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Induced plant defences in biological control of arthropod pests: a double-edged sword

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Abstract

Biological control is an important ecosystem service delivered by natural enemies. Together with breeding for plant defence, it constitutes one of the most promising alternatives to pesticides for controlling herbivores in sustainable crop production. Especially induced plant defences may be promising targets in plant breeding for resistance against arthropod pests. Because they are activated upon herbivore damage, costs are only incurred when defence is needed. Moreover, they can be more specific than constitutive defences. Nevertheless, inducible defence traits that are harming plant pest organisms may interfere with biological control agents, such as predators and parasitoids. Despite the vast fundamental knowledge on plant defence mechanisms and their effects on natural enemies, our understanding of the feasibility of combining biological control with induced plant defence in practice is relatively poor. In this review, we focus on arthropod pest control and present the most important features of biological control with natural enemies and of induced plant defence. Furthermore, we show potential synergies and conflicts among them and, finally, identify gaps and list opportunities for their combined use in crop protection. We suggest that breeders should focus on inducible resistance traits that are compatible with the natural enemies of arthropod pests, specifically traits that help communities of natural enemies to build up.
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1 INTRODUCTION

Global food security relies heavily on the control of herbivorous pests. Estimated pre-harvest losses caused by arthropod pests in major crops worldwide are seldom less than 10% and frequently much higher (see reference [1] for example). Since the 1960s, chemical pesticides have been widely used to maximize crop yields in agriculture. Nowadays, such pesticides are often combined with biological control agents, i.e. the natural enemies of pests such as predators and parasitoids, within so-called integrated pest management (IPM) programmes. However, this combination may be counter-productive as pesticides may interfere with predator performance directly and indirectly by decreasing prey quality, thereby repressing sufficient predator population build-up. Additionally, pesticides also interfere with other (beneficial) non-target organisms that provide ecosystem services (e.g. bees that provide pollination services) and pose a health risk to humans.[2,3] Moreover, pesticides usually impose high selection pressure for the evolution of resistance mechanisms in the target organisms. Because of the negative environmental and health effects, some of the most hazardous pesticides (e.g. several organophosphates and organochlorines) have been banned from the European and US markets during the last 15 years to comply with the European Commission Directive 91/414/EEC and registration requirements of the Environmental Protection Agency, respectively.[4,5]

The resulting loss of important pesticides in the pest control toolbox, combined with the increase in consumer demands, has increased the interest in biological agents to control arthropod pests. Another environmentally friendly alternative for replacing pesticides is resistance breeding. The degree to which a plant can

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resist pests depends on the efficiency of its defences in limiting the damage. Defences affect the herbivores either directly by killing or repelling them or by slowing down their development and population growth or alternatively indirectly by attracting the natural enemies of herbivores.[6] Some plant defences are constitutive, i.e. present irrespective of herbivore presence, but the majority of plant defences are to some extent herbivore-inducible, i.e. herbivore feeding or oviposition activities reinforce the constitutive defences or activate novel defences.[6,7] Inducible defences can be cost-saving compared to constitutive defences and may prevent auto-intoxication.[8] In addition, inducible defences may be more advantageous as they can be tailored to the actual attacker after the plant has recognized herbivore-specific cues.[9] Thus resistance breeding for inducible defence traits may emerge as an important alternative pest control method, especially if it is compatible with biological control.

In this review, we explore the most promising opportunities for enhancing biological control of arthropod pests on the basis of our chemical-molecular and ecological knowledge on induced plant defences. First, we provide a brief overview of the current fundamental knowledge on induced plant defences. Then, we outline how some natural enemies are being used in biological control practices within simple and more complex agricultural settings. Subsequently, we bring these topics together and discuss the (possible) consequences of interactions between plant defences and natural enemies for biological control of arthropod pests. Finally, we list the practical opportunities for fine-tuning plant breeding and natural enemy selection in order to ensure and improve sustainable crop production. Other IPM tools such as genetic engineering, behavioural and cultural techniques are not considered here as they are the focus of other review papers.[10−15]

