

How caterpillar-damaged plants protect themselves by attracting parasitic wasps

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ABSTRACT Parasitic and predatory arthropods often prevent plants from being severely damaged by killing herbivores as they feed on the plants. Recent studies show that a variety of plants, when injured by herbivores, emit chemical signals that guide natural enemies to the herbivores. It is unlikely that herbivore-damaged plants initiate the production of chemicals solely to attract parasitoids and predators. The signaling role probably evolved secondarily from plant responses that produce toxins and deterrents against herbivores and antibiotics against pathogens. To effectively function as signals for natural enemies, the emitted volatiles should be clearly distinguishable from background odors, specific for prey or host species that feed on the plant, and emitted at times when the natural enemies forage. Our studies on the phenomena of herbivore-induced emissions of volatiles in corn and cotton plants and studies conducted by others indicate that (i) the clarity of the volatile signals is high, as they are unique for herbivore damage, produced in relatively large amounts, and easily distinguishable from background odors; (ii) specificity is limited when different herbivores feed on the same plant species but high as far as odors emitted by different plant species and genotypes are concerned; (iii) the signals are timed so that they are mainly released during the daytime, when natural enemies tend to forage, and they wane slowly after herbivory stops.

Plants show some astonishing adaptations that promote the presence of predators and parasitoids. The finest examples must be the special structures grown by plants such as acacias and cecropias that result in mutualistic interactions with ants. In these interactions the plants offer the ants food in the form of food bodies and extrafloral nectaries and shelter in hollow stems and thorns (1). The main benefit that the ants seem to offer the plants in return is protection against herbivores. When we consider these extreme plant adaptations, perhaps, we should not be too surprised to find that, as some have predicted (2, 3), plants may also actively guide predators and parasitoids to herbivores. Such plant strategies are not so obvious and, therefore, have not yet received much attention. Recently, however, studies have revealed that plants that are under attack by herbivores initiate the release of chemical "signals" that natural enemies of the herbivores use to locate their victims.

Dicke and coworkers (4–6) have shown that plants that are infested by spider mites emit volatiles that are attractive to predatory mites but are not emitted when the plants are subjected to artificial damage. A similar interaction was found when we studied (7) the host location behavior of parasitoids of

lepidopterous caterpillars and observed that parasitoids oriented toward odorous cues emitted by caterpillar-damaged plants. In corn seedlings, the emission of several highly attractive terpenoids only occurs several hours after caterpillars start damaging the plants. The response is systemic, as undamaged leaves of injured plants also emit the terpenoids (8). Mere artificial damage does not induce the response in corn, but when caterpillar regurgitate is applied to such artificially damaged sites, corn seedlings emit volatiles in amounts comparable to caterpillar-damaged plants (7). After studying several plant species, it now appears that herbivore-induced emission of parasitoid and predator attractants is a common phenomenon.

The fact that predators and parasitoids effectively exploit the chemical signals provided by the plants has been the basis for the hypothesis that plants may actively recruit these natural enemies of herbivores (4, 7, 9, 10). In other words, it has been suggested that a form of communication between plants and the third trophic level has evolved. The evidence presented here supports the hypothesis of signaling between plant and insect. We propose that such interactions evolved from more direct plant defense strategies. Plants primarily combat herbivory with the production of several defensive chemicals that directly affect herbivores and pathogens. Volatiles that are emitted when such chemicals are mobilized may have been secondarily exploited by natural enemies of herbivores. Over evolutionary time, plants will have adapted their defensive responses to enhance the signaling function of the volatiles, which has resulted in the observed communication between plant and insect. Three aspects of the plant signals seem most relevant to the on-going discussion on whether or not herbivore-damaged plants actively lure natural enemies. (i) The signal should be clear enough to the insects so that it can be perceived and distinguished from background noise. (ii) The signal has to be specific enough to reliably indicate the presence of a suitable host or prey. (iii) The signal will have to be emitted during the period of time that the natural enemies forage. To address these aspects of clarity, specificity, and

Abbreviation: LOX product, lipoxygenase-derived volatile product.
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timing of the signals, we selectively review and compare the data that we have obtained from our studies on tritrophic level interactions involving corn and cotton plants.

Clarity of the Signal

For the emitted volatiles to function as useful signals to parasitoids, they should be detectable to the insects and distinguishable from background odors. We refer to a combination of these criteria as the clarity of the signal.

