

Update on Plant-Insect Interactions

Plant Volatiles as a Defense against Insect Herbivores

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Leaves normally release small quantities of volatile chemicals, but when a plant is damaged by herbivorous insects, many more volatiles are released. The chemical identity of the volatile compounds varies with the plant species and with the herbivorous insect species. These volatiles attract both parasitic and predatory insects that are natural enemies of the herbivores. They may also induce defense responses in neighboring plants. Such chemicals, which function in communication between and among species, as well as those that serve as messengers between members of the same species, are called semiochemicals (from the Greek “*semeion*,” a mark or signal) (Law and Regnier, 1971).

Semiochemicals emitted from a diverse group of plants and insects mediate key processes in the behavior of specific insects. Volatile phytochemicals can serve as airborne semiochemicals, promoting or deterring interactions between plants and insect herbivores. For example, wheat seedlings without herbivore damage attract aphids, whereas odors released from wheat seedlings with a high density of aphids repel other aphids (Quiroz et al., 1997). For swallowtail butterflies, volatiles from host plants enhance the effect of contact stimulants, increasing landing rates and oviposition relative to non-host plants (Feeny et al., 1989).

In addition to the bouquet of compounds that render leaves attractive or disagreeable to herbivores, volatile terpenoids and other compounds emitted from leaves in response to insect damage allow insect parasitoids (such as parasitic wasps) and predators to distinguish between infested and noninfested plants, and thus aid in locating hosts or prey (Fig. 1). These phytodistress signals, which result in an active interaction between herbivore-damaged plants and a third trophic level, have been described for several agro-ecosystems. Examples include lima bean and apple plants, which produce volatiles that attract predatory mites when damaged by spider mites (Takabayashi and Dicke, 1996), and corn and cotton plants, which release volatiles that attract hymenopterous parasitoids that attack larvae of several Lepidoptera species (Tumlinson et al.,

1993). In the latter case, a parasitoid female injects her eggs when she stings, and the eggs hatch into wasp larvae inside the caterpillar. Once the caterpillar has been stung, its reproductive cycle is terminated and a new generation of wasps is produced.

In all plants reported thus far, there are notable similarities in the structure of the volatile compounds that are emitted from insect-damaged leaves and from leaves distal to the site of damage. The structural uniformity in the chemical emissions from different plants with insect feeding suggests the activation of a common set of biosynthetic pathways shared by a wide range of plant families, and that the products are detectable to a broad spectrum of insect parasitoids and predators (Fig. 2). The ability of host-seeking insects to recognize and respond to such chemical cues and differentiate them from background odors indicates that insect-damaged plants emit volatile chemicals that are clearly distinguishable from those released in response to other types of damage or those released from undamaged plants. The plant's ability to differentiate between herbivore damage and a general wound response suggests the presence of elicitors associated with insect feeding that are absent from other types of leaf damage.

PLANTS RESPOND TO INSECT FEEDING DAMAGE BY RELEASING GREATER AMOUNTS OF A VARIETY OF VOLATILES

An undamaged plant maintains a baseline level of volatile metabolites that are released from the surface of the leaf and/or from accumulated storage sites in the leaf. These constitutive chemical reserves, which often include monoterpenes, sesquiterpenes, and aromatics, accumulate to high levels in specialized glands or trichomes (Paré and Tumlinson, 1997a). In addition, green-leaf odors consisting of a blend of saturated and unsaturated six-carbon alcohols, aldehydes, and esters are produced by autolytic oxidative breakdown of membrane lipids and are released when leaves are mechanically damaged. This pattern of constitutive compounds has been analyzed in the field for perennials, including beech (Tollsten and Müller, 1996) and ash (Markovic et al., 1996) trees, as well as under greenhouse conditions for many herbaceous annuals, including