2 PLANT DEFENCES IN RELATION TO BIOLOGICAL CONTROL

2.1 Direct and indirect plant defences

Plants employ various strategies to defend themselves against above or below ground herbivores.[16,17] Well-known examples of plant defences are the glandular trichomes on tomato plants that physically and chemically impede herbivory by mites and whiteflies,[18] protease inhibitors that constrain food digestion – and thereby growth and development – of herbivorous moth larvae,[19] or the toxic secondary metabolites of parsnip that obstruct webworm performance.[20] Over 200 000 defensive secondary metabolites are known from the plant kingdom, and single plant species may already produce hundreds if not thousands.[21] Several of these compounds are volatile and can thus be detected in the plant's headspace. Upon herbivory the composition of this headspace changes and this facilitates the attraction and/or arresting of the herbivores' natural enemies which are guided by these volatiles to plants with prey, which is an example of indirect defence.[22] Indirect defences can also be conferred by plant traits that accommodate natural enemies, such as domatia or extrafloral nectar, which provide shelter and food, respectively.[23,24]

2.2 Cost and benefits of induced plant defences

The distinction between constitutive and induced defences can be misleading, since many constitutive defences are also inducible. For example, when acacias are being fed upon by giraffes the length and density of thorns increases in the canopy at the grazing height.[25] The inducible component(s) of defence responses may help minimize production costs in terms of plant productivity. For example, genetically modified tomato plants with constitutive expression of otherwise inducible defences produce considerably fewer fruits than normal inducible plants.[26]

It is commonly assumed that induced defences will be favoured over constitutive defences by natural selection since inducibility (1) limits damage through auto-toxicity and/or (2) lowers the energy investment, particularly when the presence of herbivores is variable, and/or (3) allows for tailoring responses to different pests.[9] The costs of producing defences can be physiological or ecological. Physiological costs are those associated with the energy investment needed to produce and store defences, whereas ecological costs are those associated with negative changes in the interaction between plants and their environment attributable to elevated defences, such as a reduction in competitive strength with other plants,[27,28] decreased resistance to other pests[29] or decreased attractiveness to beneficial organisms such as pollinators.[30] In all cases these costs reduce plant performance or plant fitness, which may vary across environments.[31] It must be noted here that crop producers may not focus primarily on the plant's fitness but rather on aesthetic quality or plant productivity, and these may be affected differently by induced defences.

It has long been debated whether plants incur a net benefit from deploying indirect defences in nature.[32,33] An important argument against being beneficial was that parasitized herbivores may feed more and may have an extra larval instar.[34] Additionally, herbivores or hyperparasitoids may also exploit indirect defences, such as induced plant volatiles, to find their host.[35] Thus the net benefit of particular induced indirect defences may vary strongly between environments with different herbivore communities. Nevertheless, there is ample empirical evidence showing that indirect defences can benefit plants. Extrafloral nectar production consistently was found to increase plant fitness in ant-attended wild plants.[36,37] Experiments with *Arabidopsis* plants and maize or the charloc mustard *Sinapis arvensis* attacked by parasitized caterpillars revealed that seed production was not compromised or was even increased.[38−40]

2.3 Priming of induced plant defences

Plants can use environmental cues predictive of future stress, such as herbivore-induced plant volatiles, to prime their inducible defence responses.[41] Priming is a state of sensitization which results in a faster and stronger induced defence response upon future herbivore attack compared to a non-primed individual.[42,43] Priming reduces the time-lag of the induced defence response and may result in a stronger response, often at a lower cost to the plant.[44] These properties could make priming a promising add-on for fine-tuning the application of induced defences in horticulture or agriculture without compromising crop production.

Priming of defences can occur after exposure to induced plant volatiles from adjacent plants, through exposure to other (synthetic) elicitors such as beta-amino butyric acid (BABA) or through the addition of rhizobacteria.[42,45−47] The secretion of extrafloral nectar in lima beans, for example, can be primed by the volatiles released from herbivore-attacked leaves both between and within plants.[41] Maize plants that were exposed to volatiles of damaged maize seedlings emitted more parasitoid-attracting sesquiterpenes in response to feeding by a lepidopteran herbivore than unprimed plants.[45] Volatiles may also allow for 'eavesdropping' between different plant species, resulting in direct upregulation of defences. This is the case for wild tobacco plants which elevate their defences and become more resistant to herbivory after

exposure to volatiles emitted from damaged sagebrush.[48] Not only plant volatiles but also egg deposition can prime defences that are subsequently triggered faster when the neonate larvae start to feed.[49−51] Finally, it has been shown that defence priming can be realized using synthetic elicitors such as BABA.[47] Although BABA-mediated priming is especially efficient against pathogens, there are indications that it can also reduce aphid growth without having a direct negative effect on the aphid's parasitoids.[52] This suggests that it may be possible to include plant defence primers like BABA in IPM strategies.