We first discovered (7) that plants emit a strong odor when under attack by caterpillars when we studied the host-searching behavior of the braconid larval parasitoid *Cotesia marginiventris*. Rather than responding to odor cues coming directly from their hosts, females of *C. marginiventris* are strongly attracted to volatiles emitted by the caterpillar-damaged plants (7, 11). Research focused on identifying the chemicals emitted by damaged corn plants and studying the dynamics of emission. A very striking difference was found between corn seedlings that were only under recent herbivore attack and seedlings that had been fed on for >6 h (Fig. 1). Fresh feeding damage results in a significant release of (*Z*)-3-hexenal, (*E*)-2-hexenal, (*Z*)-3-hexenol, (*E*)-2-hexenol, and (*Z*)-3-hexenyl acetate. These lipoxygenase-derived volatiles (LOX products) (12), also known as "green leaf volatiles," are the only compounds detected at this stage. After several hours, however, emission of large amounts of terpenoids [linalool, (3*E*)-4,8-dimethyl-1,3,7-nonatriene, α -*trans*-bergamotene, (*E*)- β -farnesene, (*E*)-nerolidol, and (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene] and indole were observed (Fig. 1). It

was found that this emission of specific chemicals could not be induced by mechanical damage alone. Plants that had been fed upon by caterpillars for 2 h released far more of these terpenoids on the following day than plants that had been damaged with razor blades during the same 2 h. However, when caterpillar regurgitate was directly applied to sites that had been freshly damaged with a razor blade, the plants released terpenoids in amounts equal to those released by caterpillar-damaged plants (7).

The volatile emissions of cotton plants differ from corn plants in that several terpenoids are emitted immediately at the start of caterpillar feeding (Fig. 2). These terpenoids (e.g., α -pinene and β -caryophyllene) are apparently stored in glands located in the cotton leaves. The stored compounds may serve as toxins to directly discourage herbivores from feeding on the cotton leaves. Besides these stored terpenoids, the cotton plants were found to emit several other terpenoids [e.g., (*E*)- β -ocimene and (*E*)- β -farnesene] in a delayed response to caterpillar feeding (13, 14).

The chemicals emitted by the plants upon herbivory should easily be detected by insects and thus could serve as very clear signals to parasitoids and predators. One corn seedling can emit several micrograms of a particular substance per hour. This is a much greater amount than normally seen in insect pheromone communication, where a few nanograms of sex pheromone per hour can be detected in the field by receptive individuals searching for a partner (15, 16).

The signal is further enhanced by the fact that the chemical emissions are not limited to the damaged sites. For corn seedlings, all of the induced compounds are released throughout injured plants; even unharmed leaves of damaged plants showed a significant increase in the release of terpenoids (8, 17). The systemic plant response can also be induced by merely placing seedlings with their severed stems in water-diluted caterpillar regurgitate (18). Incubation of seedlings in diluted regurgitate for a number of hours induces a dramatic increase in terpenoid emissions. As a result, the seedlings become very attractive to parasitoids. Seedlings that have been placed in water for the same period remain virtually odorless. The systemic nature of the plant response is not unique for corn; lima bean shows a systemic spider mite-induced emission of volatiles that are attractive to predatory mites (6, 19), and unharmed leaves of mealybug-infested cassava plants become attractive to a parasitoid of the mealybug (20). In cotton plants, the systemic response is much more delayed; it can take several days of caterpillar feeding before induced volatiles are detected from undamaged leaves (U.S.R.R., unpublished data).

We conclude that the chemicals emitted by the plants in response to herbivory are easy to detect by insects and are clearly distinguishable from the extremely low levels of odors emitted by unharmed plants. Moreover, the blend of induced terpenoids emitted by herbivore-damaged plants is quite different from the odors emitted by unharmed or mechanically damaged plants. Unlike the LOX products and constitutive terpenoids that may be released by mechanical damage, the induced substances represent a signal that is dependably associated with the presence of herbivores. The signal is enhanced by the systemic nature of the plant response and makes the whole plant stand out as an odorous beacon that should be easily distinguishable from the surrounding plants. In short, herbivore-injured plants provide foraging natural enemies with a very clear odorous signal that indicates the presence of potential hosts or prey.