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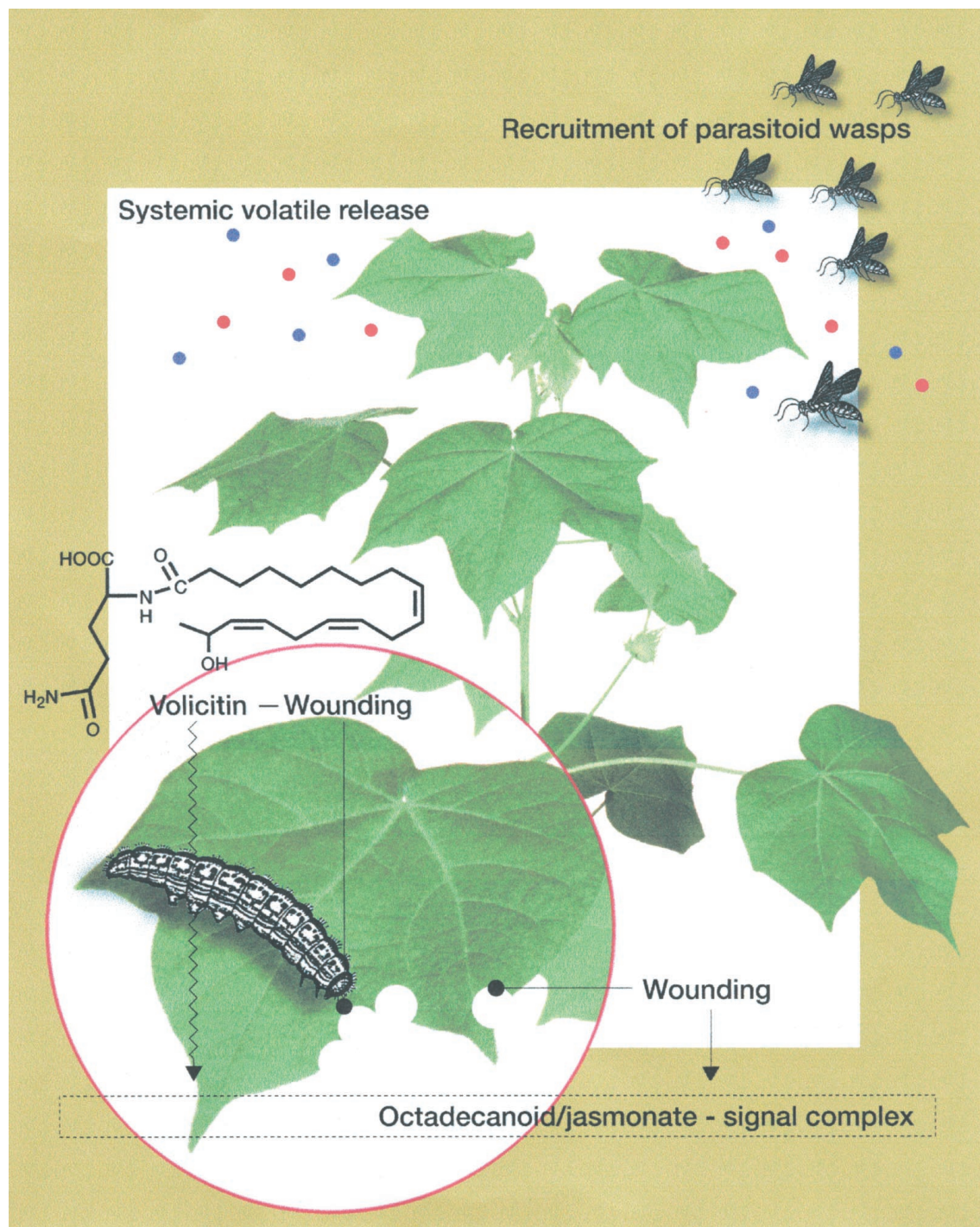


Figure 1. Schematic representation indicating an increase of volatile compounds released by plants in response to insect feeding triggered by an interaction of elicitors such as volicitin in the oral secretions of insect herbivores with damaged plant tissue. Volatile semiochemicals are then used by natural enemies of herbivores such as parasitoid wasps to locate their hosts.

brussels sprouts (Mattiacci et al., 1994) and cucumber (Takabayashi et al., 1994).

