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REVIEW ARTICLE

Early Herbivore Alert: Insect Eggs Induce Plant Defense

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Abstract Plants are able to "notice" insect egg deposition and to respond by activating direct and indirect defenses. An overview of these defenses and the underlying mechanisms is given from a tritrophic perspective. First, the interface between plant and eggs is addressed with respect to the mode of attachment of eggs on the plant surface. It is elucidated which plant cells might respond to components from insect eggs or the egg deposition. The scarce knowledge on the elicitors associated with the eggs or the egg-laying female is outlined. Since endosymbiotic microorganisms are often present on the eggs, and microorganisms are also abundant on the leaf surface, the role of these hidden players for eliciting oviposition-induced plant responses is considered. Furthermore, the question of which physiological and molecular processes are induced within the plant in response to egg deposition is addressed. Second, studies on the response of the herbivorous insect to oviposition-induced plant defenses are outlined. Third, the importance of oviposition-induced plant volatiles and contact cues for host and prey location of parasitoids and predators is discussed in the context of other informative chemicals used by carnivores when searching for food. Finally, physiological and ecological costs of oviposition-induced plant responses are addressed.

Keywords Plant defenses · Oviposition · Egg · Secretion · Endosymbiotic microorganisms · Elicitor · Terpenoids · Green leaf volatiles

Introduction

Most herbivorous insects start attacking a plant by laying eggs on it. For example, many Lepidoptera and folivorous Hymenoptera do not feed upon leaves during the adult stage, but females deposit their eggs on those plants or plant parts where

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Table 1 Oviposition-induced plant responses acting directly against the herbivore or addressing the third trophic level

Plant	Herbivore	Effect of egg deposition	Induction by	Elicitor	Induction time	Reference
Direct defenses						
Pea	Bruchids	Neoplasma growth (local response only)	Egg cement No (ovipositional) wounding	3-Hydroxy-propanoates	1 d	Doss et al., 1995, 2000; Oliver et al., 2000
Rice	Planthoppers	Ovicidal substance (local response)	Egg on watery oviposition lesion Ovipositional wounding	Unknown	2 d	Seino et al., 1996; Suzuki et al., 1996
Potato	Colorado potato leaf beetle	Hypersensitive response (local response only)	Egg shell or egg cement No (ovipositional) wounding	Unknown	1 d	Balbyshev and Lorenzen, 1997
Cabbage	Large/small white cabbage butterfly	Hypersensitive response (local response only)	Egg cement No (ovipositional) wounding (?)	Unknown	1 d	Shapiro and DeVay, 1987
	Large white cabbage butterfly	Oviposition deterrence (local response, systemic response indicated)	Egg on undamaged surface No (ovipositional) wounding (?)	Unknown	1 d	Blaakmeer et al., 1994

Indirect defenses						
Elm	Elm leaf beetle	Oviposition-induced volatiles attract parasitoids (local + systemic response)	Egg on surface-damaged leaf Female removes leaf epdermis at oviposition site	Oviduct secretion coating the egg	3 hr–5 d	Meiners and Hilker, 1997, 2000; Meiners, unpublished data
Pine	Pine sawfly	Oviposition-induced volatiles attract parasitoids (local + systemic response)	Egg in slit pine needle Female saws a needle tangentially to lay eggs inside	Oviduct secretion coating the egg; a small protein or peptide	3 d	Hilker et al., 2002a, 2005
Bean	Bug	Oviposition-induced volatiles attract parasitoids (local + systemic response)	Egg on undamaged surface No (ovipositional) wounding But plus feeding damage	Unknown	3–4 d	Colazza et al. 2004a,b
Brussels sprouts	Large white cabbage butterfly	Oviposition-induced leaf contact cues arrest parasitoids (local response)	Egg on undamaged surface No (ovipositional) wounding	Secretion of accessory gland which glues the egg onto the surface	3–4 d	Fatouros et al., 2005a

hatching larvae will find suitable food. Also, in those herbivores where adults and larvae do not have separate feeding niches, such as, for example, in many herbivorous Coleoptera and Hemiptera, the choice of a plant for egg deposition is the initial step for starting a further generation damaging the plant by feeding activity.

Numerous studies address plant defenses that are induced by feeding herbivores (Tumlinson et al., 1993; Karban and Baldwin, 1997; Agrawal et al., 1999; Dicke and van Loon, 2000; Turlings and Wäckers, 2004). These plant responses start when feeding damage and loss of foliage have already begun. However, a plant is able to act "just in time" to prevent herbivores from feeding at all. Plants have evolved several mechanisms and respond to the very first step of insect attack. Induced direct and indirect plant defenses as responses to insect egg deposition are known. These oviposition-induced reactions aim to rid the plant of eggs and/or kill them, thus preventing feeding damage by the larvae that would hatch from these eggs (Hilker and Meiners, 2002; Hilker et al., 2002b).