Specificity of the Signal

A clear signal does not necessarily mean that plants provide parasitoids and predators with a reliable signal (21, 22). For signals to be optimally useful for parasitoids, they should indicate the presence of a suitable host and, under ideal

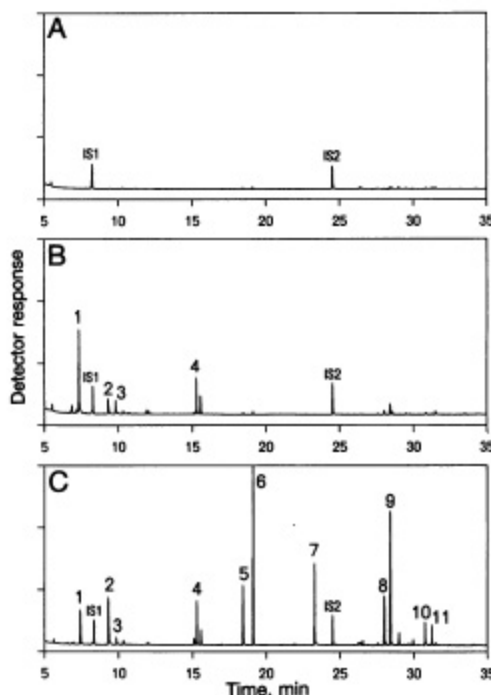


FIG. 1. Chromatographic profiles of volatiles emitted by healthy corn seedlings (undamaged) (A), by corn seedlings just after caterpillars start feeding on them (first hour of damage) (B), and several hours after feeding starts (sixth hour of damage) (C). Peaks: 1, (*Z*)-3-hexenal; 2, (*E*)-2-hexenal; 3, (*Z*)-3-hexenol; 4, (*Z*)-3-hexenyl acetate; 5, linalool; 6, (3*E*)-4,8-dimethyl-1,3,7-nonatriene; 7, indole; 8, α -*trans*-bergamotene; 9, (*E*)- β -farnesene; 10, (*E*)-nerolidol; and 11, (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. Added reference compounds were *n*-octane (IS1) and nonyl acetate (IS2).

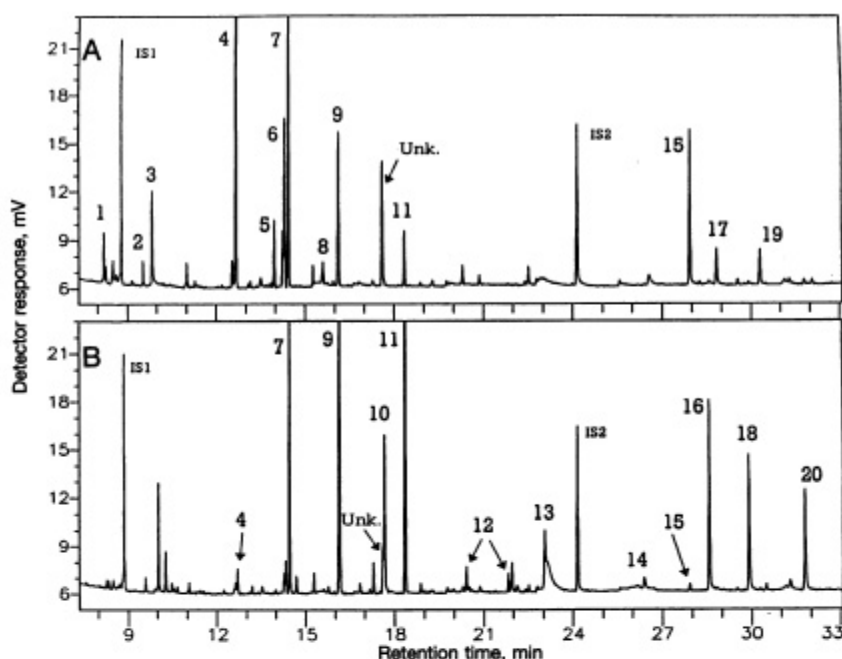


FIG. 2. Chromatographic profiles of volatiles emitted by cotton plants on the first day of caterpillar feeding (A) and third day of caterpillar feeding (B). Peaks: 1, (*Z*)-3-hexenal; 2, (*E*)-2-hexenal; 3, (*Z*)-3-hexenol; 4, α -pinene; 5, β -pinene; 6, myrcene; 7, (*Z*)-3-hexen-1-yl acetate; 8, limonene; 9, (*E*)- β -ocimene; 10, linalool; 11, (3*E*)-4,8-dimethyl-1,3,7-nonatriene; 12, isomeric hexenyl butyrates; 13, indole; 14, (*Z*)-jasmonone; 15, caryophyllene; 16, (*E*)- β -farnesene; 17, α -humulene; 18, (*E,E*)- α -farnesene; 19, γ -bisabolene; 20, (3*E,7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. Added reference compounds were *n*-octane (IS1) and nonyl acetate (IS2). Unk., unknown.

circumstances, be distinguishable from odors that are associated with nonhosts.

