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Review

The effects of herbivore-induced plant volatiles on interactions between plants and flower-visiting insects

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ABSTRACT

Plants are faced with a trade-off between on the one hand growth, development and reproduction and on the other hand defence against environmental stresses. Yet, research on insect–plant interactions has addressed plant–pollinator interactions and plant–attacker interactions separately. Plants have evolved a high diversity of constitutive and induced responses to attack, including the systemic emission of herbivore-induced plant volatiles (HIPVs). The effect of HIPVs on the behaviour of carnivorous insects has received ample attention for leaf-feeding (folivorous) species and their parasitoids and predators. Here, we review whether and to what extent HIPVs affect the interaction of plants in the flowering stage with mutualistic and antagonistic insects. Whereas the role of flower volatiles in the interactions between plants and insect pollinators has received increased attention over the last decade, studies addressing both HIPVs and pollinator behaviour are rare, despite the fact that in a number of plant species herbivory is known to affect flower traits, including size, nectar secretion and composition. In addition, folivory and florivory can also result in significant changes in flower volatile emission and in most systems investigated, pollinator visitation decreased, although exceptions have been found. Negative effects of HIPVs on pollinator visitation rates likely exert negative selection pressure on HIPV emission. The systemic nature of herbivore-induced plant responses and the behavioural responses of antagonistic and mutualistic insects, requires the study of volatile emission of entire plants in the flowering stage. We conclude that approaches to integrate the study of plant defences and pollination are essential to advance plant biology, in particular in the context of the trade-off between defence and growth/reproduction.

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1. Trade-off between growth, development and reproduction versus defence

Plants have been under natural selection to maximise their fitness, resulting in a dynamic balance between growth and defence that is affected by the environmental conditions experienced by the plant. A central paradigm in plant biology is the existence of a trade-off between on the one hand growth, development and reproduction and on the other hand defence against environmental stresses (Herms and Mattson, 1992). Thus, energy invested in defence cannot be invested in growth, development and reproduction and vice versa.

Plants are exposed to a multitude of attackers. The number of insect species is estimated to be about 6 million, half of them being herbivorous (Schoonhoven et al., 2005). Arthropod–plant interactions are characterised by a high degree of trophic specialism: about 80% of herbivorous arthropods are specialist feeders that accept only a limited number of plant species belonging to a single genus or family. To combat attackers, plants have evolved an astounding diversity of phytochemical defences. More than 100,000 secondary compounds of plant origin have been recorded and there is ample evidence for the role of secondary metabolites in the defence of plants against herbivorous insects. Many plant families produce characteristic secondary metabolites such as glucosinolates in the Brassicaceae (Hopkins et al., 2009) or alkaloids in the Solanaceae (Pomilio et al., 2008). Phytochemical-based plant defence may be constitutive, causing resistance to the large majority of herbivorous species, except for a small number of specialist feeders. Moreover, herbivory can induce additional direct and indirect defences (Dicke and Baldwin, 2010; Gardner and Agrawal, 2002; Karban and Baldwin, 1997; Kessler and Baldwin, 2002) such as, for instance, the production of herbivore-induced plant volatiles (HIPVs) that attract carnivorous enemies of herbivores (Dicke and Baldwin, 2010). It is generally assumed that the benefit of inducible over constitutive defences is cost reduction (Karban and Baldwin, 1997), especially in terms of biosynthetic costs. However, plants may also incur ecological costs related to defence investments. For instance, secondary metabolites may be exploited by specialist herbivores during host-plant selection (Hopkins et al., 2009), or herbivores may sequester plant secondary metabolites and exploit them for their own defence against carnivorous enemies (Nishida, 2002). As a result of such biosynthetic and ecological costs, plants will be under selection to optimise the balance between investments in constitutive and inducible defences. An additional benefit of inducible defences is that the plant has a plastic phenotype which is likely to retard adaptation in herbivores (Agrawal and Karban, 1999). However, the costs of induced defences have rarely been considered in the context of the trade-off between reproduction and defence (Agrawal et al., 1999). The expression of defences may affect, for instance, a plant's interactions with pollinators and when induced defence reduces pollinator visitation, this represents another ecological cost. In this review we will focus on the consequences of induced indirect defence for insect–flower interactions, i.e. in the context of the defence versus growth/reproduction trade-off. More specifically, we address how HIPVs of plants in the flowering stage may influence (a) host plant selection by adult herbivores, (b) host location by parasitoids, and (c) foraging preferences of pollinators.

