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Specificity of herbivore-induced plant defences

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Abstract

In addition to induced direct defence, plants can defend themselves indirectly by improving the effectiveness of enemies of herbivores. Plants can respond to arthropod herbivory with the induction of a blend of volatiles that attracts predators and/or parasitoids of herbivores. Carnivorous arthropods can discriminate between infested plants and mechanically wounded plants, and between plants infested by different herbivore species. The volatile blends emitted by different plant species infested by the same herbivore show large qualitative differences, whereas blends emitted by plants of the same species, but infested by different herbivore species are mostly qualitatively similar with quantitative variation. Carnivores can discriminate between blends that differ qualitatively and/or quantitatively. However, it remains unknown what differences in blends are used by carnivorous arthropods in this discrimination.

Signal-transduction pathways involved in the induction of direct and indirect defence seem to overlap. Direct and indirect defence may interfere with each other's effectiveness. For application of direct and indirect defence in agriculture, it is important to compare the relative importance of these two defence types in the same plant species.

Introduction

Insects dominate the world's fauna in terms of number of species and individuals. Plants are under the constant threat of being attacked by insects. They have evolved a fascinating array of defences that can be grouped into two categories: (1) direct defence that affects the attackers directly through e.g. toxins, repellents, digestibility reducers, spines and thorns and (2) indirect defence that promotes the effectiveness of natural enemies of herbivores through e.g. the provision of shelter, alternative food or the production of SOS-signals that enable carnivorous arthropods to locate the herbivores. Each of these two defences can be constitutively present or can be induced by attack.

This chapter will concentrate on induced defences and especially on the relative contribution of induced direct and induced indirect defence. The induction of defences may occur in response to mechanical damage and/or herbivore damage. Whether a plant responds differently to mechanical damage vs. herbivore damage or to different herbivore species is a measure of the specificity of the plant's induced response. Different degrees of specificity of the plant's response to damage can be distinguished, depending on quantitative and qualitative differences in the responses to mechanical damage, and damage inflicted by different herbivore species. Qualitative differences in plant response characterise a higher degree of specificity than quantitative differences.

Induced direct defence

Induced direct defence against herbivores has been recorded since the 1970's for more than 100 plant species in 34 families (Karban & Baldwin 1997). Induced direct defence can comprise the induction of various characteristics such as toxins, digestibility reducers, repellents and trichomes (Karban & Baldwin 1997). Several plant species, such as tomato, potato, tobacco, and cotton have been studied in considerable depth.

Specificity of induced direct defence: chemical and biological evidence.

In many cases direct defence can be induced by mechanically wounding a plant or by herbivore feeding damage, often with similar effects. For instance, mechanical wounding just like herbivore damage results in the induction of proteinase inhibitors in tomato and potato plants, leading to a reduction of the digestibility of plant tissues for herbivores (Green & Ryan 1971). Mechanical wounding and caterpillar (*Manduca sexta*) damage both induce the production of nicotine in tobacco plants, albeit that caterpillar damage results in lower levels of nicotine than mechanical damage (McCloud & Baldwin 1997). However, some reports demonstrate that induced plant responses can be specific for the type of damage that is inflicted. For instance, caterpillars (*Helicoverpa zea*),

leafminer flies (*Liriomyza trifolii*) and russet mites (*Aculops lycopersici*) induce different combinations of polyphenol oxidase, peroxidase, lipoxygenase and proteinase inhibitors in tomato plants (Stout et al. 1994).

When studying the effect on herbivores, specificity may be more difficult to detect. Different plant responses may have a similar effect on herbivores because each combination of induced responses negatively affects subsequent herbivores attacking the plant. In fact, the induction of toxins and more likely that of digestibility reducers will affect a range of insects. This is similar to the observation that constitutively present secondary plant chemicals have similar effects on a variety of herbivore species, with only specialist species being able to overcome the effects of the phytochemicals. For example, spider mite damage to cotton plants results in lower population increase during subsequent spider mite infestations (Karban & Carey 1984). Similar results are obtained with mechanical wounding or fungus (*Verticillium dahliae*) infestation (Karban et al. 1987).