Plants respond to insect feeding damage by releasing a variety of volatiles from the damaged site, and the profile of the volatiles emitted is markedly different from those of undamaged or mechanically damaged plants. In cotton,

breakage of leaf glands causes stored terpenes to be released in much higher levels, and the emissions of lipoxygenase pathway green-leaf volatiles are also increased. While the release of these metabolites correlates closely with leaf damage from insect feeding (Loughrin et al., 1994), a subset of terpenes, the nitrogen-containing com-

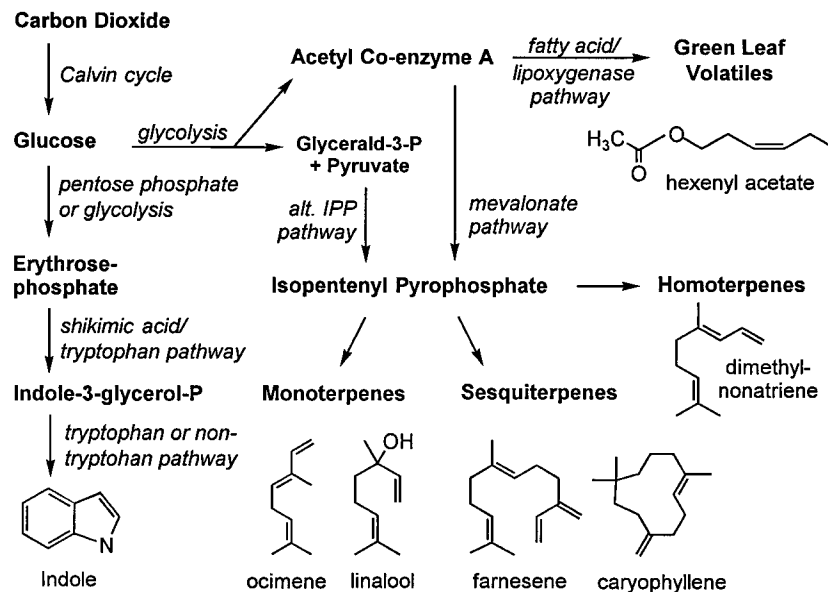


Figure 2. Biosynthetic pathways leading to the release of plant volatiles. Indole, a product of the shikimic acid pathway, is formed from indole-3-glycerol-P either as an intermediate in Trp biosynthesis or by a Trp-independent pathway leading to a family of nitrogen-containing defense compounds (e.g. 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) (Frey et al., 1997). Sesquiterpenes are synthesized via the isopentenyl pyrophosphate (IPP) intermediate following the classical mevalonate pathway, whereas monoterpenes and diterpenes are synthesized via an alternative IPP pathway with glyceraldehyde-3-P and pyruvate identified as the direct precursors of IPP (Lichtenthaler et al., 1997). The mevalonate pathway is localized in the cytosol and reactions for the non-mevalonate pathway are localized in plastids. The homoterpene (*E*)-4,8-dimethyl-1,3,7-nonatriene and (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene are derived from their 15 and 20 carbon precursors, farnesyl- and geranylgeranyl-pyrophosphate, respectively, by a series of enzymatic steps with the overall loss of four carbon units (Donath and Boland, 1994). The green-leaf volatiles are derived from linolenic acid via a 13-hydroperoxylinolenic acid intermediate (Blee, 1998). This oxidized linolenic acid, instead of losing water and committing the molecule down the defense signaling jasmonic acid pathway, is cleaved to form two fragments of 12 and six carbon units (Fig. 3). The variety of green-leaf volatiles are formed from this second pathway by multiple rearrangement steps of the six-carbon (*Z*)-3-hexenal.

compound indole, and hexenyl acetate are also released in much higher levels with insect feeding, but in a diurnal cycle that is decoupled from short-term insect damage. These compounds, linalool and (*E*)- β -ocimene (monoterpenes), (*E,E*)- α -farnesene and (*E*)- β -farnesene (sesquiterpenes), nonatriene and tridecatetraene (homoterpenes), and indole and (*Z*)-3-hexenyl acetate, have an emissions profile more similar to the light cycle, with low emissions at night and high levels during the periods of maximal photosynthesis.