Direct plant defenses induced by insect egg deposition may affect either the eggs themselves or the egg-laying female (Table 1). Egg deposition can induce the formation of a neoplasm that elevates the egg from the plant surface. Such exposed eggs easily drop off the plant (Doss et al., 1995, 2000). Rice plants even produce an ovicidal substance that kills the eggs in response to egg deposition by planthoppers (Seino et al., 1996; Suzuki et al., 1996; Yamasaki et al., 2003). Another mechanism to get rid of the eggs is to form necrotic tissue where eggs are laid. Such a hypersensitive response detaches the eggs from the plant surface and makes them fall to the ground. Larvae hatching on the ground suffer a rarely high mortality and rarely find their way back to their host plant (Shapiro and DeVay, 1987; Balbyshev and Lorenzen, 1997). A further direct defense mechanism induced by egg deposition addresses the egg-laying female by rendering those leaves deterrent that already carry eggs or that are adjacent to egg-laden leaves (Blaakmeer et al., 1994).

The known indirect plant defense mechanisms induced by egg deposition act by supporting egg parasitoids to locate their hosts (Table 1). For three tritrophic systems, it has been shown that insect egg deposition induces a plant volatile pattern that attracts egg parasitoids (elm: Meiners and Hilker, 1997, 2000; pine: Hilker et al., 2002a; beans: Colazza et al., 2004a), whereas the study of a further system consisting of *Brassica*, *Pieris*, and *Trichogramma* suggests that egg deposition induces the change of plant surface chemicals, thus arresting the egg parasitoids by contact cues in the vicinity of the eggs (Fatouros et al., 2005a).

Up to now, leaves especially are known as the plant organs responding to insect egg deposition by defensive mechanisms (see Table 1). The only exceptions are fruits, i.e., pea pods forming neoplasms in response to egg deposition (Doss et al., 1995, 2000), and stems of rice plants producing ovicidal benzyl benzoate after egg deposition (Seino et al., 1996). No seeds are known to "whisper for help" (Steidle et al., 2005) by emission of oviposition-induced volatiles, even though small seeds also can emit sufficient amounts of volatiles to attract herbivores, regardless of whether they carry eggs or not (Ignacimuthu et al., 2000). Although it is not known if egg deposition can induce defensive responses in, e.g., seeds, roots, or flowers, we suggest that these and plant organs other than leaves are capable of reacting to the presence of insect eggs and activating effective defensive mechanisms.

Almost all plant organs are well known to be able to form galls when attacked by gall insects (Shorthouse and Rohfritsch, 1992). Whereas numerous plant galls are induced by larval feeding activity in plant tissue, several plant galls are induced by oviposition or by both ovipositional wounding and larval feeding activity (Rohfritsch, 1992; Hilker et al., 2002b). Gall formation of plants may be considered as a mechanism initially evolved for defensive purposes by isolating the galling insect, which in turn has counteradapted to this plant response and evolved the ability to exploit the growing plant tissue for shelter and nutrition (Zweigelt, 1931). Thus, studies on the response of plant organs other than leaves to insect egg deposition will be necessary to understand the plasticity of plant defenses against this first step of attack by herbivores.

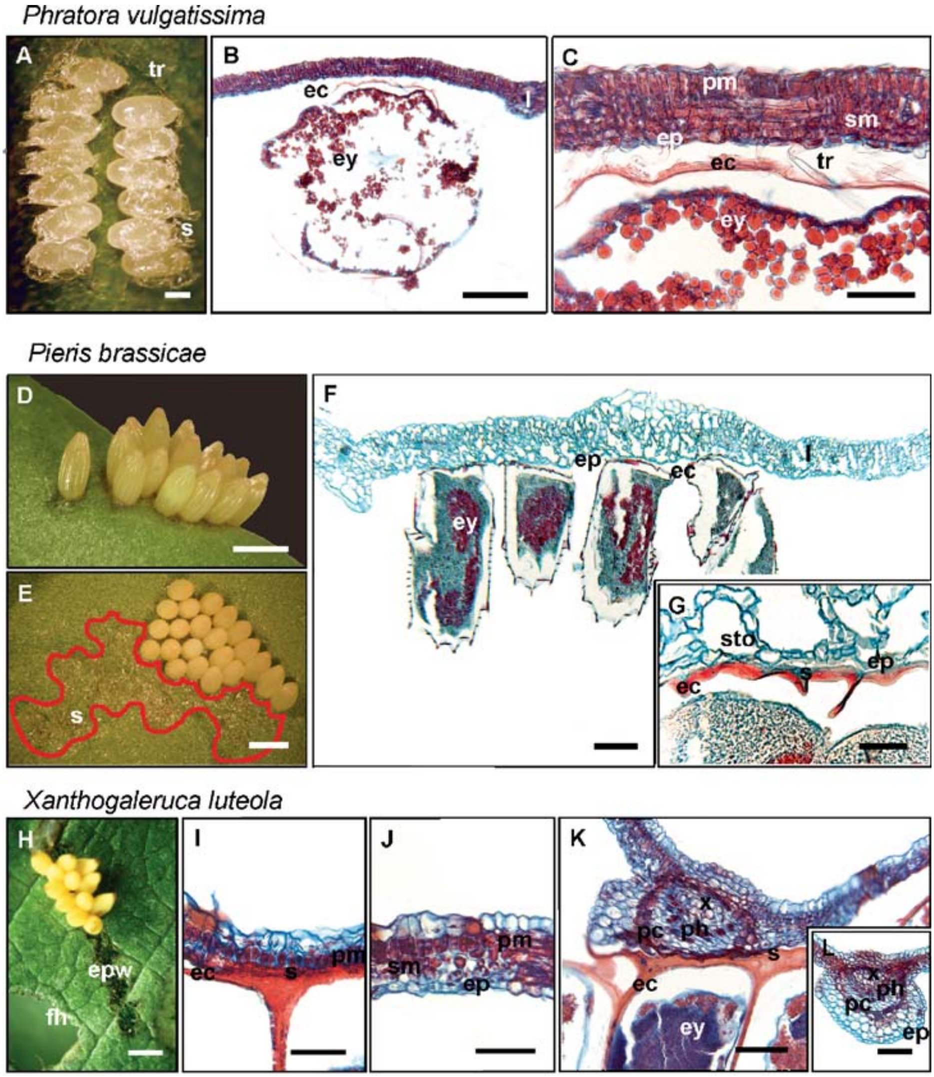
When considering plants in the tritrophic systems studied so far for their response to insect egg deposition, numerous questions on both the mechanisms and ecological functions arise. How does the plant "notice" an egg deposition? Is there any evidence that the egg-laying herbivore female counteradapts or even exploits the plant's response to egg deposition? How does the egg parasitoid recognize oviposition-induced volatile patterns within a jungle of other volatile cues? How important are these oviposition-induced plant cues for host location behavior of egg parasitoids in comparison to other informative chemicals? In the following, these and other questions will be addressed with respect to molecular, physiological, behavioral, and evolutionary aspects.