Induced indirect defence

The major form of induced indirect defence is the emission of herbivore-induced plant volatiles that attract carnivorous enemies of the herbivores. This induced defence has been reported since the 1980's for more than 20 plant species in 13 families (see review by Dicke 1998). Two major categories of plant response may be distinguished (Dicke 1998). (1) The emission of large amounts of novel compounds that dominate the blend from herbivore-induced plants. These novel compounds are not, or only in trace amounts, emitted by undamaged plants or by mechanically wounded plants. Examples comprise Lima bean, corn, and cucumber. (2) Plants that emit qualitatively similar but quantitatively different blends in response to herbivory or mechanical wounding or when undamaged. Examples are e.g. tomato, potato, and cabbage. A large amount of information is present on the effect of these induced plant volatiles on the behaviour of carnivorous arthropods such as predators and parasitoids. Herbivore-induced plant volatiles are very important to carnivorous arthropods. Their herbivore victims usually do not emit large amounts of volatiles: they are small components in the environment, and the emission of volatiles that attract their enemies is strongly selected against. Volatiles from undamaged plants, though more abundant than herbivore volatiles, do not provide information to carnivores on herbivore presence. In contrast, plant volatiles induced by herbivory are both well-detectable and often reliable indicators of not only herbivore presence but also herbivore identity. Thus, herbivore-induced plant volatiles provide a solution to the reliability-detectability problem that carnivorous arthropods face and

consequently the production of herbivore-induced plant volatiles is an important mechanism of increasing the effectiveness of carnivorous enemies of herbivores (Vet & Dicke 1992).

Specificity of herbivore-induced plant volatiles: chemical and behavioural evidence.

Induced carnivore attraction can occur rather specifically. This is obvious from chemical as well as behavioural evidence. Many plant species emit volatile blends that are qualitatively very different in response to mechanical or herbivore damage (Dicke 1998). For instance, Lima bean leaves infested with spider mites emit a blend that is qualitatively very different from that emitted from mechanically wounded Lima bean leaves (Dicke et al. 1990). The predatory thrips *Scolothrips takahashii* discriminates among volatiles from spider-mite infested Lima bean leaves and mechanically wounded Lima bean leaves; they are not attracted by mechanically wounded leaves (Shimoda et al. 1997). However, even when qualitative differences are absent or minor, carnivores may discriminate between mechanically damaged and herbivore-damaged plants. Cabbage leaves infested with *P. brassicae* caterpillars emit a qualitatively similar blend as mechanically wounded cabbage leaves, but caterpillar-infested leaves emit larger amounts and for a longer time period after damaging the plant halts (Mattiacci et al. 1994). The parasitoid *Cotesia glomerata* is attracted by mechanically wounded cabbage leaves, but when offered vs. cabbage leaves infested with their hosts, *Pieris brassicae* caterpillars, they prefer the volatiles from caterpillar-infested cabbage leaves (Steinberg et al. 1993). Plants can also emit different volatile blends in response to pathogens or herbivores. For instance, bean plants (*Phaseolus vulgaris* cv. Red Mexican) that are infested with the bacterium *Pseudomonas syringae* pv. *phaseolica* emit a blend of volatiles that is produced through the lipoxygenase pathway, with (Z)-3-hexen-1ol as major component, but no terpenoids are emitted (Croft et al. 1993, A.J. Slusarenko, pers. comm.). In contrast, when bean plants of the same cultivar are infested with the spider mite *Tetranychus urticae*, the plants emit a blend in which (Z)-3-hexen-1ol is a minor component, several terpenoids are induced and the homoterpene 4,8-dimethyl-1,3(E),7-nonatriene is the dominant blend component (M. Dicke & M.A. Posthumus, unpubl. data; Figure 1).

In addition to differences in response to mechanical wounding, pathogen infestation and herbivory, plants may also emit different blends when infested by different herbivore species. For instance, apple foliage infested with either of two herbivorous mite species, *Panonychus ulmi* or *Tetranychus urticae*, emit blends that, although qualitatively similar, differ in the relative contribution of the compounds to the total blend (Takabayashi et al.