2. Induced direct and indirect defences

Two types of induced plant defence are distinguished: (a) direct defence that affects the performance or behaviour of its attacker directly, e.g. through an increased concentration of secondary metabolites (Gols et al., 2008; Steppuhn et al., 2004), including plant volatiles (De Moraes et al., 2001; Kessler and Baldwin, 2001) and (b) indirect defence that enhances the effectiveness of natural enemies of herbivores through the production of HIPV (Dicke and Baldwin, 2010), and through the induction of extrafloral nectar (EFN) (Dicke, 2009; Heil, 2008). The induced production of volatile organic compounds (VOCs) that attract carnivorous arthropods can occur in response to herbivore feeding damage (Vet and Dicke, 1992) or egg deposition (Hilker and Meiners, 2006), both aboveground (Arimura et al., 2005) and belowground (Erb et al., 2009a). The emission of such HIPVs has been documented for plant responses to insects belonging to five orders (Lepidoptera, Diptera, Thysanoptera, Coleoptera and Hemiptera) and mites (Mumm and Dicke, 2010). HIPVs include compounds produced through various biosynthetic pathways, including the octadecanoid pathway leading to fatty-acid derived green leaf volatiles (GLVs), the MEP (methyl-erythritol phosphate) pathway leading to monoterpenes and diterpenes, the mevalonate pathway giving rise to sesquiterpenes, and the shikimate pathway leading to a large diversity of aromatic metabolites (Fig. 1). Moreover, secondary metabolites

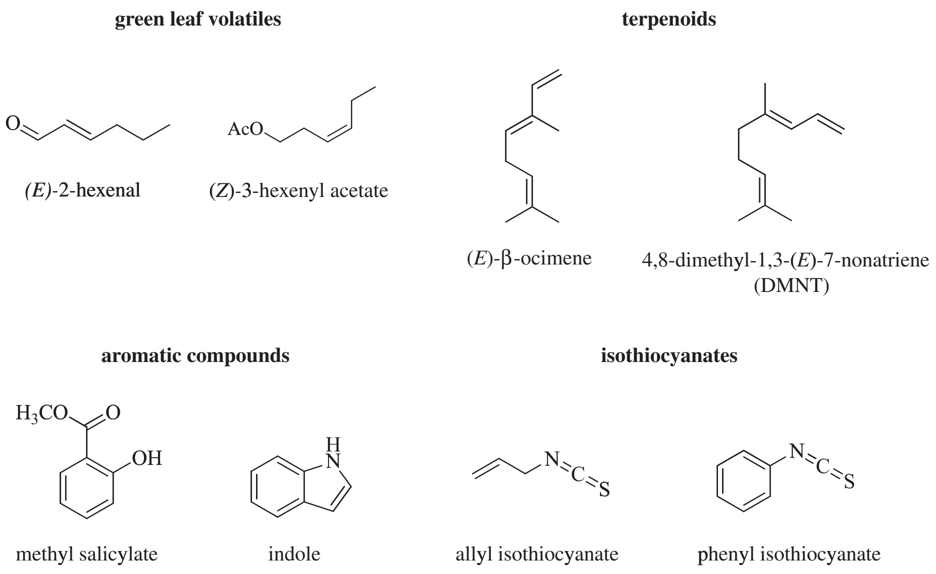

Fig. 1. Examples of HIPVs produced through different biosynthetic pathways or that are catalytic products of plant secondary metabolites.