

NOCTUIDAE-INDUCED PLANT VOLATILES: CURRENT SITUATION AND PROSPECTS

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Recebido em 13/01/2014; aceito em 25/07/2014; publicado na web em 05/09/2014

Noctuids are phytophagous lepidopterans with some species causing significant damage to agriculture. The host plants, in turn, have developed defense mechanisms to cope with them, for instance chemical defenses. In this study we review the literature on plant volatiles induced by noctuids, and discuss the methodologies used to induce the production of volatiles that are usually employed in plant defense mechanisms. Future prospects involving this line of research in pest control are also discussed.

Keywords: herbivory-induced plant volatiles; elicitors; tritrophic interactions.

INTRODUCTION

Noctuid moths are classified in the superfamily Noctuoidea, which include about 30,000 described species. These nocturnal moths are characterized by a robust tagma, and wings with a high density of wing scales.¹ Noctuid caterpillars, as a rule, are phytophagous. The family encompasses extremely important agricultural pests that cause huge economic losses. In Brazil, they attack and damage soybean, corn, wheat, beans, and cotton.

In an effort to reduce the environmental impact of modern agriculture, biological control methods are often proposed as alternatives to synthetic insecticides. In this context, natural enemies, which can be attracted and manipulated in abundance during outbreaks through the use of plant volatiles, represent an environmentally friendly alternative to insecticides. However, because the interactions among different crops, herbivores and their natural enemies are complex, the implementation of indirect defense mechanisms in agroecosystems needs to be carefully planned.²

Usually when host plants are injured by herbivores they can respond to it through the so-called “induced plant responses”. The latter are strategies plants use to defend themselves from herbivore attacks.³

In the last two decades, great progress has been made in understanding the mechanisms of emission and biosynthesis of plant volatiles. Several studies have provided evidence that herbivore-induced plant volatiles (HIPVs) can mediate two kinds of defenses: direct defenses, which have an immediate negative impact on the herbivore, and may increase plant resistance^{4,5} and repellency; and indirect defenses, which include the attraction of the insects’ natural enemies.⁶⁻¹²

HIPVs may mediate interactions between plants and arthropods, among microorganisms and among plants in various ecosystems. The profile of volatile compounds released by plants may vary quantitatively and qualitatively, depending on the cultivar (genotype),¹³ the stage of development of the plant (age of the leaf, plant tissues), the environmental conditions where the plant grows, as well as the number of herbivore species attacking it.^{11,14}

Plants of many species, when attacked, can release certain compounds, for instance terpenoids and methyl salicylate. Other volatiles can only be released by one plant species or a group of species.⁹ However, differences among volatiles released within the same plant

species are usually smaller than differences among volatiles released by different species.¹⁵

HIPVs are derived from different metabolic pathways. While some compounds are released immediately after herbivore attack, the synthesis of other compounds is truly induced, and their release takes some time after the initial infestation.¹⁶

After the first contact with a herbivore, the almost instantaneous response of a plant is the emission of chemicals from the lipoxygenase metabolic pathway, also known as green leaf volatiles. Among the latter are (3Z)-hexenal, and (2E)-hexenal.¹⁷⁻²¹

Compounds such as indole, various terpene derivatives from the isoprene pathway such as (E)- β -farnesene, linalool, (E)- β -ocimene and other unsaturated compounds, for instance (3E)-4,8-dimethyl-1,3,7-nonatriene, and (3E, 7E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene are synthesized *de novo* a few hours after the first herbivore attack (Figure 1).^{9,22}

In particular, the role of two major HIPV groups, terpenoids and green leaf volatiles, has gained increased interest because they can be used as additional tools in the control of agricultural pests, owing to their ability to attract natural enemies or repel insects of economic importance.^{11,23,24}

The aim of this contribution is to give an overview of the plant volatiles induced by noctuids, as well as to present and discuss the methodologies used in the induction of these volatiles, which are usually part of the defense mechanisms of plants. The prospects involving this line of research in pest control are also discussed.