Evidence for herbivore-specific signals is limited. Variation in emitted odors was found in apple cultivars in response to spider mite infestation (23). The apple leaves showed mainly quantitative differences in emissions of several compounds when leaves infested by the two-spotted spider mite *Tetranychus urticae* and the red spider mite *Panonychus ulmi* were compared. Predatory mites are able to distinguish between the different odors (24).

In corn and cotton, differences were mainly observed in the emissions of the noninduced releases of the LOX products. These volatiles, (*Z*)-3-hexen-1-ol, (*E*)-2-hexen-1-ol, (*Z*)-3-hexen-1-ol, and (*Z*)-3-hexen-1-yl acetate, are released immediately when the plants are damaged (Figs. 1 and 2). The observed differences in emissions of LOX products (U.S.R.R., unpublished data) may occur because of variations in feeding patterns exhibited by different caterpillar species. No significant quantitative or qualitative differences were measured in the induced compounds emitted by corn. Despite this, the parasitoids do show some ability to learn to distinguish between odors from different caterpillar species feeding on the same plant variety. Thus, *C. marginiventris* was found to distinguish between *Spodoptera exigua* and *Spodoptera frugiperda* on corn (25). These two closely related noctuids happen to show a very significant ratio difference in the emitted LOX products.

Generally, specificity of induced compounds seems to be limited when different herbivores damage the same plant variety. However, significant quantitative differences can be found in volatiles emitted by different genotypes of the same plant species (refs. 23 and 24 and unpublished data). Clear qualitative differences can be observed in volatiles emitted by different plant species upon herbivore-inflicted injury (25). Still, several compounds, particularly (3*E*)-4,8-dimethyl-1,3,7-

nonatriene and (3*E,7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene and to a lesser degree linalool, ocimenes, farnesenes, etc., are induced in many plant species as a result of herbivore damage (25, 26).

The nature of the signals is obviously under the control of the plants. If, as we suspect, the plant-produced chemicals are targeting the herbivores and/or pathogens, then possible variations in chemicals that the plants produce may mainly result from different defense strategies that the plants may employ against different adversaries. Perhaps the plants do not need to release highly specific signals that differ when different herbivores attack it. The plants do not necessarily suffer when natural enemies make "mistakes" and are attracted to signals that are induced by herbivores they cannot attack. As long as the "right" natural enemies are attracted as well, the signal has served its purpose for the plant. It seems therefore up to the natural enemies to deal with some of the unreliable aspects of the signals (21, 22, 27). Parasitoids also use other signals such as close-range contact chemicals and visual (22) and vibrational (28) cues. The parasitoids will use these in combination with the volatile chemicals to discriminate among suitable and unsuitable hosts and host sites.

Timing of the Signals

It seems that signals would be best emitted as soon as, or at least shortly after, a herbivore starts damaging a plant. Moreover, the volatiles should be most effective if they are emitted during the time of day when natural enemies are most likely to forage. To establish whether the timing of volatile release is in tune with the parasitoids' needs, we designed several experiments to monitor odor emissions by corn and cotton plants over a longer period of time. For this, we used a system that allows nondestructive collection of volatiles from growing plants (29). With this system, volatiles can be sampled at

periodic intervals throughout one or more photoperiods. Thus, we monitored the volatiles released by corn and cotton plants at 2- and 3-h intervals, respectively, for up to 3 days.

In Figs. 3 and 4, we have plotted the emissions of several compounds that are representative of the total blend. They can be categorized in three groups. The LOX products are released instantaneously upon damaging the plants and their release rapidly wanes after damage ceases (Fig. 3A). Cotton plants, unlike corn plants, also release several terpenoids as soon as damage occurs (Fig. 4B). As with the LOX compounds, the release of these terpenoids drops as soon as damage is stopped (i.e., when caterpillars are removed) (14). The source of these "constitutive" compounds is probably glands in the leaves that are ruptured when the caterpillars chew on them. Under continuous damage, the release of these compounds fluctuates only slightly and slowly wanes as, perhaps, their quantities dwindle or the caterpillars feed less vigorously (Fig. 4B). As was shown above, the release of many of the terpenoids occurs only several hours after the damage starts. In the case of corn, the plants were only damaged and treated with regurgitate once. The result was a delayed, but dramatic increase in terpenoid emissions during daytime hours that was still detected on the third day after initial damage (Fig. 3B). In the experiment with cotton, caterpillars were placed on the plant on the first day and left there throughout the collection period. While, as in corn, the release of the induced compounds drops significantly at night (Fig. 4C), the release of the "constitutive" compounds does not (Fig. 4B).