3 THE BIOLOGICAL CONTROL TOOLBOX

3.1 Types of biological pest control

Generally three types of biological control are distinguished: classical, augmentative and conservation.[53] Classical biological control aims for long-term control of exotic pests by introducing populations of exotic natural enemies. Augmentative biological control uses mass-produced indigenous natural enemies either to achieve curative control of a pest by mass release (inundation) or to achieve prophylactic control of a potential pest (inoculative introductions).[54] Conservation biological control aims to conserve and promote naturally occurring populations of natural enemies using various techniques of habitat modification and resource supplementation. Biological pest control is widely used in greenhouse vegetable crops, soft fruits and ornamentals, but increasingly also in open field crops and some arable crops.

Different techniques have been developed and implemented so far to attract and retain biological control agents in horticultural and agricultural farmlands. This has been accomplished for instance by providing overwintering shelters, so called 'beetle banks', in winter wheat[55] and alternative or supplementary food sources in the main crop or nearby vegetation. This approach is applied in annual crops such as vegetables[56] and perennial systems such as orchards and vineyards,[57,58] but increasingly also in greenhouse crops.[59]

3.2 Obstacles in biological pest control

Biological control has been applied successfully in many crops, but not in all crops do natural enemies establish equally well. Impediments for establishment include (1) a (temporary) lack of prey for predators or hosts for parasitoids, (2) a lack of non-prey food, such as nectar, honeydew or pollen, (3) a lack of suitable oviposition sites and shelter and (4) the presence of plant traits which adversely affect predators and parasitoids.[60]

Alternative or supplementary food such as nectar and pollen allows natural enemies to survive periods without prey or hosts. In addition, several natural enemies are fully dependent on nectar and/or pollen during part of their life stages. For instance adult parasitoids, hoverflies and gall midges need nectar to survive, to fuel flight activity and to stimulate oviposition.[24] Several species of predatory mites can establish populations on pollen alone. Plant-provided oviposition sites include soft plant tissues, used by anthocorid and mirid predatory bugs.[61] Predatory mites often survive and reproduce better on plants with so-called acarodomatia, which are either small holes or tufts of hairs that serve as refuges protecting eggs and/or mobile stages against unfavourable environmental conditions and predation.[62] Lack of these supportive traits can seriously limit establishment of the pests' natural enemies.

Morphological plant traits that can have negative effects on the foraging activity of parasitoids and predators include leaf pubescence, glandular trichomes and waxy surfaces (but see also below).[60] Glandular trichomes have strong detrimental effects on most natural enemies,[63] although some species of predatory bugs are adapted to sticky plants, which allow them to feed on the carrion of entrapped insects as a food source[64] and provide their offspring protection against predation. Finally, some specialist insect pests may selectively sequester resistance compounds from their host plant and use them for their own defence against their natural enemies.[65] A well-known example is the selective sequestration of glucosinolates and the concomitant enzyme myrosinase in the cabbage aphid *Brevicoryne brassicae* (L.), which 'makes them walking mustard oil bombs'[66] that are less palatable to predators and parasitoids. Thus, breeding for resistance to generalist pests and pathogens by increasing the levels of glucosinolates[67] may incur the risk of reducing the effectiveness of biocontrol agents.

3.3 Methods to accommodate natural enemies

The notion that catering to the resource requirements of parasitoids and predators can greatly improve population establishment has sparked novel strategies targeted at both the naturally occurring as well as mass released natural enemies.[59] One of these strategies are insectary and banker plants; these are specifically selected plants that provide alternative food resources such as nectar, pollen or alternative prey to predators and parasitoids.[24,68] Insectary plants are typically used as pure stands of a single species or as mixtures in strips within the main crop (orchards, vineyards) or at field margins,[69,70] whereas banker plants are non-crop plants grown within a greenhouse.[71] Insectary plants may also evoke negative effects by providing nutritional benefits to pests or by attracting higher order predators and hyperparasitoids. Selection of the plant species based on experimental evidence may help avoid these potential pitfalls.[68,70] Plant species used in the so-called 'push − pull' strategy to repel herbivores out of the crop may also be used to attract the natural enemies of these herbivores in the crop.[72] Recent studies have shown that this targeted approach can help enhance natural enemy levels, pest control and even generate yield benefits (George D *et al.*, unpublished).