Noctuid-induced volatiles as a plant defense mechanisms

Plants are not passive to the injuries caused by insect herbivores. They are able to erect physical barriers such as spikes and trichomes, and also respond to damage by synthesizing and releasing a wide variety of volatile compounds, which have the potential to regulate pest populations.²⁵⁻²⁷

Plant defenses are commonly divided into two different types: a) constitutive defenses, which include physical or chemical barriers. These are present in the plant before the herbivore attack; and b) induced defenses, which are only produced or translocated when there is an injury or stressful stimulus.²⁸⁻³¹ Induced defenses have been the subject of a considerable number of recent studies, because of their potentially significant impact on pest control. This impact

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is not only momentary. In fact, it may extend to future generations, which may incorporate such compounds to their defense mechanism, transforming an induced defense into a constitutive one.^{5,32}

In general, the amount of volatiles emitted from intact leaves is relatively small, making them imperceptible to herbivores. On the other hand, a HIPV mixture is qualitatively and quantitatively different from volatiles released by intact leaves, marking the plant not only for its natural enemies, but also for other herbivores.¹¹

In studies involving tomatoes (*Lycopersicon esculentum*, Mill.), it was observed that after an attack by the herbivore *Trichoplusia ni* (Hübner, 1802), (3Z)-hexenyl acetate, (E)- β -ocimene, and β -caryophyllene were produced.³³ In another study, lima beans (*Phaseolus lunatus* L.), after being attacked by the cotton worm, *Spodoptera littoralis* (Boisduval, 1833), released the volatiles described above.³⁴

The production of indole, ethylene, and a combination of the sesquiterpenes β -caryophyllene, (E)- α -bergamotene, and (E)- β -farnesene by maize (*Zea mays* L.) was recorded after plants were attacked by the moth *Spodoptera exigua* (Hübner, 1808).³⁵

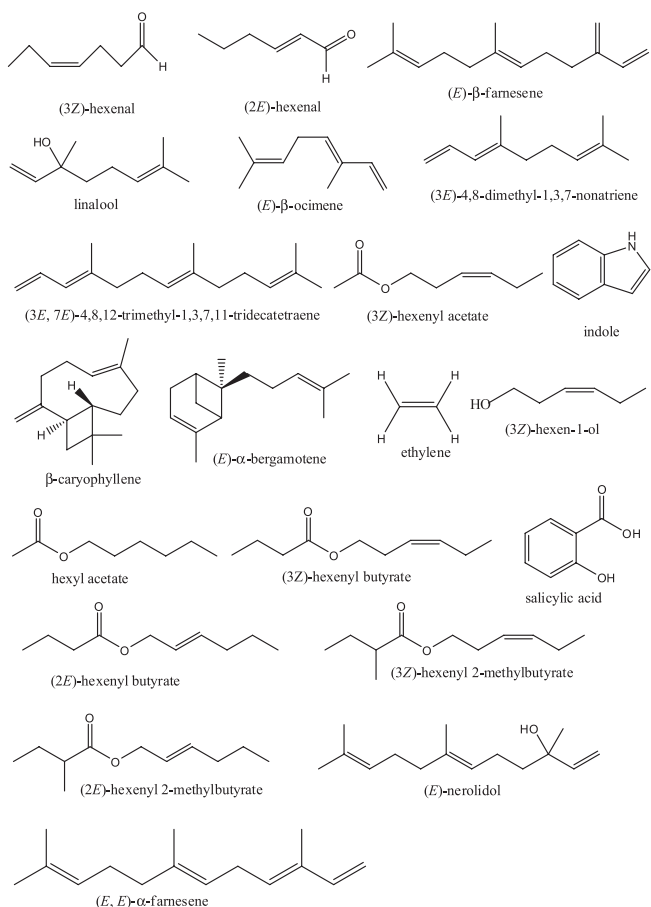


Figure 1. Noctuid-induced volatiles used in the defense mechanisms of plants

Another example of the production of volatile compounds was described when cotton (*Gossypium hirsutum* L.) was attacked by the moth *Helicoverpa zea* (Boddie, 1850). In this case, the volatiles were identified as (3Z)-hexenyl acetate, hexyl acetate, (E)- β -ocimene, (3E)-4,8-dimethyl-1,3,7-nonatriene, (3Z)-hexenyl butyrate, (2E)-hexenyl butyrate, (3Z)-hexenyl 2-methylbutyrate, (2E)-hexenyl 2-methylbutyrate and indole.³⁶