Chemical labeling studies have established that the compounds released in much greater quantities during the day and specifically in response to insect damage are synthesized *de novo* and are not stored in the plant (Paré and Tumlinson, 1997b). These induced compounds rapidly incorporate a high level of label when plants damaged by feeding caterpillars are held in volatile collection chambers under an atmosphere containing ^{13}C -CO₂. The high incorporation of ^{13}C detected by mass spectral analysis, and the rapid turnover of this label in experiments where short pulses of ^{13}C -CO₂ were used indicate that its production is tightly coupled with photosynthesis. A consistent, several-hour delay between when insect feeding begins and emission of the induced volatiles supports the hypothesis that a series of biochemical reactions, including gene expression, protein assembly, and/or enzyme induction, is required for the synthesis and release of these compounds.

RELEASE OF VOLATILES FROM UNDAUNED LEAVES OF A DAMAGED PLANT INDICATES A SYSTEMIC SIGNAL

In addition to the release of volatiles at the site of herbivore feeding, analysis of volatile emissions from unharmed leaves of insect-damaged plants has established that there is a systemic response. In both corn (Turlings and Tumlinson, 1992) and cotton (Röse et al., 1996), leaves distal to the site of herbivore feeding showed an increase in the release of volatiles. The chemical blend of volatiles from undamaged cotton leaves differs from the volatiles collected from the entire plant. The products of the lipoxygenase pathway, including the hexenals and hexenols, which are released from freshly cut or damaged tissue, are not detected in the systemically released volatiles, with the exception of (*Z*)-3-hexenyl acetate. One explanation is that these six-carbon compounds can only be released from undamaged leaf tissue when they are converted to the acetate form (Paré and Tumlinson, 1998).

The activation of the lipoxygenase pathway in undamaged leaves suggests a mechanism analogous to that proposed by Farmer and Ryan (1992), wherein a mobile signal such as systemin can transmit information from the damaged site to distal leaves, triggering the lipoxygenase pathway and resulting in a cascade of signals activating several

defense responses in plants. Some of the monoterpenes and sesquiterpenes, as well as indole and isomeric hexenyl butyrates and 2-methyl butyrates, are also only released from damaged leaves (Röse et al., 1996). The induced terpenoids that are synthesized *de novo* in cotton leaves in response to herbivore damage are also released systemically from undamaged leaves of a caterpillar-damaged plant. Chemical labeling experiments established that the systemic volatiles are synthesized at the site of release, suggesting that a mobile chemical messenger is transported from the damage location to distal, undamaged leaves to trigger synthesis and volatile release (Paré and Tumlinson, 1998).

Chemical labeling experiments using herbivore-damaged plants in combination with an analysis of the volatiles released has only been reported for cotton. However, since many of the compounds emitted from corn during the day have also been shown to be induced in cotton, and the quantities released increase with increased light intensity, it can be speculated that these volatiles are also synthesized *de novo* in corn plants. It is interesting that similar compounds are emitted in response to insect herbivore damage in several agricultural species, including cucumber, apple, lima bean, corn, and cotton (see Table I). Both among individual plants of the same species and between different plant species, whether the blend of volatile compounds is induced through a common signaling pathway or if their emissions are triggered by different signaling mechanisms is not yet known.

THE SYNTHESIS OF VOLATILES HAS A HIGH METABOLIC COST

Terpenes are an important source of olefinic compounds involved in the formation of phytotoxic products. For example, in conifers (Buchbauer et al., 1994) and broadleaf tree species (Monson and Fall, 1989), an array of terpene hydrocarbons are released from plants during times of photosynthesis. These naturally produced isoprenoids are known to form photooxidants and ozone in combination with nitrogen oxides. As a result, increased amounts of terpenes can act as pollutants, increasing the stress to the plant. The metabolic cost of these phytochemical emissions can also be high. In particular, terpenoids are more expensive to manufacture per gram than most other primary and secondary metabolites due to the need for extensive chemical reduction (Gershenson, 1994). Defensive compound

production costs in terms of reproductive success can depend on the level of herbivory. When herbivore levels are low, chemically induced wild-type tobacco plants produce fewer seeds than their noninduced counterparts. With intermediate herbivory, chemically induced plants experience less feeding on the foliage and have a higher fitness level than noninduced, insect-damaged control plants (Baldwin, 1998; Mitchell-Olds et al., 1998). It appears that volatiles need to be judiciously synthesized and safely stored, as increased synthesis can be costly and potentially toxic to the plant. However, decreases in terpene accumulation may make an individual plant more vulnerable to insect pest attacks or temperature stress.