Another novel strategy is the application of synthetic plant volatiles that are attractive to natural enemies, similar to those induced by herbivores. This approach has been used to attract predatory mirids, anthocorids, coccinellids and lacewings in several crops.[73−75] Synthetic plant volatiles can be used to attract natural enemies and repel herbivores at the same time,[76] or for 'attract-and-reward' approaches to attract natural enemies to insectary plants where they are rewarded with alternative food.[77] The latter approach has been tested under field conditions for sweet corn, broccoli, wine-grapes and *Brassica* crops using buckwheat as the insectary plant and the common plant compound methyl salicylate as volatile attractant.[78,79] Although it is yet unclear to what extent this approach enhances crop production, volatiles may increase the parasitization rate of aphids but may also increase the abundance of hyperparasitoids or herbivores.[79,80]

4 INDUCED PLANT DEFENCES AND BIOLOGICAL PEST CONTROL

4.1 Synergies and conflicts

Plants usually employ multiple lines of defence concurrently, rather than relying on individual defence mechanisms. This generates scope for possible interactions (both positive and negative) between different defence strategies.[81] Positive interactions
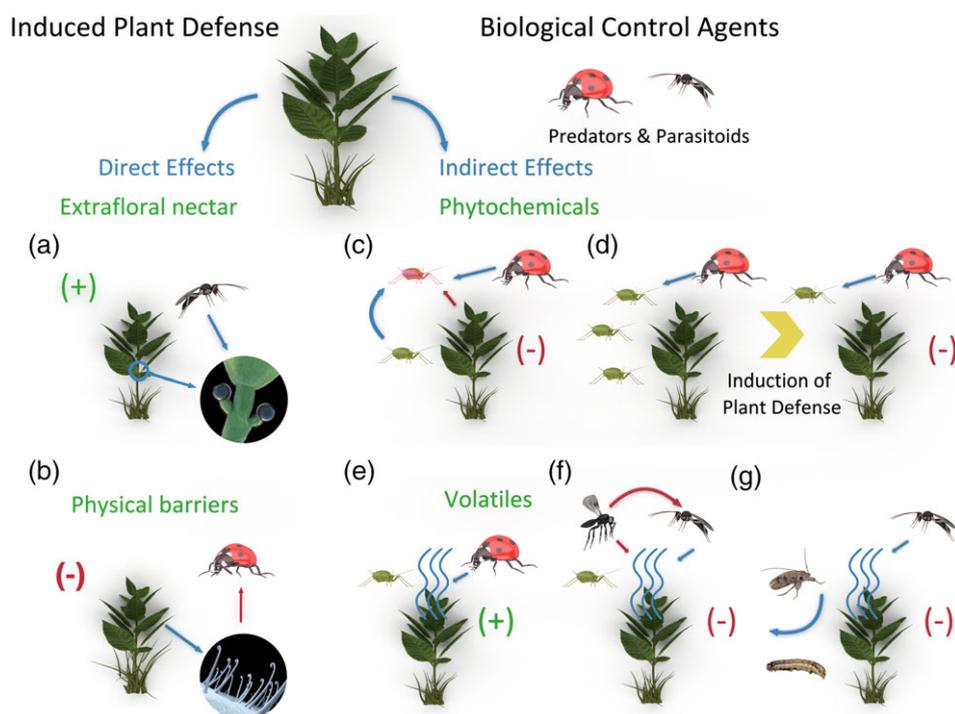
Figure 1. Variation in direct and indirect effects of induced plant defence on natural enemies may determine the outcome of biological control. Natural enemies can benefit from induced plant responses, e.g. from the release of volatile signals guiding predators or parasitoids to infested plants. Natural enemies can also be affected by induced plant responses themselves. These *direct effects* could be (a) positive, e.g. for induced extrafloral nectar secretion,[23] or (b) negative, e.g. for increased trichome densities hindering the movement or oviposition of the biological control agent.[112] *Indirectly*, natural enemies may be affected by an altered quality (c), quantity (d) and/or developmental time of the herbivorous prey.[81,113] On the other hand, induced volatiles may attract not only natural enemies (e) but also intraguild predators and hyperparasitoids (f) and may inform herbivores on the damage status of their host (g).[35,114,115]

between direct defensive traits and natural enemies occur when plant chemistry or plant morphology slow down the development of herbivores, thus extending the time window during which the herbivores are vulnerable to attack.[82] Plant direct defences may also induce the mobility of the feeding herbivore.[83,84] This can be another mechanism that favours biological control as mobile herbivores are typically more exposed to visually hunting and ground dwelling enemies.