Some noctuids oviposit preferentially on intact plants rather than on damaged plants, responding to the volatiles produced by the latter. This avoids exposing the offspring to a greater risk of predation and

parasitism, as well to inter- and intra-specific competition. An example of this is the moth *Helicoverpa virescens* (Fabricius, 1777). Females of this species explore the signs of volatiles induced on tobacco (*Nicotiana tabacum* L.) by conspecific larvae. The volatiles released during the scotophase are different from those released in the photophase and have great amounts of (3Z)-hexen-1-ol, which repels female moths, allowing them to locate oviposition sites on plants that are not damaged.³⁷

Trichoplusia ni (Hübner, 1802) moths, after sensing cotton plant (*G. hirsutum* L.) volatiles induced by conspecific caterpillars, seek uninfested plants to oviposit.³⁸

In rice (*Oryza sativa* L.), volatiles induced by the oriental leafworm moth, *Spodoptera litura* (Fabricius, 1775), repel the brown leafhopper *Nilaparvata lugens* (Stål, 1854). However, the volatiles induced by *N. lugens* do not seem to deter con-specific insects.³⁹

When subjected to continuous mechanical damage performed by a device known as “mechanical caterpillar”, which mimics the feeding of *S. littoralis* (Boisduval, 1833) caterpillars, leaves of the lima bean (*P. lunatus* L.) release a volatile mixture that is qualitatively similar to the mixture induced by caterpillars.⁴⁰ Arimura and collaborators observed that leaves of the lima bean (*P. lunatus* L.) that had been mechanically damaged by the mechanical caterpillar released volatile mixtures that were qualitatively different in the photophase and scotophase.⁴¹ During photophase there was an increased release of β -ocimene and (3Z)-hexenyl acetate, whereas during scotophase the production of β -ocimene was low. This example demonstrates that plants are capable of generating different blends of volatiles that affect different organisms at different times of the day, which optimizes their defense mechanisms.⁴¹

Herbivores may also benefit from the volatiles they induce. The latter may serve as olfactory cues to locate host plants or to find mating partners.⁴²⁻⁴⁵ Carroll (2008) and colleagues found that the cowpea (*Vigna unguiculata* L.), after being damaged by *Spodoptera frugiperda* (Smith, 1797) caterpillars, releases (3E)-4,8-dimethyl-1,3,7-nonatriene, which serves as a chemical track to locate and recognize the host plant.⁴⁶

Tritrophic interactions

Research has shown that plant volatiles induced by herbivory act directly on herbivores and indirectly on their natural enemies.^{3,10,47} This has generated a lot of interest in the scientific community, in view of the enormous potential natural enemies have as biological control agents.¹¹

After being infested by immature noctuids, some plants alter the composition of the compounds they emit. As a result, parasitoid females become more selective and look more consistently for these volatiles to locate the herbivores they attack. This is a complex task for natural enemies, because they need to be able to discriminate among the mixtures that are rich in volatile compounds.^{2,48} The success of parasitoids in this challenge depends largely on their degree of specialization,⁴⁹ as well as their previous experience.⁵⁰

The first evidence that plants can modify their pattern of emission of volatiles in response to damage caused by noctuids, and attract parasitoids as a result of that, was given by Turlings and collaborators (1990), who found that the parasitoid *C. marginiventris* (Cresson) was attracted to seedlings of maize (*Z. mays* L.) attacked by *S. exigua* (Hübner, 1808) caterpillars. The latter induce the release of (3Z)-hexen-1-ol, indole, (3E)-4,8-dimethyl-1,3,7-nonatriene, linalool and (E)- β -bergamotene.⁵¹