The Plant and its Response to Insect Egg Deposition

The Interface between Plant and Eggs

Since so far mostly leaves have been studied and found to display oviposition-induced defenses, a closer morphological view of the interface between leaves and eggs of herbivorous insects is presented here (Table 1). The degree of how tightly an egg is associated with the leaf varies greatly and may also depend on the physicochemical characteristics of the leaf surface (Müller and Riederer, 2005). Eggs may be attached just loosely to a leaf like the eggs of the willow leaf beetle, *Phratora vulgatissima*, which are laid on the lower side of a willow leaf (Fig. 1A, B). In this species, the secretion coating the eggs has only very loose contact with the plant surface. The egg adheres especially to the trichomes of the lower plant surface (Fig. 1C). The eggs of many lepidopteran species are tightly glued onto the lower leaf surface. In *Pieris brassicae*, sometimes surface scratches are visible on Brussels sprouts leaves with eggs (Nina Fatouros, personal communication). In the samples studied here, the surface of Chinese cabbage leaves with eggs has not been observed to be damaged before oviposition (Fig. 1D). The transparent shiny secretion of the accessory glands of *P. brassicae* females is not only found directly associated with the eggs, but also smeared on leaf tissue around the egg mass. Where secretion touches the leaf surface, the tissue becomes brownish (Fig. 1E). It is not yet known whether this is due to the closure of stomata by the secretion (Fig. 1F, G) and subsequent death of the cells, or whether it is a hypersensitive response. In contrast, some herbivorous insects damage the leaf at the site of oviposition. This damage may be limited to the epidermis and the adjacent spongy parenchyma, as has been observed for the elm leaf beetle (Fig. 1H–J). The elm leaf beetle prefers to lay eggs on leaf veins (Meiners and Hilker, 1997), thus getting close to the vascular bundles after removal of the epidermis (Fig. 1K, L). Other herbivorous insects severely damage leaf tissue, as has been described for the egg deposition of pine sawflies, which slit a needle tangentially with the ovipositor, remove parenchymatic tissue, and damage one vascular bundle (Hilker et al., 2002a).

The different degrees of egg attachment on or insertion into leaf tissue suggest that different cells of a leaf are able to perceive the information that an egg has been laid. When eggs of *P. brassicae* just touch the wax layer, egg components eliciting the plant's defensive response probably need to move across the wax layer to the epidermal cell wall (Fatouros et al., 2005a). In the elm leaf beetle, the elicitor inducing the oviposition-induced defense (Meiners and Hilker, 2000) is probably interacting with the parenchymatic tissue. Since sawflies deeply disrupt pine needle tissue, all types of damaged cells (e.g., epidermal cells, parenchymatic tissue, endodermal cells) need to be considered as being able to perceive the information of a recent egg deposition (Hilker et al., 2002a).



Microorganisms in the Interface between Plants and Eggs

Are leaves, insect eggs, and/or their mothers the only interacting organisms for oviposition-induced plant responses, or are hidden players such as microorganisms involved (Dicke and Hilker, 2003)? When damage is inflicted to leaf tissue prior to oviposition (see Table 1), microorganisms might invade wounds and contribute to the oviposition-induced response. These microorganisms or their products might be transferred from the insect into the wound. Furthermore, microorganisms living on the plant surface where they may occur as symbionts, commensalists, or phytopathogens might be involved in the induction process (Dickinson and Preece, 1976; Morris et al., 1996; Kinkel, 1997; Varma et al., 2004). However, wounding is known to be insufficient to induce indirect defensive responses that attract egg parasitoids. In bean leaves, feeding damage *per se* does not induce the release of volatiles that attract the egg parasitoid *Trissolcus basalis* (Colazza et al., 2004a). Also, feeding damaged elms do not emit volatiles that attract egg parasitoids (Meiners and Hilker, 1997). Neither do the ovipositional wounds conducted by the elm leaf beetle (with the mandibles) or by the pine sawfly (with the ovipositor) induce a volatile pattern to which the respective egg parasitoid responds positively (Meiners and Hilker, 2000; Hilker et al., 2002a). Thus, induction of plant defensive responses by insect egg deposition obviously requires elicitors that are specific for the egg or egg-associated components rather than elicitors produced by microorganisms living on the plant surface.