With or without insect feeding, plants usually release a variety of terpenes during periods of high temperature. Although the biological function of terpene production is not fully understood, one proposed explanation for these emissions is that it is a strategy for responding to high temperatures (Mlot, 1995). It has been suggested that fat-soluble hydrocarbons dissolve into the thylakoid membrane and keep the chloroplast from degrading when temperatures exceed the plant's biological optimum. These hydrocarbons evaporate as the temperature rises, so that terpene volatilization cools the chloroplasts. However, since the evaporative cooling of terpenes is relatively small compared with a solvent such as water, this explanation is not universally accepted.

VOLATILES FROM INSECT-DAMAGED PLANTS ATTRACT NATURAL ENEMIES OF THE HERBIVORES

The task for a female parasitoid to locate lepidopteran caterpillar hosts would most often be unproductive if she were simply to rely on visual cues. Unlike insect pollinators seeking out well-marked flower targets, parasitoids are searching for small herbivores that are often well camouflaged and mostly inhabit the undersides of leaves. Therefore, the chances of parasitoids finding hosts by random searching are remote. Both McCall et al. (1993) and Steinberg et al. (1993) have shown by wind tunnel flights and GC analysis the weak allure and low abundance that herbivore odors alone provide for parasitoids. In contrast, the chemicals released from herbivore-damaged plants appear to contain critical chemical information that draws parasitoids to air streams spiked with these plant odors in the laboratory and to damaged plants placed among a group of undamaged neighbors in the field.

Table I. Diverse plant species with shared volatile terpenes released in response to herbivory

Plant	(E)- β -Ocimene	Linalool	(E)-4,8-Dimethyl-1,3,7-Nonatriene	(E,E)- α -Farnesene	(E)- β -Farnesene	(E,E)-4,8,12-Trimethyl-1,3,7,11-Tridecatetraene	Reference
Cucumber	+		+	+		+	Takabayashi et al. (1994)
Apple	+		+	+		+	Takabayashi et al. (1991)
Lima bean	+	+	+		+	+	Takabayashi et al. (1994)
Cotton	+	+	+	+	+	+	Paré and Tumlinson (1997a)
Corn	+	+	+	+	+	+	Turlings et al. (1990)
Tobacco	+	+		+	+		De Moraes et al. (1998)
Potato	+	+		+	+		Bolter et al. (1997)

To examine whether systemically released chemicals alone provide sufficient chemical cues to attract parasitic wasps, herbivore-damaged leaves were removed immediately before flight tests. Wind tunnel experiments showed that systemically released components were detectable at levels sufficient to direct parasitoids to their hosts (Cortese et al., 1997). In cotton and tobacco field trials using female wasps (*Cardiochiles nigriceps*), the ratio of landings on host (tobacco budworm) damaged versus undamaged plants was high: approximately 95% to 5%, respectively, in systemic or whole-plant volatile emissions (De Moraes et al., 1998). Interestingly, this specialist parasitic wasp, using chemical cues released by the plant, can distinguish plants infested by her host *Heliothis virescens* from those infested by *Helicoverpa zea*, a closely related, non-host herbivore species. In tobacco, cotton, and maize, each plant produces a herbivore-specific blend of volatile components in response to a particular herbivore species feeding on the leaves, and these differences are observable by GC chemical analyses and detectable by parasitic wasps.

PARASITIC WASPS LEARN CHEMICAL CUES ASSOCIATED WITH HOSTS

Although the volatile compounds released by insect herbivore damage are similar among the several plant species studied thus far, the specific blends are quite distinct, varying in both the number of compounds and the actual structures produced. Thus, the task of finding a host is more complicated for the parasitoid when the host feeds on several different plant species. The wasps have overcome this obstacle by developing the ability to learn chemical cues associated with the presence of a host (Lewis and Tumlinson, 1988). The chemicals to which a female wasp is exposed during interactions with her host familiarize her with particular host location cues. A successful host experience increases the wasp's responsiveness to host-associated chemicals. For example, an oviposition experience on the plant-host complex significantly increases the oriented flight and landing responses of females of the aphid parasitoid *Aphidius ervi* relative to those that aren't allowed to sting but that are exposed to undamaged or host-damaged plants (Du et al., 1997). This underscores the importance of the oviposition experience in combination with host-damaged plant cues. Interestingly, female wasps can also learn volatile odors associated with food sources and use them to locate necessary food (Lewis and Takasu, 1990).