1991). Carnivorous mites discriminate between volatiles emitted by apple plants infested by either of the two herbivorous mite species. The predators *Amblyseius finlandicus* and *A. andersoni* are attracted to apple foliage infested with *P. ulmi*, their preferred prey species and not to apple foliage infested with *T. urticae*, while the carnivore *Phytoseiulus persimilis*, a specialist predator of *T. urticae* has the reverse response (Sabelis & Dicke 1985). These quantitative differences in blend composition may allow the predatory mites to discriminate. However, it cannot be excluded that qualitative differences in components that were present below the detection level of the equipment, play a role. In some systems, chemical analyses reveal hardly any differences in blend composition, either in qualitative or in quantitative respect, while carnivorous enemies of the herbivores are able to discriminate among the blends. An example is the discrimination by the parasitoid *Cotesia glomerata* between cabbage plants infested by either caterpillars of *P. brassicae* or caterpillars of *P. rapae* (Geervliet et al. 1998). Chemical analyses revealed no qualitative differences and only minor quantitative differences among the blends of cabbage plants infested by either caterpillar species (Blaakmeer et al. 1994, Geervliet et al. 1997). The discrimination by the parasitoids was only recorded after several oviposition experiences (Geervliet et al. 1998). Learning to discriminate among very similar odour blends has been recorded for other carnivorous arthropods as well (Turlings et al. 1993, Vet et al. 1998, Dicke & Vet 1998). Moreover, a few examples are known where parasitoids that had no previous oviposition experience discriminated between odour blends emitted by plants infested with different herbivores. In these instances, the odour blends differed qualitatively (Takabayashi et al. 1995, Powell et al. 1998). The ability of carnivores to discriminate between plants infested by different herbivore species has been recorded for a range of plant-herbivore-carnivore systems (see Dicke & Vet 1998 for review).

What variation in blend composition is important to carnivorous arthropods?

Initially, odour blends emitted by herbivore-infested plants seemed to have a simple composition, comprising ca. 10-20 compounds (Dicke et al. 1990, Turlings et al. 1990). However, with the development of more sensitive analytical methods, more and more blend components have been identified. For instance, in 1990 we reported 17 compounds in the blend emitted by spider-mite infested Lima bean plants (Dicke et al. 1990). Recent analyses resulted in the identification of more than 60 compounds from the same odour blend (Dicke et al., unpublished data). Odour blends emitted by herbivore-infested plants may be composed of 100 or more compounds, many of which occur as minor constituents (Gols et al., unpublished data). The composition of the

volatile blends induced by herbivory varies with plant species, plant genotype, leaf age, time of the day and herbivore species or instar that damages the plant (Turlings et al. 1995, Takabayashi & Dicke 1996). Among plant species, blend composition varies qualitatively in many components although shared compounds also occur. Commonly induced compounds are e.g. the two homoterpenes 4,8,-dimethyl-1,3(*E*),7-nonatriene and 4,8,12-trimethyl-1,3(*E*),7(*E*),11-tridecatetraene (Dicke et al. 1990, Turlings et al. 1990, 1995, Takabayashi & Dicke 1996). In contrast, among plants of the same species blend composition varies predominantly quantitatively, leading to blends that differ in ratios of similar compounds (Takabayashi et al. 1991, Turlings et al. 1993, De Moraes et al. 1998).

Although a lot of knowledge exists on the chemical compositions of herbivore-induced plant odour blends and on the behavioural responses of carnivorous arthropods to the blends emitted by herbivore-damaged plants, little is known about the relative importance of blend components for the response of carnivores. This is partly due to the blends having a complex composition, which sharply contrasts to e.g. the composition of sex pheromones of moths. For instance, in studies on sex pheromones, the total number of compounds emitted from the pheromone gland is usually restricted to 2-10 (Carde & Minks 1997), while infested plants can emit tens to more than 100 different compounds (Turlings et al. 1993, Mattiacci et al. 1994, Gols et al. unpublished data). The parasitoid *Cotesia marginiventris* is attracted to a synthetic mixture of the 11 major components of the blend emitted by corn plants infested by their hosts, *Spodoptera exigua*. However, although the synthetic mixture was composed as a close mimic of the natural mixture, the parasitoids' response to the natural and synthetic mixture significantly differed (Turlings et al. 1991). This may have been due to minor components in the natural blend or to small differences in the 11 major compounds between the natural blend and the synthetic blend. The predatory mite *Phytoseiulus persimilis* is attracted to four chemicals identified in the blend emitted by Lima bean plants infested with their prey, the spider mite *Tetranychus urticae*, even though the compounds were offered individually (Dicke et al. 1990a). No comparison of the effect of the single components or a synthetic mixture of them and a natural odour blend has been made for this predatory mite.