Thaler showed that, in agricultural systems, *Spodoptera exigua* (Hübner, 1808) caterpillars placed on tomato (*L. esculentum* L.) plants previously pulverized with jasmonic acid, suffered higher rates of parasitism by *Hyposoter exiguae* (Viereck) than control plants.⁵²

The specialist parasitoid *Cardiochiles nigriceps* Viereck, for example, is able to distinguish whether cotton (*G. hirsutum* L.) and tobacco (*N. tabacum* L.) are infested with its host, *H. virescens* (Fabricius, 1777) or with the non-host caterpillar, *H. zea* (Boddie, 1850).⁵³

The generalist parasitoid *M. rufiventris* (Kok.), which attacks the early stages of its hosts in natural environments, was unable to discriminate among different instars of *S. littoralis* (Boisduval, 1833) caterpillars based on the volatiles they induced on maize (*Z. mays* L.).⁵⁴

The release of specific terpenes attract the natural enemies of noctuids, as observed for maize (*Z. mays* L.) plants, which release large amounts of the sesquiterpene (*E*)- β -caryophyllene after they have been damaged by *S. littoralis* (Boisduval, 1833) caterpillars. This sesquiterpene serves as a chemical clue that attracts the caterpillar's natural enemy, the parasitoid wasp *C. marginiventris* (Cresson).^{55,56}

Volatile compounds emitted by maize seedlings after being attacked by the generalist caterpillars *S. littoralis* (Boisduval, 1833) and *S. exigua* (Hubner, 1808) have been well characterized for over two decades.^{7,57,58} Volatile compounds are generally green leaf volatiles and include aldehydes and esters, linalool, (3*E*)-4,8-dimethyl-1,3,7-nonatriene, and indole. However, the greatest proportion of the mixture consists of (*E*)-farnesene, (*E*)- α -bergamotene and sesquiterpene hydrocarbons. This volatile mixture attracts parasitoid wasps.⁵⁸

Most research on noctuid-induced volatiles stems originates from studies on damaged plant tissue caused by caterpillars while feeding. However, in addition to feeding, oviposition by adult moths also induces the production of volatiles that attract egg parasitoids, for instance *Trichogramma*. Several species of this genus are generalist

egg parasitoids of several lepidopteran pests.⁵⁹ There is evidence that plants may emit volatiles upon oviposition on the surface of their leaves, indicating a synergistic effect between egg mass and oviduct secretion.⁶⁰

In insect-plant trophic relationships, each receive and send chemical signals that determine the outcome of the interaction. Chemoreceptors in the mouthparts, antennae and tarsi, for example, help phytophagous insects as certain the suitability of a plant as a food source. Conversely, plant cells recognize and respond to aspects of the insects such as their movements, the wounds they inflict, and the compounds present in their oral secretions.⁶¹ Rostás and Wölfling, in 2009, observed that volatiles are induced in barley (*Hordeum vulgare* L.) plants when *S. frugiperda* (Smith, 1797) caterpillars walk on them, and that these volatiles are attractive to the parasitoid wasp *C. Marginiventris* (Cresson).⁶²

Some studies have shown that synthetic chemical mixtures can simulate the volatiles released by plants damaged by noctuid moths. For example, *Cotesia kariyai* (Watanabe) parasitoids are attracted in a wind tunnel containing filter paper treated with a mixture of (2*E*)-hexenal, (3*Z*)-hexen-1-ol, (3*Z*)-hexenyl acetate, myrcene and linalool released from plants infested by *Mythimna separata* (Walker, 1865) caterpillars.⁶³

Evidence that terpenoids and green leaf volatiles are most often induced after noctuid attacks may contribute to a better understanding of trophic interactions and the development of more effective techniques for the biological control of these pests. The induced volatiles attracting the noctuids natural enemies are shown in Table 1.