Although there is some delay, the plants seem to respond quickly enough for parasitoids and predators to effectively exploit the volatile signals. Moreover, the plants give off the strongest signals during the photoperiod, when natural enemies tend to forage (30, 31). We do not wish to suggest that the plants have adapted their responses solely to be tuned in to the active periods of parasitoids and predators. It is more likely that one of the reasons natural enemies forage mostly during the day is because that is when most chemical (and also visual) cues are available to them. It is possible that the plant's diurnal metabolism allows for volatile emissions only during the day. On the other hand, the biology of night-blooming plants

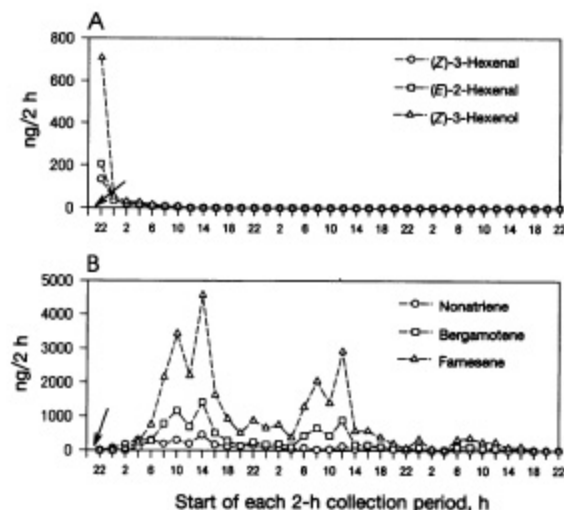


FIG. 3. Selected compounds emitted by corn seedlings over the course of several days. Two corn seedlings were damaged by scratching the surface of their leaves and treating the damaged sites with caterpillar regurgitate at 21:45 h of the first day (arrows). The volatile emissions were then measured every 2 h over a 3-day period. (A) LOX products from corn. (B) Induced compounds from corn.

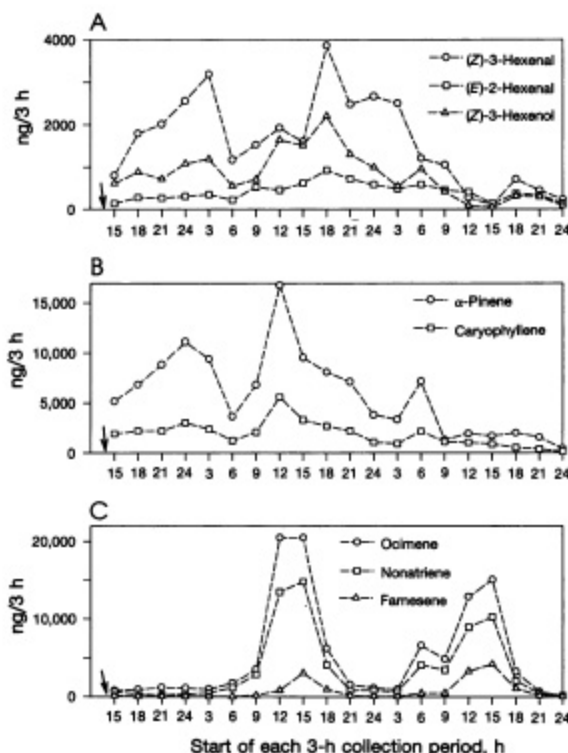


FIG. 4. Selected compounds emitted by cotton plants over the course of several days. Five *S. exigua* caterpillars were placed on a 1.5-month-old cotton plant at 14:00 h of the first day (arrows). The volatile emissions were then measured every 3 h over a 2.5-day period (16). (A) LOX products from cotton. (B) Constitutive compounds from cotton. (C) Induced compounds from cotton.

suggests that there is no physiological constraint on when volatiles could be emitted (32).

Discussion

As herbivores have adapted to be inconspicuous to their natural enemies, it can be expected that they emit very little in terms of odors that can be detected by foraging parasitoids and predators (27, 33). On the other hand, plants that are under attack by herbivores benefit from the presence of the natural enemies because it may lead to the elimination of the herbivores. Plants may therefore have developed means, such as chemical signals, to reveal the presence of the herbivores.

