BioGreenhouse

Plant health

Induced plant responses and natural enemies

Plants react to external stimuli (biotic and abiotic stress) with a series of defence responses. These responses may be either constitutive or induced only after attack. Induced defences to herbivory in particular, comprise direct traits that affect herbivore performance and behaviour, as well as indirect traits affecting the behaviour of natural enemies. Besides their involvement in indirect plant defence, the performance and behaviour of natural enemies may also be affected by direct responses. Natural enemies of herbivores may be either positively or negatively affected by plant defences. Here, the main effects of induced plant responses on natural enemies are briefly reviewed with the aim to highlight the role of induced defence in conservation biological control.

Plant responses to herbivory

Plants employ a series of defences to protect themselves against herbivory. Responses that are produced upon herbivore attack are known as inducible defences and these may impact herbivores, either directly, or indirectly (Figure 1). Direct defences include the production of toxins, antifeedants, and morphological or other plant traits that deter herbivory by affecting herbivore performance and behaviour. In addition, indirect defences combat herbivory by recruiting the natural enemies of herbivores via the emission of distinct volatile signals or food rewards produced upon herbivore attack (Figure 2).

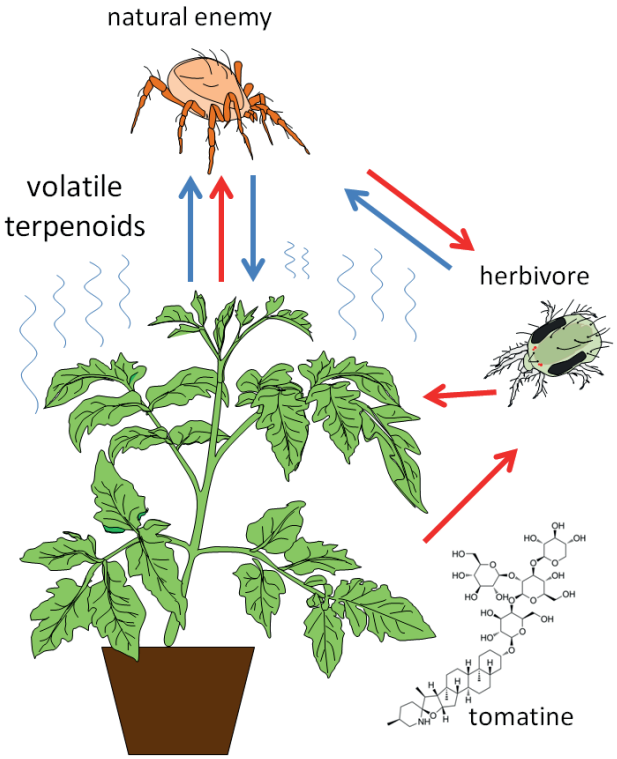

Figure 1. Schematic diagram showing the ways induced plants responses to herbivory may influence a simple food web (red arrows: negative effects, blue arrows: positive effects).

Both direct and indirect defences play important roles in interactions among herbivores and their natural enemies. Herbivore recognition by the plants is mediated by specific elicitors produced either by the damaged tissue or by herbivore-associated elicitors (e.g. compounds found in the saliva and oral secretions of the herbivores).

Figure 2. Extrafloral nectaries of *Vicia sativa*.

Damage patterns may also play an important role in the identification of specific herbivores by the plant, while herbivores belonging to different feeding guilds may impact the activation of defence responses in distinct ways. Central regulators of plant defence (both direct and indirect) are a set of phytohormones (mainly jasmonic acid, salicylic acid and ethylene) that mediate signal recognition and activation of defences.

With regard to pest control, so far direct defences have been mainly considered for their impact on herbivores (bottom-up control), while natural enemies (top-down control) are mostly involved in indirect responses to herbivore attack.

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COST is supported by the EU Framework Programme Horizon 2020

Induced defence and natural enemies

Mounting defences is a costly process. Ideally, plants invest to the induction of either direct or indirect defences to optimize the net benefit of suppressing herbivore populations. Whereas indirect defences facilitate host selection and acceptance behaviour of herbivores by predators and parasitoids, direct responses may impose a hurdle in pest control in cases when natural enemies are affected in a negative way. Either positive or negative, effects of induced plant responses on natural enemies are directly and/or indirectly expressed (Table 1).

Table 1. Examples of defence traits differentially affecting natural enemies

Defence type	Trait/Mechanism	Effect on natural enemies
Direct	morphological barriers (e.g. trichomes)	negative (-) / positive (+) / no effect (n)
	phytochemicals (toxins, antifeedants etc.)	-/n
Indirect	prey quality / quantity alteration	-
	herbivore growth delay	-/+
	host avoidance by herbivores (volatiles)	-
	attraction to host/prey	+
	competitors/intraguild predator attraction	-/n
	food rewards (e.g. extrafloral nectar)	+

Direct effects

Natural enemies may be directly exposed to toxins produced upon herbivore attack and/or sequestrated in herbivore's tissue or haemolymph. Such effects are prominent in parasitoids. Food rewards (e.g. nectar) may positively influence the performance of parasitoids and predators, while the increased production of glandular trichomes may negatively affect the performance of natural enemies.

Indirect effects

Induced plant responses may indirectly affect natural enemies through changes in herbivore (host) quality and/or quantity. Moreover, delayed herbivore developmental growth may facilitate their foraging efficiency, while volatiles may also attract competitors and intraguild predators additionally to informing herbivores on the damage status of their host plants.

Applied aspects

Conservation of natural enemies in the greenhouse may be enhanced by recruiting the main components of indirect defence i.e. herbivore-induced volatiles (HIPVs) and production of food rewards, while eliminating negative effects of direct defence.

Triggering plant responses

Exogenous application of defence-related chemicals (e.g. JA, MeJA, MeSA) has been shown to enhance the attraction of natural enemies on plants. Moreover, exposure of plants to synthetic HIPVs resulted in increased production of terpenoids, phenolics and proteinase inhibitors.

Breeding for resistance

Cultivars that produce enhanced HIPVs or extrafloral nectar upon attack may be included in breeding programs to optimize biological pest control.

Moreover, effects of plant responses on natural enemies should be taken into consideration when breeding for resistance against herbivory.

Future directions

Induced plant defence is a major force mediating plant-herbivore interactions aiming to the suppression of herbivore populations. Such interactions may be defined by, but also reciprocally impact, the third trophic level. Applied research should focus on the optimization of pest control by identifying defence compatible natural enemies, as well as defence-related tools (e.g. exogenous application of defence-inducing chemicals, selection of resistant to herbivores, albeit harmless to natural enemies crops) to attract, sustain and enhance the populations of natural enemies inside the greenhouse.

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Acknowledgement: This work was supported by COST Action FA1105 "Towards a sustainable and productive EU organic greenhouse horticulture".

DOI: http://dx.doi.org/10.18174/373605

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Grasso DA, Pandolfi C, Bazihizina N, Nocentini D, Nepi M, Mancuso S. 2015. AoB PLANTS 7: plv002; doi:10.1093/aobpla/plv002