ENVIRONMENTAL CONDITIONS MODULATE VOLATILE EMISSIONS

Differences in the amount of volatiles released by individual plants can vary with environmental conditions that influence the plant's physiology. Several species, including corn, cotton, and lima bean, respond to reduced light (due to either lower light intensity or shorter daylength) with a decline in the release of herbivore-induced volatiles. Based on studies with lima bean, water stress also seems to directly affect volatile release (Takabayashi et al., 1994). With

less water available for the plant, elevated levels of volatiles are released from infested individuals relative to non-water-stressed controls. Correlating this with insect preference showed that predatory mites selected plants that were infested and water-stressed over those that were infested but not water-stressed (Takabayashi et al., 1994). The addition of high levels of mineral and/or organic nitrogen fertilizers significantly decreased the constitutive volatiles extracted from celery (Van Wassenhove et al., 1990). With volatile analysis and flight studies for plants under different nutritional conditions, the role of these volatiles in attracting wasps to their herbivore hosts may be more clearly assigned.

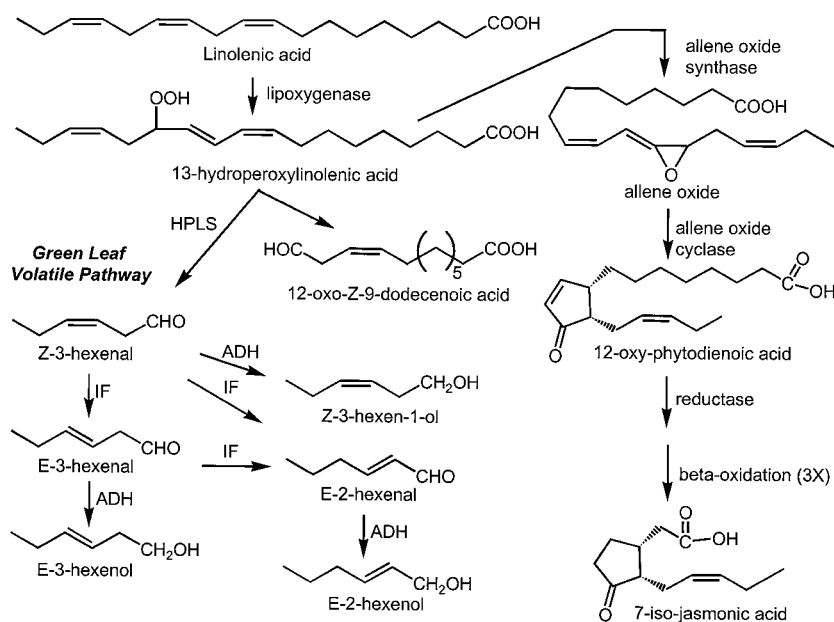
ENZYMES AND ELICITORS FROM INSECT HERBIVORES TRIGGER VOLATILE RELEASE

Key to the emissions of plant signals for the foraging success of parasitoids are substances in the oral secretion of herbivores. Recent work suggests that volatile emissions and other plant defense responses are potentiated by a component or components associated with the feeding herbivore that allows the plant to differentiate between general wounding and damage due to chewing insects. In cotton, induced volatiles that are synthesized in response to wounding are released in greater quantities as a result of caterpillar feeding than as a result of mechanical damage alone (Paré and Tumlinson, 1997a). In tobacco, higher concentrations of the defense-signaling molecule jasmonic acid result from herbivore damage by hornworm caterpillars than from mechanical damage designed to mimic herbivory (McCloud and Baldwin, 1998). At the transcriptional level, potato mRNAs involved in plant defense accumulate more rapidly with insect-derived elicitor(s) in contact with the damaged leaves than with mechanical damage alone (Korth and Dixon, 1997).

