (1/2 disk, 50 mm in

diameter; Nr. LS 14, Schleicher and Schuell) and introduced into the olfactometer.

Herbivore and parasitoid survival

To investigate the effect of indole on the survival of *S. littoralis* and *M. rufiventris*, 20 *S. littoralis* larvae were kept in nonhermetic plastic boxes (8 cm in diameter and 5 cm in height) and exposed to one mated parasitoid female for 24 hours. Second-instar *S. littoralis* larvae were used for the parasitism by *M. rufiventris*. Before exposing them to the parasitoids, *S. littoralis* larvae were exposed to control or indole dispensers, as described above, for 24 hours. After parasitism, larvae were again subjected to the same treatment until parasitoid emergence. As control treatment, *S. littoralis* larvae were exposed to control or indole dispensers without parasitism ($n = 7$). Each day, the number of dead *S. littoralis* larvae was recorded. Characteristic growth depression of *S. littoralis* larvae was recorded as a sign of successful parasitoid development, and the number of emerging parasitoid cocoons was counted at the end of the experiment.

A similar setup was used to test the impact of wild-type and *igl*-mutant plants on herbivore and parasitoid survival. Second-instar larvae were reared on 10-day-old wild-type and *igl*-mutant plants for 24 hours. Twenty *S. littoralis* larvae were then put in nonhermetic plastic boxes (8 cm in diameter and 5 cm in height) and exposed to one mated parasitoid female for 24 hours ($n = 12$). *M. rufiventris* attack rates were monitored for the first 30 min. One attack corresponds to an *M. rufiventris* female inserting its ovipositor into the host larva. If no attack was observed within the first 5 min after exposure, then the parasitoids were replaced. The larvae were then put back on the respective plant genotypes until parasitoid emergence. The number of dead *S. littoralis* larvae was recorded, and the number of emerging parasitoid cocoons was counted at the end of the experiment.

Herbivore choice experiments

To determine whether parasitoid exposure modulates the response of *S. littoralis* caterpillars to indole, we performed choice tests in which naïve and parasitoid-exposed caterpillars were released in a modified four-arm olfactometer, as previously described (31). The olfactometer consisted of a central glass choice arena with four arms and an upward connection for a glass bulb, as described above. The choice arena was connected to four glass bottles. Volatile dispensers releasing the test odor (indole or 1-hexenol) were placed in one arm, and an empty dispenser was placed in another arm. The two remaining arms were left empty. The position of the odor sources was changed between each experimental assay. The system was left connected for half an hour before releasing caterpillars in the center of the choice arena. The larvae would crawl out of the chamber and enter one of the four arms. After 30 min, larval numbers in each arm were counted, and the larvae that did not make the choice were considered as having made no choice.

We tested caterpillars of two treatment types: “scared” and “naïve” caterpillars. To obtain scared caterpillars, groups of 30 second-instar larvae were placed in small cages (5 cm in diameter and 2 cm in height) covered with a nylon mesh and put into a nonhermetic plastic box (8 cm in diameter and 5 cm in height) with 10 parasitoid females, so the larvae were in close proximity to the parasitoid but without direct contact. Thirty minutes later, the larvae were taken out of the box and released into the choice arena immediately. Naïve caterpillars that did not experience the presence of parasitoids were tested in the

same olfactometer setup. Three such releases were performed for each replicate and pooled for analysis. Using this system, we first tested the response of naïve *S. littoralis* larvae to pure indole by giving the larvae a choice between indole-releasing dispensers and empty arms ($n = 6$). Second, we replaced the naïve larvae with the parasitoid-exposed caterpillars to do the same bioassay as above ($n = 4$). Using the same experimental procedure, we investigated the caterpillar responses to the attractant 1-hexanol ($n = 6$).

Volatile collection and analysis

To identify the indole-dependent changes in *S. littoralis* body odors, we first analyzed the volatiles from caterpillars using SPME coupled with GC-MS. Fifteen naïve or indole-exposed second-instar larvae were put into a 10-ml sealed glass vial, and a stainless steel screen kept them blocked on the bottom of the vial. An SPME fiber (100- μ m polydimethylsiloxane coating; Supelco) was exposed to the vial headspace for 60 min at room temperature without agitation and then introduced into the injector inlet for 2 min at 250°C in splitless mode. The compounds adsorbed on the fiber were then analyzed by GC-MS (Agilent 7820A GC interfaced with an Agilent 5977E MSD, Palo Alto), as previously described (57), with a few modifications. After fiber insertion, the column temperature was maintained at 60°C for 1 min and then increased to 250°C at 5°C min⁻¹, followed by a final stage of 4 min at 250°C. The resulting GC-MS chromatograms were processed with Progenesis Q1 (Nonlinear Dynamics) using a resolution of 200 full width at half maximum and default settings for spectral alignment and peak picking. Furthermore, chromatograms were inspected manually for differential peaks. We also analyzed the larval body odors by directly injecting 1 μ l of aliquot of indole-exposed or control-treated caterpillars' surface extracts (as described above) into the GC-MS system ($n = 6$). Two modified methods were processed to separate and identify the high- and low-boiling larval surface volatiles within these extracts (57, 58): (i) The oven temperature was maintained at 150°C for 2 min after injection and then increased to 320°C at 5°C min⁻¹, followed by a postrun of 3 min at 325°C; and (ii) the oven temperature was maintained at 40°C for 1 min and then increased to 250°C at 6°C min⁻¹, followed by a postrun of 3 min at 250°C. Data analysis was carried out as described above.

Statistical analysis

The functional relationship between parasitoid and larval behavioral responses and the different odor sources offered in the four-arm olfactometer was analyzed with a generalized linear model (a log linear model) with the software package R (version 3.3.1). To compensate for the overdispersion of wasps within the olfactometer, we based the models on a quasi-Poisson distribution, followed by pairwise comparisons of LSM. *P* values were corrected using the FDR method. For a detailed description, see the study of Turlings *et al.* (55). Results from the two *igl* mutants and the two wild-type lines were pooled for analysis. Differences in mortality, growth depression, and parasitism success between control and indole treatments were analyzed for significance using Student's *t* tests.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/5/eaar4767/DC1>

fig. S1. Indole is not re-released from exposed caterpillars.

fig. S2. Parasitoid exposure does not influence caterpillar attraction to 1-hexanol.

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An herbivore-induced plant volatile reduces parasitoid attraction by changing the smell of caterpillars

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