The ability of carnivorous arthropods to discriminate among odour blends is significantly characterised by phenotypic plasticity. Important factors affecting behavioural responses are e.g. starvation, specific hunger, successful and unsuccessful foraging experiences (Vet & Dicke 1992, Turlings et al. 1993, Dicke et al. 1998, Vet et al. 1998, Vet, this volume). For instance, the parasitoid *C. marginiventris* was strongly attracted to a

synthetic odour blend made to mimic the natural, plant-emitted, odour blend after the wasps had a successful oviposition experience in the presence of the synthetic blend, but not after a successful experience in the presence of the natural odour blend (Turlings et al. 1991). Very subtle differences between odour blends may be learned by parasitoids and qualitative differences in odour blends can be learned with more ease than quantitative differences (Vet et al. 1998, Vet, this volume).

Some knowledge on the importance of variation in the composition of plant volatile blends for the behavioural response of arthropods is available for herbivorous beetles. The Colorado potato beetle is strongly attracted by volatiles emitted by potato foliage, either when undamaged, mechanically wounded, or damaged by herbivores (Visser & Ave, 1978, Bolter et al. 1997). Volatiles emitted by potato plants are not specific for potato, but are emitted by a wide variety of plant species. However, the composition of the *blend* is characteristic for potato. When individual components were added to the natural blend of potato so that quantitative variation in blend components was achieved, the behavioural response of the beetles was disturbed in several, but not all, treatments (Visser & Ave, 1978).

Elucidating how carnivores cope with variation in blends of herbivore-induced plant volatiles will be an exciting challenge, now that chemical information on variation in blend composition and the factors influencing behavioural responses of carnivores are well-known.

Specificity of SOS-signals: how do plants do it?

The differences in plant responses to herbivory and mechanical wounding can be explained by the involvement of herbivore oral secretions. The application of oral secretion onto a mechanical wound results in the same response as herbivory (Turlings et al. 1990, Mattiacci et al. 1994, 1995, Alborn et al. 1997). Oral secretions may also be applied through the plant's cut stem and then induce odour emission from undamaged plant leaves (Turlings et al. 1995). Oral secretions may also explain the specificity of the plant's response to different herbivores. For instance, corn plants infested with 1st/2nd instar caterpillars of *Pseudaletia separata* emit a different volatile blend than corn plants infested with 5th/6th instars. Plants infested with 1st/2nd instars attract the parasitoid *Cotesia kariyai* while plants infested with 5th/6th instars do not. When oral secretions from young and old caterpillars were applied onto a mechanical wound a similar difference in response of the parasitoids was recorded (Takabayashi et al. 1995). Interestingly, a single component of a herbivore's oral secretion can induce a complex volatile blend that is similar to the blend induced by herbivory (Mattiacci et al. 1995,

Alborn et al. 1997). The blend components result from several different biosynthetic pathways such as the isoprenoid, shikimic acid and lipoxygenase pathways. It remains unclear how a single herbivore elicitor can induce different pathways resulting in quantitative differences in blend composition. Herbivory (Blechert et al. 1995) and oral secretion (McCloud & Baldwin 1997) can induce jasmonic acid in plants and jasmonic acid application to Lima bean or corn plants results in the induction of e.g. the homoterpene 4,8,-dimethyl-1,3(*E*),7-nonatriene, which is also induced by herbivory (Hopke et al. 1994). However, it seems that jasmonic acid cannot fully explain the plant's response. For instance, the homoterpene 4,8,12-trimethyl-1,3(*E*),7(*E*),11-tridecatetraene is not induced in bean plants by jasmonic acid application (Hopke et al. 1994, Dicke et al., unpublished data). Also, in induced direct defence, jasmonic acid seems unable to explain the plant response completely (McCloud & Baldwin 1997). Induced indirect defence is expressed systemically (Takabayashi et al. 1991b, Turlings & Tumlinson 1992, Dicke et al. 1993) and a systemic elicitor can be extracted from plants (Dicke et al. 1993). The nature of this systemic elicitor remains unidentified. In systemic induction of nicotine production in tobacco plants jasmonic acid is involved and it may be the systemically transported elicitor (McCloud & Baldwin 1997).