Plant defensive responses to feeding activity have been discussed as being elicited by components produced by microorganisms in the insect gut and then released via

Fig. 1 Mode of attachment of eggs of herbivorous insects to leaf surface. (A) Egg mass of the willow leaf beetle *P. vulgatissima* on a hairy leaf of *Salix viminalis*. Leaf trichomes (tr). Transparent secretion (s) visible on the top of the eggs. Bar = 500 μm. (B) Cross section (overview) through a leaf of *S. viminalis* with an egg of *P. vulgatissima* on the lower surface. Overview. ey, egg yolk; ec, egg chorion; l, leaf. Bar = 200 μm. (C) Close view on cross section through a leaf of *S. viminalis* with an egg (eg) of *P. vulgatissima* on the lower surface. It is just adhered to the trichomes (tr) and hardly has any contact with the lower epidermis (ep). sm, spongy mesophyll; pm, parenchymatic mesophyll; ec, egg chorion; ey, egg yolk. Bar = 50 μm. (D) Egg mass of *P. brassicae* on the lower surface of a *Brassica oleraceae* leaf. Bar = 1 mm. (E) Egg mass of *P. brassicae* partially removed from the leaf. The red lining shows where the eggs lay prior to removal. Leaf tissue turns brownish underneath the eggs and right next to them around the egg mass. s, shiny transparent secretion. Bar = 1 mm. (F) Cross section (overview) through a cabbage leaf (l) with eggs (ey, egg yolk; ec, egg chorion) of *P. brassicae*. The epidermis (ep) is not damaged. The eggs are closely attached to the epidermis. Bar = 200 μm. (G) Close view on cross section through a cabbage leaf with eggs of *P. brassicae*. The egg chorion (ec) covered by secretion (s) is tightly attached to the epidermis (ep) and is even covering the stomata (sto). Bar = 50 μm. (H) Egg mass of the elm leaf beetle *X. luteola* on the lower surface of an elm leaf, *Ulmus minor*. The lower part of the egg mass has been removed. At the place where eggs have been removed, the epidermal wounding (epw) is visible, which a female is conducting at the oviposition site with her mouth parts prior to egg laying. This epidermal wounding is clearly distinguishable from a feeding hole (fh) visible on the lower left side of the photo. Bar = 1 mm. (I) Cross section (close view) through an elm leaf with eggs of the elm leaf beetle. The epidermal cells and spongy mesophyll cells are removed so that the egg with chorion (ec) and secretion (s) adheres to the parenchymatic mesophyll cells (pm). Bar = 100 μm. (J) Cross section (close view) through an elm leaf without eggs. ep, epidermis; sm, spongy mesophyll; pm, parenchymatic mesophyll cells. Bar = 507 μm. (K) Cross section (close view) through an elm leaf vein with an egg mass of the elm leaf beetle on it. The epidermal cells and mesophyll cells are removed so that the eggs with their secretion (s) are closely attached to the parenchymatic cells surrounding the vascular bundle (ph, phloem; x, xylem; ec, egg chorion; ey, egg yolk). Bar = 100 μm. (L) Cross section (close view) through an elm leaf vein without egg mass. The intact vascular bundle is visible with the xylem (x), phloem (ph), and the parenchymatic cells (pc) surrounding the vascular bundle. Bar = 100 μm the regurgitate into the plant wound during feeding (Spiteller et al., 2000). However, Tumlinson and Lait (2005) have argued that the bacterial biosynthesis rates of the analogs of eliciting components presented by Spiteller et al. (2000) are much too low to meet the requirements for a necessary rapid elicitor accumulation. Instead, they found evidence that fatty acid amide elicitors are biosynthesized in the membranes of the crop and anterior midgut tissues of lepidopteran larvae (Lait et al., 2003). Up to now, there are no hints that endosymbiotic microorganisms are involved in the production of egg-associated elicitors, even though symbiotic microorganisms are well known to be deposited with the eggs (e.g., Hilker, 1994; Kellner, 2002).

The Elicitor of Oviposition-Induced Plant Responses

If the plant is not wounded by oviposition and eggs just "touch" the plant surface, the components necessary for eliciting an oviposition-induced plant response might act either just via induction by touching or they may need to pass the waxy plant cuticula to reach the epidermal cells.

Plant responses to touch and wind have been summarized by Schaller and Weiler (2002). These responses range from changes of the cytosolic calcium concentration to an increase in ethylene production. Both changes of calcium concentrations (Arimura et al., 2000; Maffei et al., 2004) and accumulation of reactive oxygen species are also well known to occur in response to feeding herbivores (e.g., Felton and Eichenseer, 1999, and references therein).