In the case of indirect plant defences, which act on herbivores through the attraction or accommodation of natural enemies, plants and biological control should ideally work mutualistically. Plants providing honest signals, food or shelter for predators and parasitoids usually enhance the efficacy by which these intended receivers protect the plants.[85] Defence traits that strengthen each other can be expected to be expressed jointly. A good example of this is the positive correlation in the occurrence of extrafloral nectar and domatia as shown among *Viburnum* spp.,[86] underlining the fact that these traits work in concert to support biological control. However, when herbivores also exploit these traits to find their host plants, and there are insufficient effective natural enemies, the functioning of these indirect defences can break down. Another conflict may arise when plants are dishonest. Some plants mimic the presence of herbivores and, as a result, attract natural enemies of pests under false pretences.[87] An example is the chemical mimicry of aphid sex or alarm pheromones by a range of plant species, which results in the attraction of aphid predators, frequently even duping them into depositing eggs.[88] Under these circumstances natural enemies may learn that responding to these signals is not rewarding and may ignore them in favour of other,

honest signals. This may happen, for example, when plants are selected or genetically modified to enhance constitutive emissions of volatiles attracting natural enemies without rewards.

Direct defences against herbivores tend to have an impact on the natural enemies of these herbivores as well (Fig. 1). Such plant defence impacts on natural enemies can be direct, e.g. when plant feeding predators are exposed to secondary metabolites, or indirect, mediated through the herbivore. When the net impact of defensive plant traits on biological control agents is positive, plant defences and biological control can act additively or even synergistically in reducing pest levels. However, if plant defensive traits impair the functioning of natural enemies, this can generate conflicts in terms of pest control.[89] In this regard the combination of defensive traits may generate unexpected potential conflicts as well. For example, inducible plant defences that negatively affect spider mite reproduction also constrain egg consumption by predatory mites.[90] In addition, plant secondary metabolites expressed as (inducible) direct defence also leach into nectar. Toxic nectar may represent a pleiotropic constraint of having phloem-transported defensive chemicals[91] but also increase visitation frequencies by pollinators as was shown for wild tobacco.[92,93] While most examples of 'toxic nectar' involve floral nectar, this can also occur in extrafloral nectar.[94] Knowing which direct defences could backfire by negatively affecting natural enemies is important information for plant breeders: sustainable crop protection could gain momentum by routinely testing the compatibility of novel resistances with biological control agents on the one hand or by removing undesired resistances that interfere with biological control.
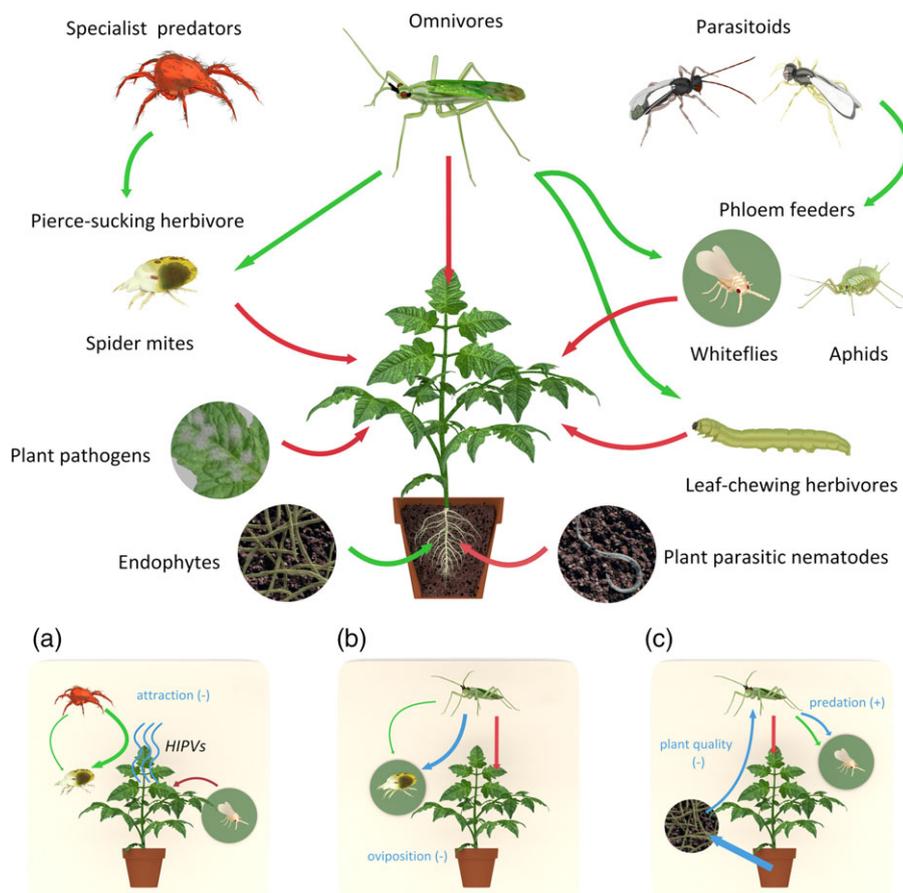
Figure 2. Tomato food web of arthropod pests with different modes of plant feeding and their natural enemies, pathogens and endophytes that can occur in a tomato crop. Plant responses induced by herbivores, omnivores, pathogens or endophytes can affect food web interactions in various ways. For example, a pre-infestation by whiteflies reduced the response of specialist predatory mites to spider mites,[116] which can disrupt biological control (A), whereas pre-infestation by omnivorous predatory bugs decreased oviposition rates of spider mites,[111] which may enhance biological control (B). Induced plant responses may also alter the feeding behaviour of omnivorous predators. For example, induced plant responses to endophytes can reduce the plant quality for omnivorous predators that may consequently increase prey feeding and thus facilitate biological pest control (C). Although only few of such food web interactions have been studied, they should be considered when combining biological control and breeding for resistant plants.