Table 1. Noctuid-induced volatiles and the natural enemies they attract

HIPVs	Plant	Noctuidae	Natural Enemy	Reference
β -caryophyllene	<i>N. tabacum</i>	<i>H. virescens</i>	<i>Cardiochiles nigriceps</i>	53
(<i>E</i>)- β -farnesene	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	97
	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	23
	<i>Z. mays</i>	<i>S. exigua</i>	<i>C. marginiventris</i>	51
(<i>E</i>)-4,8-dimethyl-1,3,7-nonatriene	<i>Z. mays</i>	<i>M. separata</i>	<i>Exorista japonica</i>	98
	<i>Z. mays</i>	<i>P. separata</i>	<i>C. kariyai</i>	99
	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	55
(<i>E</i>)-caryophyllene	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	23
	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	23
β -ocimene	<i>N. tabacum</i>	<i>H. virescens</i>	<i>C. nigriceps</i>	53
	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	97
(<i>E</i>)- α -bergamotene	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	23
	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	23
(<i>E</i>)- β -bergamotene	<i>Z. mays</i>	<i>S. exigua</i>	<i>C. marginiventris</i>	51
	<i>Z. mays</i>	<i>S. exigua</i>	<i>C. marginiventris</i>	51
	<i>Z. mays</i>	<i>S. exigua</i>	<i>C. marginiventris</i>	51
linalool	<i>Z. mays</i>	<i>M. separata</i>	<i>E. japonica</i>	100
	<i>Z. mays</i>	<i>M. separata</i>	<i>Campoletis chloridae</i>	101
α -pinene	<i>Z. mays</i>	<i>M. separata</i>	<i>C. kariyai</i>	102
1-hexanol	<i>Z. mays</i>	<i>M. separata</i>	<i>E. japonica</i>	100
(2 <i>E</i>)-hexen-1-ol	<i>Z. mays</i>	<i>M. separata</i>	<i>E. japonica</i>	100
	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	24
	<i>Z. mays</i>	<i>M. separata</i>	<i>C. kariyai</i>	103
(3 <i>Z</i>)-hexenyl acetate	<i>Z. mays</i>	<i>M. separata</i>	<i>E. japonica</i>	100
	<i>Z. mays</i>	<i>M. separata</i>	<i>C. kariyai</i>	102
	<i>Z. mays</i>	<i>M. separata</i>	<i>C. chloridae</i>	101
	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	24
	<i>Z. mays</i>	<i>M. separata</i>	<i>E. japonica</i>	100
(3 <i>Z</i>)-hexen-1-ol	<i>Z. mays</i>	<i>S. littoralis</i>	<i>C. marginiventris</i>	24
	<i>Z. mays</i>	<i>S. exigua</i>	<i>C. marginiventris</i>	51
	<i>Z. mays</i>	<i>S. exigua</i>	<i>C. marginiventris</i>	51
indole	<i>Z. mays</i>	<i>M. separata</i>	<i>E. japonica</i>	98
	<i>Z. mays</i>	<i>P. separata</i>	<i>C. kariyai</i>	99

Elicitors as inducers of volatiles production

Recent research on the reaction of plants to herbivore damage suggests that there are elicitors associated with the oral secretions of insects. They allow plants to distinguish between ordinary damage and injury caused by phytophagy.⁶⁴

After the damage and the introduction of elicitors, a series of biochemical processes takes place in the plant, culminating in a systemic response that may involve a change in gene expression and synthesis of chemical compounds. Plants may adjust their responses to insect feeding depending on the kind of elicitor the insect releases, activating several signal transduction pathways that lead to the induction and production of a variety of secondary metabolites, especially terpenoids and green leaf volatiles. All these signal transduction pathways are regulated by several plant hormones. These plant hormones are activated by damage caused by phytophagous insects, as well as by mechanical damage. In addition, the synergistic and antagonistic relationships between these hormones may cause a suppression or over expression of certain volatiles.^{11,39,65-67}