If just the touch of the plant surface by insect eggs is not sufficient to elicit the defensive response and when no wounding occurs along with egg deposition, then the eliciting components associated with the eggs need to gain access to the plant epidermal cell. Thus, they need to be either highly lipophilic to pass the waxy plant surface, or need to possess the ability to "cut" their way enzymatically through the plant cuticula, or need to be accompanied by components smoothing their way (compare e.g., Rosetto et al., 2003). When the elicitor has reached the epidermal cell wall, it might act via receptors or form channels to enter the cell. Truitt et al. (2004) provide evidence that volicitin, an elicitor from the regurgitate of lepidopteran larvae that induces indirect plant defenses, is binding with a plasma membrane protein of the wounded plant (Alborn et al., 1997). When considering the ability of an elicitor to induce plant volatiles, Engelberth et al. (2000) suggest that formation of "pores" is also a possible mechanism. Several channel-forming components especially from phytopathogenic fungi are known to change permeability of biomembranes (Minardi, 1995; Zimmermann et al., 1999; Engelberth et al. 2000). However, they have not been described yet from insect eggs.

If plant cells are wounded by oviposition, an elicitor might enter them via the disrupted cell membrane. In addition, microwounding of the leaf surface that is visible only at high magnification will need closer consideration in future. For example, insect females might easily scratch the leaf surface by ovipositor hairs when laying eggs. Similarly, crawling of insect larvae also has been found to leave microwoundings on the leaf surface that are only visible by REM (Hall et al., 2004). These "larval footsteps" induce significant plant responses, such as increases of superoxide concentrations and GABA accumulation (Bown et al., 2002).

The chemistry of the elicitor of a direct plant defensive response to egg deposition is known only from bruchid beetles (Table 1). Their eggs laid onto pea pods induce the formation of neoplasms. The elicitors are long-chain α, γmonounsaturated C_{22} diols and α, γ-mono- and diunsaturated C_{24} diols, mono- or diesterified with 3-hydroxypropanoic acid.

The elicitors of indirect oviposition-induced plant defensive responses studied so far have been detected in the secretion coating the eggs and adhering them to plant tissue. In both the elm leaf beetle and in the pine sawfly, this secretion is produced in the *oviductus communis* (Meiners and Hilker, 2000; Hilker et al., 2002a). When applying these secretions onto artificial wounds of leaf tissue that mimic the wounding applied by the female prior to egg deposition (see above), the oviduct secretion *per se* is able to induce the indirect plant response, and no eggs are necessary for this eliciting process. For the pine sawfly, it has been shown that the oviduct secretion looses its activity when treated with a proteinase. The oviduct secretion only keeps its eliciting activity if kept in Ringer solution. Storage in just water results in a loss of activity. Hemolymph of the pine sawfly has no eliciting activity. A comparison of hemolymph and oviduct secretion by SDS-PAGE revealed that oviduct secretion contains a small protein that is not present in the hemolymph. Therefore, this protein is a candidate component that needs to be isolated and tested for its eliciting activity in future studies by applying it into wounded pine needle tissue like the sawfly females does during oviposition (Hilker et al., 2005).

A further candidate as elicitor of oviposition-induced plant responses might be jasmonic acid (JA), which has been detected inside the eggs of several lepidopteran species in much higher concentrations than in plant tissue or larval diet. “Chorions appear to contain small amounts of JA” (Tooker and De Moraes, 2005). It is not yet known whether JA is indeed present at the very outer surface of the eggs. The fact that the leaf surface is usually not visibly damaged when moths deposit eggs raises the question of how JA can invade the plant cell through a waxy egg chorion and a lipophilic plant cuticle.

Plant physiological and molecular processes that are initiated by an oviposition-associated elicitor are almost a black box. When considering the direct plant response to bruchid eggs, enhanced mitogenesis was observed. However, it is unknown how this is controlled and leads to a neoplasm with limited growth. In rice plants, a specific gene (*ovc*) is induced by egg deposition of a planthopper. This gene is involved in the production of the ovicidal substance, benzyl benzoate (Yamasaki et al., 2003). Indirect plant responses to insect egg deposition require modification of the biosynthetic activity of the terpenoid pathways especially, since changes of the quantity and/or quality of the plant’s terpenoid volatiles have been detected for egg-laden bean and elm leaves as well as for pine needles with eggs (Wegener et al., 2001; Mumm et al., 2003; Colazza et al., 2004b). For example, pine needles with eggs emit the sesquiterpene (*E*)-β-farnesene in higher quantities than do egg-free pine needles (Mumm et al., 2003). Current studies address the question of how the increase of (*E*)-β-farnesene in the headspace of egg-laden pine needles is regulated at the molecular level.

Systemically Induced Plant Responses

In elm, pine, and beans (see Table 1), the defensive plant response is not strictly limited to the site of egg deposition, but egg-free leaves adjacent to the site of oviposition also release volatiles attractive for the egg parasitoids. Egg-free leaves adjacent to egg-laden ones might just adsorb the oviposition-induced volatiles produced by egg-carrying leaves and release them again with some delay. However, it has been proved experimentally that no such adsorbance, but systemic induction, occurs. Egg-free leaves adjacent to egg-laden ones indeed show a systemically induced response (Meiners and Hilker, 2000; Hilker et al., 2002a; Colazza et al., 2004a).

How is the signal systemically transferred in the plant from the egg-laden part to the adjacent egg-free part? Application of jasmonic acid (JA) through the cut elm and pine twig, respectively, revealed that this treatment also leads to a volatile pattern attracting the respective egg parasitoids. Comparisons of the components of the headspace of JA-treated twigs and untreated controls show that the pattern is not identical to the one of oviposition-induced twigs, but very similar. For example, JA-treated pine twigs also show a significant enhancement of the emission of (*E*)-β-farnesene. These results indicate that JA might act as a hormone transferring the information from the oviposition-induced site to adjacent, egg-free parts of the plant.