4.2 Future directions

We argue that, despite the extensive knowledge base, not much of existing basic research on natural plant resistance strategies has been translated into applications that have been put into agricultural practice. Notable exceptions are push – pull farming in Africa[76,95] and commercial pollen supplements to feed predatory mites.[96] This seems odd because these opportunities have been widely acknowledged. An important reason, we feel, is that plant protection using pesticides has long removed the incentive for plant breeders and practitioners to search and apply plant-resistance traits to enhance biocontrol programmes. In addition, natural enemy behaviour in the field is only poorly understood as our current knowledge mainly relies on laboratory studies with the application of manipulation of volatile emissions under field conditions being scarce.[97,98] However, the increasing demand for reduced pesticide usage has re-ignited interest in this field. We see several opportunities for integrating natural plant resistances in crop breeding and IPM programmes.

4.2.1 Re-introducing natural resistance

Crops have often lost the full repertoire of resistance mechanisms that can be found among their wild relatives.[99] Some of these traits, like sticky trichomes, are simply impractical for

breeders while other traits may have been lost accidentally or, for defences that are costly, as a consequence of maximizing yield. Several programmes have been initiated to explore which of these resistance factors can be transferred back into commercial varieties to meet our demand of more environmentally friendly crop protection.[18,100,101] Re-introducing plant defences may affect product flavour and/or crop yield and thus these effects should also be considered in the process of developing new varieties, especially when the loss of a resistance trait was intended.[102] In addition, genetic engineering of 'green chemistry', i.e. inducible production of natural insecticides or semiochemicals,[13] may provide some extra control tools.

4.2.2 Removing redundant defences

Some defences interfere with biological control and do more harm than good. Possibly such defences can be removed via breeding but it is essential to first evaluate the impact on biological control agents (e.g. see Fig. 2). Alternatively, one could try to select for natural enemies that can cope with the plant defences to which they are exposed directly or via their prey. In nature, predators and parasitoids have to cope with these defences as well and it is reasonable to assume that natural populations may harbour variation in susceptibility, similar to pesticide-resistant

natural enemies.[103] In principle, these traits could be introduced into commercial biological control agents to make them more compatible with the plant resistances currently present in our crops.