Thus far, two oral secretion products from chewing insects have been identified that augment the release of plant volatiles. A β -glucosidase present in the regurgitant of *Pieris brassicae* caterpillars triggers the same emissions of volatiles in cabbage plants as induced by feeding caterpillars (Mattiacci et al., 1995). Since enzyme activity in the regurgitant is retained when caterpillars are fed a β -glucosidase-free diet, enzyme activity does not appear to be plant derived. Presumably, the enzyme acts to cleave sugars coupled to organic compounds that then become more volatile and are released. In contrast, a low- M_r fatty acid derivative, *N*-(17-hydroxylinolenoyl)-L-Gln (volicitin), has been identified from the oral secretions of beet armyworm caterpillars and induces corn seedlings to release volatile chemical signals (Alborn et al., 1997).

Analysis of volicitin from beet armyworms fed ^{13}C -labeled corn seedlings demonstrated that the caterpillar synthesizes this elicitor by adding a hydroxyl group and Gln to linolenic acid obtained directly from the plant on which the caterpillar feeds (Paré et al., 1998). Thus, although the precursor of volicitin is obtained from plants, the bioactive product has only been found in the caterpillar. This strongly suggests that these molecules play an important yet still unknown role in metabolism or some

Figure 3. Select intermediates in the metabolic conversion of linolenic acid to jasmonic acid and a series of hexenyl or green-leaf volatiles catalyzed by the enzymes hydroperoxide lyase (HPLS), isomerization factor (IF), and alcohol dehydrogenase (ADH) (Blee, 1998).



other process critical to the life of the herbivorous insects. Although it is known that the plant provides linolenic acid, which is essential for most lepidopteran larvae (Stanley-Samuelson, 1994), it is seemingly detrimental to the insect to chemically convert this fatty acid into an elicitor that triggers plant defense. The full implications of this are not yet understood.

It has been suggested that jasmonic acid, which is produced from linolenic acid by the octadecanoid signaling pathway (see Fig. 3), is a key regulatory component in the transduction sequence that triggers synthesis and release of volatile compounds by plants (Krumm et al., 1995). Jasmonates also stimulate other physiological and defensive processes in plants (Farmer and Ryan, 1992), and the amino acid conjugates of jasmonic acid are involved in physiological and developmental processes in many plants (Kramell et al., 1995). Therefore, the structure of volicitin, an octadecatrienoate conjugated to an amino acid, suggests that the elicitor molecule interacts with the octadecanoid pathway in herbivore-damaged plants.

THE MECHANISMS THAT REGULATE THE SYNTHESIS AND RELEASE OF PLANT VOLATILES ARE POORLY UNDERSTOOD

There is still much to learn about the chemical interactions between plants and insect herbivores that lead to the synthesis and release of volatiles by the plants. Only one herbivore-specific volatile elicitor, volicitin, has been identified, but we know from preliminary investigations of the chemistry and activity of oral secretions of other insect herbivores that other compounds, some analogous in structure to volicitin, are also active. Furthermore, damage of a plant by different herbivore species can induce the release of volatile blends with different proportions of constituents. Thus, distinct responses are induced by elicitors of different structures from different herbivore species. How-

ever, we don't know the biochemical mechanisms by which these elicitors trigger biosynthesis and release of plant volatiles. Do they interact with the octadecanoid signaling pathway, and if so, how? Do they regulate the release of linolenic acid, the production of jasmonic acid, or the activation of the oxidative burst, all of which are associated with the wounding of plant tissue? Also, we have no knowledge of the mechanism leading to the systemic release of volatiles. Does the original, herbivore-produced elicitor serve as a mobile messenger, triggering whole-plant volatile synthesis? Or are secondary messengers employed to transmit the signal to sites distal to the site of damage? Furthermore, why do herbivores produce compounds that activate plant chemical defenses? What function, if any, do these compounds serve in herbivore metabolism or defense?

The answers to these and similar questions should lead to the development of more effective methods for the biological control of insect pests with natural enemies. It may also lead to the development of new plant varieties with enhanced chemical defenses or to methods of "inoculating" plants with elicitors to increase their resistance to insect pests.

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