The Egg-Laying Herbivore

The defensive responses of a plant may deliver not only information on the herbivore presence to the third trophic level, but also on the degree of infestation and the defense status to the herbivores themselves. Several studies are available showing that the emission of leaf volatiles in response to herbivore attack is exploited by the herbivores themselves. As outlined below, most of these studies address the herbivore's response to feeding-induced plant volatiles. We are just starting to analyze the herbivore's behavior in response to oviposition-induced volatiles.

The Herbivore's Response to Feeding-Induced Plant Volatiles

If herbivore-induced plant volatiles convey information on the presence of competitors or the risk of high predation and parasitization, herbivorous insects should avoid such plants. Indeed, herbivorous females about to oviposit can be strongly deterred by feeding-induced plant volatiles. For example, the cabbage looper, *Trichoplusia ni*, is less attracted to cabbage damaged by larval feeding and laid fewer eggs on feeding-damaged plants (Landolt, 1993). In addition, females of *Heliothis virescens* are significantly deterred from oviposition by the nocturnal volatiles of feeding-damaged tobacco plants (De Moraes et al., 2001). Similarly, females of *Manduca quinquemaculata* lay fewer eggs on feeding-damaged and JA-treated plants (Kessler and Baldwin, 2001).

If herbivore-induced plant volatiles inform herbivores about the presence of a suitable host plant or the presence of mates or gregarious partners, they are expected to be attracted to these plants (Loughrin et al., 1996; Ruther et al., 2000). Several studies are available showing herbivore attraction to feeding-induced plants (Landolt, 1993; Harari et al., 1994; Loughrin et al., 1996; Bolter et al., 1997; Dicke and van Loon, 2000; Kalberer et al., 2001; Prokopy and Roitberg, 2001; Horiuchi et al., 2003). For example, female *Plutella xylostella* show oviposition preferences for cabbage plants already damaged by conspecific larvae, even though these plants also attract larval parasitoids. Shiojiri and Takabayashi (2003) suggest that this oviposition behavior of *P. xylostella* may be beneficial for the herbivore since it might result in an encounter-dilution effect against the larval parasitoid.

The Herbivore's Response to Oviposition-Induced Plant Volatiles

As suggested by Kessler and Baldwin (2002), the exploitation of herbivore-induced plant volatiles by the herbivores themselves might favor selection for genetic variation in emission of induced volatile compounds in natural plant populations. In the systems studied so far, the phenotypic variation of induced plant odor is obviously not sufficient to prevent its exploitation by herbivores. For example, studies on the response of the elm leaf beetle to oviposition-induced elm volatiles indicate that this beetle is able to adjust its response to plant volatiles according to the infestation rate.

Females of the elm leaf beetle *Xanthogaleruca luteola* orientate to volatiles of both untreated elm leaves and differently treated ones (treatment by feeding, mechanical damage, oviduct secretion). However, when elm twigs are heavily infested by eggs and additionally damaged by feeding of conspecifics, female *X. luteola* clearly avoid such twigs. Odor from uninfested leaves is significantly preferred to odor from heavily infested leaves (feeding damage and eggs). In contrast, at low infestation levels, the beetle's response changes. Odor from uninfested leaves is no longer preferred, but instead volatiles from elm twigs poorly infested by some conspecifics (feeding damage and egg deposition) become highly attractive. The elm leaf beetle females also prefer to lay eggs upon uninfested leaves over heavily infested ones (Meiners et al., 2005).

The herbivore's response to elm leaf odor in dependence of the infestation level would be especially adaptive if the egg parasitoid's response to oviposition-induced elm leaf odor also follows these dependencies. The egg parasitoid *Oomyzus gallerucae* is attracted by odor from elm leaves with eggs and feeding damage (Table 1). Odor from feeding damaged leaves without eggs does not attract the egg parasitoid (Meiners and Hilker, 1997, 2000). However, we do not know yet whether the egg parasitoid prefers odor from leaves with a high egg load to odor from leaves with few eggs and little feeding damage. If so, the herbivore's risk of egg parasitization at low infestation levels is expected to be lower, thus rendering the herbivore's preference for low-infested leaves over heavily infested ones advantageous.

Elms might differ in their thresholds and lag times to produce and emit induced volatiles. Underwood et al. (2005) show in a model and in a field study that increasing lags and thresholds for the production of induced resistance traits might cause increasing aggregation of herbivores and their damage. Herbivores might have adapted to link the induced plant volatiles (kairomones) with the potential presence of suitable host plants. Local densities of elms, beetles, and parasitoids might determine the outcome of this tritrophic interaction (Meiners et al., 2005).

Egg Parasitoids and Predators

Complexity of Plant Odor and the Role for Host/Prey Location

Indirect oviposition-induced plant responses address egg parasitoids and predators of eggs. Plant volatiles or changes of leaf surface chemicals induced by egg deposition provide reliable information on the presence of hosts and prey. Furthermore, the large plant biomass when laden with eggs releases oviposition-induced volatile information in quantities that can easily be detected. However, egg parasitoids and predators are also able to respond to volatiles from plants without host eggs (see review by Romeis et al., 2005) or with feeding damage only (Kessler and Baldwin, 2001).