Are direct and indirect defence similarly induced?

Signal-transduction pathways of induced direct and indirect defence seem to overlap. In both types of induced defence, the octadecanoid acid pathway through jasmonic acid seems to be central. However, the fact that different herbivores or their oral secretions can lead to different volatile blends also indicates that there are likely to be regulatory mechanisms that function differently in the two types of induced defence.

A problem for a sound comparison of signal-transduction in induced direct and induced indirect defence, though, is that signal-transduction in induced indirect defence is mainly studied for two plant species, bean and corn, that are characterised by differential responses to mechanical and herbivore damage in terms of induced volatiles. On the other hand, signal-transduction in induced direct defence is studied mostly for plants that have similar responses, in terms of induced volatiles, to these two different types of damage: tomato, potato, and cabbage. For an appropriate comparison of signal-transduction in induced direct and indirect defence it is important that future studies combine an investigation of each of these defence types in a single plant species. Possibly, some plant species are characterised by specific responses to different types of damage, while other plant species are characterised by non-specific responses.

Relative importance of direct defence vs. indirect defence

The two types of defence, direct and indirect defence, available to plants may interfere with each other's effectiveness. For instance, tomato plants have an important direct defence in the form of glandular trichomes. These trichomes immobilise and intoxicate herbivores (van Haren et al. 1987). However, these trichomes also negatively affect carnivorous arthropods, resulting in high carnivore mortality rates and thus in an impairment of indirect defence. Consequently, if tomato plants would attract enemies of herbivores, the carnivores would die on the plant rather than feed on the herbivores. It would be interesting to investigate whether the intensities of direct and indirect defence are negatively correlated. Some observations seem to support this. For instance, the emission of a herbivore-induced volatile blend that is similar to the blend induced by wounding seems more primitive than the emission of a blend that is dominated by novel compounds. Plants that do not emit novel dominant blend components are well-characterised by particular secondary metabolites that function as strong direct defences. Solanaceous plants like tomato and potato and crucifers like cabbage are well-known for alkaloids or glucosinolates respectively that confer strong resistance against many insect species. These plants emit similar blends in response to herbivory and mechanical wounding (Mattiacci et al. 1994, Bolter et al. 1997, Dicke et al. 1998). They are often used as food only by a limited number of specialist herbivores such as the Colorado potato beetle or cabbage whites. In contrast, plants that emit novel compounds that dominate the induced blend are plants such as corn and bean. These plants do not have such highly specialised secondary metabolites and can be used as food by various herbivore species. For a thorough elucidation of the question whether the development of direct and indirect defence are negatively correlated, a comparison of direct and indirect defence characteristics in a range of plant species is necessary.

Crop protection: combining direct and indirect defence

The question of the relative importance of direct and indirect defence is important for applications in agriculture. Direct defence can be applied in host plant resistance and indirect defence in biological control through predators or parasitoids. Pest management strategies have mostly been developed either through host plant resistance or through biological control. However, with a reduction of pesticide use the two methods of pest control will increasingly be applied in the same crop. Therefore, developments in either of the two pest control methods should take into consideration what the effects are on the other method so as to reach a synergistic set of control methods rather than a net reduction in pest control effectiveness.

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Figure legends

Figure 1: Headspace composition of uninfested or spider-mite-infested (*Tetranychus urticae*) bean plants (*Phaseolus vulgaris*, cultivar Red Mexican) Total peak areas (arbitrary units) recorded for spider-mite infested plants was 427 and 834, and for undamaged plants 65 and 0

Compound numbers: 1= 2-butanone; 2= 3-pentanone; 3= 2-methylpropanenitrile; 4= 1-penten-3-one; 5= 2-butanol; 6= 1-penten-3-ol; 7= limonene; 8= (*E*)-2-hexenal; 9= (*E*)- β -ocimene; 10= (*E*)-4,8-dimethyl-1,3,7-nonatriene; 11= (*Z*)-3-hexen-1-ol acetate; 12= (*Z*)-3-hexen-1-ol; 13= 2-methylpropanal oxime; 14= 1-octen-3-ol; 15= methyl salicylate; 16= (*E,E*)-4,8,12-trimethyl-1,3,7,11-tetradecaene; 17= benzyl alcohol; 18= indole

Figure 1