Oral secretions of some noctuids seem to act as elicitors for the production of jasmonic acid, one of the major indicators of herbivore damage. Jasmonic acid is synthesized from linolenic acid through the octadecanoid pathway, which induces the expression of several genes that are directly and indirectly associated with plant defenses.⁶⁸⁻⁷⁴ This same pathway induces the production of hydrogen peroxide (H_2O_2), an oxidant that can act initially as a signaling molecule in plant defense.⁷⁵

Different types of elicitors have been identified. The elicitor volicitin was first isolated from oral secretions of *S. exigua* (Hubner, 1808) caterpillars. It seems to be the product of the reaction of 17-hydroxy linolenic acid, derived from the plant, with glutamine, derived from the caterpillars, in a reaction that must occur in the oral cavity of the latter.⁷⁶⁻⁷⁸

When the oral secretion of *S. exigua* (Hubner, 1808) was applied on the leaves of cotton (*G. hirsutum* L.) over a mechanical wound, it caused the synergistic production and release of the following volatile compounds: (*E,E*)- α -farnesene, (*E*)- β -farnesene, (*E*)- β -ocimene, linalool, (*3E*)-4,8-dimethyl-1,3,7-nonatriene, (*3E,7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, and indole, the same compounds emitted during herbivory.⁷⁹

Larvae of the caterpillar *S. exigua* (Hubner, 1808) may also trigger the emission of systemic volatiles on the surfaces of uninjured leaves, as observed by Turlings and Tumlinson (1992). In this case, when healthy leaves of maize (*Z. mays* L.) were treated with oral secretions of the caterpillar, they systemically released large amounts of volatile substances such as linalool, (*3E*)-4,8-dimethyl-1,3,7-nonatriene and (*3E,7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene.

Another elicitor isolated and identified from the oral secretions of *S. frugiperda* (Smith, 1797) caterpillars is a peptide disulfide known as inceptine.⁸⁰ This peptide induces in plants a rapid and sequential production of jasmonic acid, ethylene, salicylic acid, and (*3E*)-4,8-dimethyl-1,3,7-nonatriene.⁸¹

Turlings and collaborators investigated the reactions of maize (*Z. mays* L.) seedlings grown in solutions containing regurgitate from larvae of various noctuid species (*S. frugiperda*, Smith, 1797; *H. zea*, Boddie, 1850; *T. ni*, Hübner, 1802; *Anticarsia gemmatilis*, Hübner, 1818) and also from a grasshopper, *Schistocerca americana* (Drury 1773). In their results, the production of the following compounds, which are characteristic of plants damaged by herbivory, were induced: (*3Z*)-hexenyl acetate, linalool, (*3E*)-4,8-dimethyl-1,3,7-nonatriene, (*E*)- α -bergamotene, (*E*)- β -farnesene, (*E*)-nerolidol, (*3E,7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene and indole.⁸²

Moreover, when glucose oxidase, an enzyme isolated from the salivary glands of *H. zea* (Boddie, 1850), was applied on tobacco (*N.*