Volatiles from feeding-induced plants do not provide carnivores with information on the presence of eggs, but just give a hint on the infestation of the plant. Carnivores responding to these volatiles are not expected to be specialized to prey upon eggs, but instead to be generalists. If they are specialists, they might be forced to take a chemical detour (Vet and Dicke, 1992) because other cues are not available. Indeed, the generalist carnivorous bug *Geocoris pallens* is attracted by feeding-induced plant volatiles and then preys upon the eggs found on such plants (Kessler and Baldwin, 2001). Among the feeding-induced plant volatiles, the release of the so-called general green leaf volatiles (i.e., C_6 aldehydes, C_6 alcohols and their esters) has been shown in numerous studies to increase after feeding damage (Karban and Baldwin, 1997; Dicke and Hilker, 2003). Also, carnivores specialized on insect eggs have been shown to be attracted by these volatiles. For example, *Trichogramma chilonis* shows a positive response to green leaf volatiles such as (*Z*)-3-hexenyl acetate and hexyl acetate (Reddy et al., 2002). These volatiles are also known to be emitted in small amounts by uninfested plants, and volatiles from uninfested plants often have been found to act as attractants or parasitization stimuli for *Trichogramma* spp. (for references: see Romeis et al., 2005). Also, surface extracts of leaves without eggs can stimulate parasitization (Nordlund, 1994; Dirie and Gabriel, 1998). However, volatiles from undamaged host plants may also act as repellents for egg parasitoids (Nordlund, 1994; Romeis et al., 1997, 1998). Thus, the response of egg parasitoids to plant volatiles is of high genotypic and phenotypic plasticity (De Jong and Pak, 1984; Bjorksten and Hoffmann, 1998; McGregor and Henderson, 1998). Among the factors influencing the egg parasitoid's response to chemical stimuli, the role of previous experience to these chemicals has been studied intensively (Vet and Dicke, 1992; Steidle and van Loon 2002a,b).

The chemical context in which plant volatiles are perceived is important for a parasitoid's response. During host location, the larval parasitoid *Microplitis croceipes* can learn compounds in a mixture (Meiners et al. 2003). Another braconid wasp, *Cotesia kariyai*, learns a blend of unspecific plant compounds better when it is embedded in a blend of specifically host-induced compounds (Fukushima et al., 2002). This context specificity of the response of parasitoids to plant volatiles seems to play a role when considering responses of egg parasitoids to oviposition-induced plant volatiles.

The olfactory background in which the stimuli are presented can affect recognition of individual compounds (Meiners et al., 2003). Studies on the response of *Chrysonotomyia ruforum* to pine volatiles induced by oviposition of the pine sawfly (Table 1) revealed that it is important for the egg parasitoid to perceive the oviposition-induced volatile together with the background of noninduced pine volatiles. (*E*)-β-Farnesene is the only component detected that occurs in significantly higher quantities in oviposition-induced pine than in egg-free controls (Mumm et al., 2003). However, even experienced egg parasitoids are not attracted to (*E*)-β-farnesene, at either concentration tested. When this sesquiterpene is offered in a mixture with odor from egg-free pine, however, it becomes attractive. Odor from egg-free pine does not attract the parasitoid (Mumm and Hilker, 2005). Thus, to attract this parasitoid it is necessary to contrast the oviposition-induced volatile with other plant volatiles. Although a background contrast is well known to be important for the perception of color, the importance of background odor has been somewhat neglected so far for the detection of specific volatiles (Smith, 1998; Kelling et al., 2002). However, since induction of plant volatiles by egg deposition often involves small quantitative or qualitative changes of the plant odor, the background context at which these induced volatiles are perceived might be very important to detect them within the plethora of other volatiles.

Time Frame of Oviposition-Induced Plant Responses

Oomyzus gallerucae, the major egg parasitoid of the elm leaf beetle, was shown to respond to volatiles from elm leaves with eggs 3 hr after herbivore egg deposition (Table 1). The attractiveness of odor from elm leaves with eggs vanishes when eggs are being laid for more than 5 d on an elm leaf and are close to larval hatching (Meiners, unpublished data). In other systems, the time scale of indirect plant responses to oviposition is larger. *Chrysonotmyia ruforum*, a eulophid wasp parasitizing the eggs of the pine sawfly *Diprion pini*, is not attracted by odor from pine needles with 1-d-old eggs, but 3 d after egg deposition, odor from pine needles is attractive (Hilker, unpublished data; Hilker et al., 2002a). *T. basalis*, an egg parasitoid of the Southern green stink bug *Nezara* viridula, is attracted to volatiles from egg-laden bean leaves until the host eggs are about 3 to 4 d old. After 5 d, *Nezara* eggs become unsuitable for parasitization (Colazza et al., 2004a).