From our own (7, 11, 13, 14, 18) and other (4-6, 20, 23) studies, we conclude that plants have the ability to respond to herbivore attack by emitting blends of volatiles that are detected and exploited by parasitoids for host location. By collecting and monitoring these odors, it was found that the volatile blends are specific for plant species, emitted in relatively large amounts, and easily distinguishable from background odors. The emission of the odors is timed well; odors are emitted within several hours after the herbivores start damaging the plants, and odors are mainly produced during daytime, when most parasitoids forage.

The plant response appears specific for herbivore damage and cannot be induced with mere mechanical damage. Specificity of the induction by different herbivore species is, however, very limited. Insect oral secretions play a major role in the induction. We tested the oral secretions of five caterpillar species and one grasshopper, and all induce a similar response in corn. There are some quantitative differences, but

in all cases the same blend of volatiles is emitted in very similar ratios by corn seedlings of a particular variety (18). However, differences are observed in the amounts and ratios of LOX compounds that are released when different caterpillars feed on the same plant variety.

Distinct qualitative differences do occur between the odors emitted by different plant species (compare Figs. 1 and 2) and to a much lesser extent between varieties of the same plant species (unpublished data). Female parasitic wasps seem to respond to these odors accordingly; they can distinguish between odors from different plants but are not always able to distinguish between different herbivores on the same plant. The specialist parasitoid *Microplitis croceipes* was not readily able to distinguish odors emitted by plants attacked by hosts from odors emitted by plants under attack by nonhosts (34). Moreover, *M. croceipes* and the generalist *C. marginiventris* were at least as much attracted to plants treated with caterpillar regurgitate as to plants treated with grasshopper regurgitate (18). These wasps are more capable of distinguishing between odors from different plant species but need to have had experience with hosts on a particular plant to prefer the plant's odors (25, 34).

Learning of the odors that are associated with hosts is an extremely important aspect of the host-searching behavior of parasitoids (25, 35, 36). This ability is also what may help the wasps detect subtle differences between cues associated with suitable hosts and other nonprofitable cues. Sometimes these differences may only be learned after several experiences (34, 37). Variation in odor blends that allows the wasps to smell the differences between hosts and nonhosts on plants may be caused by the ratio differences in green leafy compounds, rather than differences in the induced compounds.

The evidence presented here strongly supports the view that herbivore-induced emissions of volatiles serve to attract natural enemies of the herbivores. Two of the aspects of the signals, clarity and timing, seem to be perfectly attuned with the parasitoids' biology. As discussed above, the nonspecific nature of many of the signals can be explained from the plant's perspective; as long as the correct natural enemies are attracted, the plants do not suffer if other parasitoids and predators "mistakenly" trace the odors as well. Still, we want to emphasize that it is unlikely that the induced production of the volatiles, mainly terpenoids, has evolved solely under the selective pressures of the plant-parasitoid or plant-predator interactions. It seems far more likely that the more direct interaction between plant and its attackers formed the basis of an induced resistance by the plant. The production of terpenoids has mainly been associated with plants that are challenged by microorganisms (38). Phytopathologists term these chemicals, which have antimicrobial properties, "phytoalexins." For a plant attacked by herbivores, it may also be prudent to mobilize antibiotics to protect vulnerable herbivore-inflicted wounds. The plant-produced compounds could also be targeting the herbivores directly. In fact, some of the terpenoids emitted by corn and cotton (i.e., nerolidol and caryophyllene) have been shown to negatively affect the development of herbivores and can even kill them (39, 40). We suspect that the less direct defense strategy of attracting natural enemies has evolved from the direct defenses that the plants employ against their attackers. This may involve the same chemicals that, therefore, serve multiple functions or precursors and degradation products of chemicals that serve as toxins and antibiotics.

Conclusions on the coevolution of plant-insect interactions should not be drawn from studies with crop cultivars that have been subjected to extensive artificial selection. On the other hand, the studies on herbivore-induced emissions of volatiles clearly suggest that an intricate interaction between the plants and the natural enemies of herbivores is one of the driving forces that may have led to and maintained the trait of signaling from plant to

insect. A better understanding of the physiological and biochemical mechanisms behind this phenomena, as well as ecological studies on similar more naturally evolved systems, may help to fully grasp the significance of the chemical signals emitted by plants in response to herbivory.

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