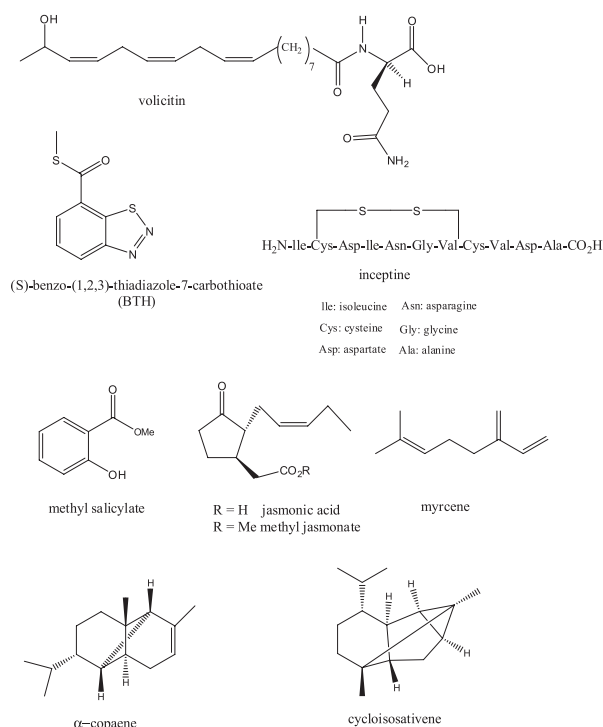


Figure 2. Structures of the elicitors volicitin, inceptine and BHT and of some HIPVs

tabacum L.) leaves, it inhibited the synthesis of volatile compounds. This enzyme might be responsible for the observed feeding resistance of this herbivore.⁸³

Systemic release of volatiles induced by herbivory

After being damaged by herbivores, plants respond fast, releasing specific signals. These signals trigger the biochemical and physiological changes that occur not only in the attacked leaves, but also in the healthy leaves, and activate the systemic production of various compounds such as triterpenes, saponins, cardioactive glycosides, indole, and nitrogen compounds such as alkaloids, non-protein amino acids, cyanogenic glycosides, and common volatile essential oils, all of which are known to reduce herbivory.⁸⁴

Rose and collaborators, in 1996, discovered that cotton (*G. hirsutum* L.) plants damaged by larvae of *S. exigua* (Hübner, 1808) caterpillars consistently released the following compounds: (*3Z*)-hexenyl acetate, (*E*)- β -ocimene, linalool, (*3E*)-4,8-dimethyl-1,3,7-nonatriene, (*E*)- β -farnesene, (*E,E*)- α -farnesene and (*3E,7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. Latter, in 1998, the same authors reported the systemic release of identical compounds by cotton (*G. hirsutum* L.) plants, induced by *H. zea* caterpillars (Boddie, 1850). These compounds are also implicated in the attraction of the parasitoids *C. marginiventris* (Cresson) and *Microplitis croceipes* (Cresson).^{79,85}

Another well-studied example is the application of exogenous (S)-benzo-(1,2,3)-thiadiazole-7-carbothioate (BHT) on cotton (*G. hirsutum* L.) plants, causing systemic acquired resistance, mimicking volatiles induced by the bollworm *Helicoverpa armigera* (Hübner, 1805).⁸⁶ The application of the same elicitor on corn (*Z. mays* L.) plants mimics the damage caused by *S. littoralis* (Boisduval, 1833) caterpillars, attracting three parasitoids: *C. marginiventris* (Cresson), *Campoplex sonorensis* (Cameron) and *Microplitis rufiventris* (Kok.).⁸⁷

Likewise, Rose and Tumlinson (2004) found that damage caused by *H. zea* (Boddie, 1850) caterpillars on cotton (*G. hirsutum* L.)

flowers induced the systemic release by intact leaves, after 72 hours, of the volatiles (3Z)-hexenyl acetate, (E)- β -ocimene, linalool, (3E)-4,8-dimethyl-1,3,7-nonatriene, (E)- β -farnesene, (E,E)- α -farnesene, and indole. This is an example of damage in the reproductive part of the plant triggering a systemic response in the vegetative portion.⁸⁸

After removing *S. exigua* (Hubner, 1808) caterpillars from the lower leaves of cotton (*G. hirsutum* L.), Rose and Tumlinson (2005) observed the systemic induction and continuous release of the volatiles (E)- β -ocimene, linalool, (3E)-4,8-dimethyl-1,3,7-nonatriene, (E)- β -farnesene, (E,E)- α -farnesene and (3E,7E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, continuing for several days after removal of the insects.⁸⁹

Undamaged leaves of soybean (*Glycine max* L.) produced (E,E)- α -farnesene, (3Z)-hexenyl acetate and methyl salicylate when soybean seedlings had been attacked by *S. frugiperda* (Smith, 1797) caterpillars. That study revealed that the transport of the signal was stronger and faster toward the acropetal direction.⁹⁰

The works mentioned above show that the emission of volatiles by plants attacked by noctuids is not limited to the sites of damage. It also occurs in regions that had not been directly attacked.