4.2.3 Using defence elicitors

Pest monitoring programmes can be used not only for deciding when to apply pesticides but also to optimize timing of defence elicitor applications. Treating plants with such elicitors basically mimics the 'natural' initiation of systemic resistance due to insect feeding albeit much faster and possibly stronger. Several of such products have been identified, such as jasmonate, benzothiadiazole (BTH) and BABA, but their usage may be restricted by legislation. In principle, applying elicitors could also allow the use of mutant crop plants that do not accumulate insect-induced defence hormones upon insect feeding, thus fine-tuning the trade-off between resistance and yield and/or flavour. However, due to the multitude of plant traits affected by such elicitors, including plant growth and reproduction parameters, uncoupling defence elicitation from herbivory bears risks for crop yield and product suitability.

4.2.4 Customizing and/or improving inducible plant defences

Many natural enemies can use prey-associated volatile signals for finding hosts, offering opportunities for enhancing this process by breeding or engineering of plants that produce clearer and possibly more localized volatile signals. As the genes regulating the production of herbivore-induced plant volatiles are well known[104] it is relatively easy to select for increased volatile emissions. These emissions preferably should be inducible to avoid 'false' signals.[87] Providing a volatile cue without a reward may backfire when biological control agents learn to associate such cues with the absence of prey or when plant pollinators like honeybees perceive treated plants as 'enemy-crowded' spaces and thus avoid them.[105] Such potential side-effects must be thoroughly tested under realistic field or greenhouse conditions before manipulated volatile emissions can be applied in cropping systems as their function in indirect defence has been mostly studied in the laboratory. Similarly, identifying the plant's susceptibility targets may offer ample opportunities for modifying regulatory networks and customizing induced direct defences without affecting the plant primary process significantly.[106]

4.2.5 Facilitating natural enemies

Arthropod natural enemies require more than one resource: they are looking not only for prey but also for other foods, shelter and sometimes for conspecifics. Helping natural enemies in their general needs may improve arrestment, persistence and performance. For example, the use of plant volatiles to attract them could be combined with offering alternative food. Some of this food could be plant-produced, such as extrafloral nectar. Its production is often inducible and even plants without nectaries can produce inducible nectar for effective indirect defence under field conditions.[107,108] Natural enemy facilitation may also be achieved by plant breeding for traits that accommodate natural enemies such as low densities of trichomes, increased densities of domatia and increasing plant-produced alternative food.

4.2.6 Evaluating multiple effects of induced plant defences

Increasing the diversity of biological control agents may be required when facing multiple pests or when a single pest can be more efficiently controlled with more than one biological control agent. Under these circumstances, it is imperative to understand what drives the interactions among species in these artificially or naturally constructed food webs. Induced plant responses to multiple biotic stresses (e.g. herbivores, plant pathogens) and their biological control agents (e.g. zoophytophagous predators, beneficial microbes) may be mediated by interacting plant signalling pathways. For example, plant susceptibility to a pathogen may increase in the presence of a zoophytophagous predator as a result of antagonism between salicylic acid and jasmonic acid mediated plant responses to the pathogen and the predator, respectively.[109–111] To enhance biological control, it is therefore important to identify and apply biological control agents that not only can cope with the induction of defences by pests but also can manipulate these in favour of plant productivity. In this context, there may be opportunities for enhancing the synergistic effects or attenuating the negative interactions between these organisms. For example, infesting plants with beneficial microbes to combat a foliar pathogen may variably affect induced plant susceptibility to the phytophagy of zoophytophagous predators or result in increased predation against a herbivorous prey. On the other hand, applying defence elicitors to enhance plant resistance against a single herbivore may provide empty niches for secondary pests such as other herbivores or plant pathogens and may also affect other plant traits in an unwanted way.

Although natural plant defences clearly can be put to work for crop protection, simply stacking defences, green chemistry and biological control in IPM may do more harm than good. Plant defences may interfere directly by negatively affecting predator performance and indirectly by affecting prey quality and eventually crop yield. This may not always clearly reveal itself since natural enemies may still be effective albeit less efficiently than they could be. Taking a community perspective, biological control is important to reveal opportunities for combining induced plant defence with biological control using natural enemies. Carefully exploring the net benefits of combining these different approaches may prevent this multipurpose tool from turning into a double-edged sword.

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