The studies by Fatouros et al. (2005a) indicate that a trichogrammatid egg parasitoid is arrested by oviposition-induced leaf surface chemicals at a time when eggs are most suitable for parasitization, i.e., 3 d after egg deposition. *Trichogramma brassicae* females most successfully parasitize 3-d-old eggs of the large white cabbage butterfly. About 80% of 3-d-old eggs are parasitized, whereas the rate of successful parasitization of freshly laid eggs and 1-d-old eggs is about 40% and 55%, respectively. The trichogrammatid wasp is also arrested on leaves with freshly laid eggs and 1-d-old eggs. However, this arrestment is due to scales and possibly other deposits left by the ovipositing female. When these host cues have lost their arresting activity 3 d after oviposition, the eggs seem to have induced a change of surface chemicals that act as arrestants at this time. Thus, in this system, the trichogrammatid wasp is first arrested by host cues, and only later, when host eggs have become most suitable, do oviposition-induced leaf contact cues seem to play a role.

All of these examples indicate a fine-tuned and cost-efficient time frame for the release of volatile or contact synomones by egg-infested plants. This is characterized by providing notice of the presence of suitable eggs and by ceasing the emission of synomones when the eggs are unsuitable. This guarantees that parasitoids will respond to an honest signal, and fosters the evolution of perceiving those signals and responding to them.

Oviposition-Induced Synomones and/or Kairomones

What is the importance of host cues and oviposition-induced plant signals for host location? Fatouros et al. (2005a) did not detect an olfactory response of *T. brassicae* to volatiles from Brussels sprouts leaves with eggs. When studying the question of how this wasp locates host eggs from a distance, *T. brassicae* was found to locate mated host female butterflies by the anti-aphrodisiac benzyl cyanide, which the butterfly male transfers to the female during mating (Andersson et al., 2003). After location of a mated female butterfly, the wasp mounts the female, hitchhikes with her to the oviposition site, and descends as soon as eggs are laid (Fatouros et al., 2005b).

If egg parasitoids do not hitchhike with a host female (Clausen, 1976), highly volatile host female sex pheromones may attract them from some distance (e.g., Zuk and Kolluru, 1998). However, these pheromones just "promise" the presence of laid eggs. Also, aggregation pheromones, chemical cues from scales and frass, which all are known to act as kairomones for egg parasitoids (Vet and Dicke, 1992), just indicate that a host is around, but do not indicate with high reliability the presence of eggs. In contrast, oviposition-induced volatiles released locally and systemically by a large plant biomass reliably indicate the presence of laid eggs. Oviposition-induced plant volatiles, however, are obviously not always induced as soon as eggs are laid (see Table 1). Furthermore, an additional capability of egg parasitoids to respond to kairomones from, e.g., host frass (*O. gallerucae*), host sex pheromones (*Chrysonotomyia ruforum*), or volatiles from host females in the preovipositional state (*T. basalis*, *T. brassicae*) can act as a backup system for the egg parasitoids in cases when plants do not respond or do not respond strongly enough to egg depositions (Meiners and Hilker, 1997; Colazza et al., 1999; Hilker et al., 2000, Fatouros et al., 2005b).

Conclusions

A plant responding to oviposition of herbivorous arthropods is possibly acting early enough to prevent feeding damage by the larvae hatching from these eggs. Such an "early alert" may be especially advantageous for annual plants, which have a much smaller time and biomass budget with which to face feeding damage than perennials (Hilker et al., 2002a). However, trees also respond to insect oviposition by induction of volatiles (Table 1). Recently, oviposition-induced *Pinus sylvestris* was shown to lower photosynthetic activity in needles adjacent to the oviposition site (Schroeder et al., 2005). Thus, induced resistance (affecting the herbivore) might be paid here by reduced tolerance (affecting the plant) (Herms and Mattson, 1992). Further studies are needed that elucidate the costs or benefits of oviposition-induced plant responses with plant reproductive parameters as currency (e.g., fruit set, seed production).

The plant's investment in "early alert" responses to egg deposition might be wasted if the eggs were to suffer mortality due to unsuitable abiotic conditions, such as, for example, high dryness. We need to study whether a plant is able to perceive egg mortality and stop the inductive process. Further, a plant might be able to minimize costs of induction by limiting the induced response only to a narrow time frame when eggs are most acceptable to egg parasitoids. The study by Fatouros et al. (2005a) on induction of Brussels sprouts by *Pieris* eggs indicates such a narrow time window during which induction by egg deposition occurs. However, other studies, such as the one described above on induction of elm by leaf beetle eggs, show a much broader time frame of induction (Meiners, unpublished data). We do not yet understand which parameters drive the selection of narrow and broad time frames for induction by egg deposition.

When induction of plant defense by insect egg deposition is considered an "early alert" strategy, it might be objected that plants induced by volatiles released from their neighbor plants respond even earlier, i.e., prior to being encountered by a herbivore. Up to now, chemical information transfer has only been shown between feeding-damaged and undamaged plants (Dicke and Bruin, 2001). However, if a plant could also "listen" to oviposition-induced cues of its neighbor plants, this "information" might be the earliest possible information on the danger of attack by an herbivore. Such "listening" to oviposition-induced cues of the neighbor plant might enhance the inducibility of the nonattacked plant in such a way that it could respond sooner or stronger when egg deposition occurs. We do not know yet whether cues from oviposition-induced plants are able to "inform" non-attacked plants next to egg-laden ones about danger. Future studies also need to elucidate whether oviposition-induced cues are able to act as an early alert in interplant communication.

Finally, we need to examine whether there is a trade-off between induction of plant defenses by oviposition and feeding, or whether these defensive strategies addressing different stages of the herbivore act effectively *in concert*.

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