Studies on the application of induced volatiles for the control of noctuids in the field

Herbivore-induced plant volatiles can be manipulated in the following ways to improve biological control in agriculture: a) through use of synthetic volatiles; b) by increasing HIPV emissions through the application of phytohormone elicitors; and c) by applying genetic engineering to increase HIPVs production.⁹¹ Compared with the large number of studies on plant defense using HIPVs under laboratory conditions, only a few studies have been conducted under field conditions.^{92,93}

Application of the phytohormone jasmonic acid in a tomato orchard increased the attraction of the parasitoid *H. exiguae*, favoring the control of *S. exigua* caterpillars, regardless of the stage of development or density of the herbivores.^{52,94}

Controlled release dispersal of the following synthetic green leaf volatiles was used on maize: (Z)-3-hexenal, (Z)-3-hexenol, (E)-2-hexenal, and (Z)-3-hexenyl acetate. These compounds were used to monitor the attraction of *S. frugiperda* caterpillar and its natural enemies. Plants exposed to these volatiles emitted larger amounts of the sesquiterpenes cycloisosalvene, α -copaene, (E)- β -caryophyllene, (E)- β -farnesene and (E)- α -bergamotene than plants that were not exposed. However, parasitism of *S. frugiperda* did not increase.⁹⁵

Methyl jasmonate, an elicitor of defense against many insects, and (S)-benzo-(1,2,3)-thiadiazole-7-carbothioate (BHT), an elicitor of resistance against certain pathogens, were applied on maize. The application of both compounds under field conditions failed to consistently affect *S. frugiperda* infestations and did not increase parasitism of its caterpillar.⁹⁶

CONCLUSION

Given that the main role of volatiles is protection against herbivores and pathogens, studies on plant defenses against herbivores are very important, not only from an evolutionary point of view, but also from an applied standpoint, given that the main role of induced volatiles is protection against herbivory and pathogens. The possibility to use HIPVs to manipulate the foraging behavior of parasitoids and reduce the damage caused by herbivores is a sound alternative to synthetic pesticides, because these compounds are specific, non-toxic and biodegradable, bringing benefits to modern agriculture.

In recent decades we have come to a broader understanding of

the endogenous mechanisms and biochemical pathways induced by herbivory. In response to injury, plants alter the synthesis of secondary metabolites and their level of gene expression. One of the main challenges in this field is the identification of genes responsible for the production of volatiles, opening the prospects for the commercialization of transgenic plants that can produce them.

With advanced technologies, new tools such as genomics, proteomics, transcriptomics, metabolomics, lipidomics, and bioinformatics have opened new perspectives to address biological issues more efficiently. Extensive qualitative and quantitative analysis of the spatial and temporal variations of entire gene systems, proteins, secondary metabolites and other molecular components will contribute to a better understanding of the regulatory properties of the biosynthetic pathways involved in the production of induced volatiles.

When the genes responsible for the biosynthesis of volatiles induced by herbivory are identified, it will be possible to use genetic engineering to induce the production of specific compounds, or mixtures of compounds, in crops that do not naturally produce them, or to increase the flux of these compounds by 'priming' (pre-exposing them to volatile organic compounds) these crops to respond more efficiently. One strategy to increment this type of control is the use of a variety of plants that are faster at producing volatiles after noctuid attacks, even when insect densities are low. Another strategy is the exogenous application of elicitors that induce these volatiles, increasing the recruitment of natural enemies.

ACKNOWLEDGEMENTS

We thank CAPES, CNPq-INCT "Controle Biorracional de Insetos-Praga" and Fundação Araucária for their financial support.

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