

Opinion

Optimizing Crops for Biocontrol of Pests and Disease

Johan A. Stenberg,¹ Martin Heil,^{2,*} Inger Åhman,³ and Christer Björkman⁴

Volatile compounds and extrafloral nectar are common defenses of wild plants; however, in crops they bear an as-yet underused potential for biological control of pests and diseases. Odor emission and nectar secretion are multigene traits in wild plants, and thus form difficult targets for breeding. Furthermore, domestication has changed the capacity of crops to express these traits. We propose that breeding crops for an enhanced capacity for tritrophic interactions and volatile-mediated direct resistance to herbivores and pathogens can contribute to environmentally-friendly and sustainable agriculture. Natural plant volatiles with antifungal or repellent properties can serve as direct resistance agents. In addition, volatiles mediating tritrophic interactions can be combined with nectar-based food rewards for carnivores to boost indirect plant defense.

Domestication and Biocontrol

Crop domestication aims to enhance the quality of plants for human use. In addition to yield, **domestication** (see [Glossary](#)) most commonly has altered the size, taste, and nutritional quality of the plant parts of interest, favoring synchronous ripening, homogenous plant sizes, apical dominance, determinate growth, indehiscent fruits, or other characteristics of relevance for cultivation and harvesting, as well as modifying traits that facilitate transport and storage [1–3]. Furthermore, enhanced resistance to pathogens or abiotic stress represents an integrated goal in most plant breeding programs [4,5]. Breeding for resistance to herbivores ('pests') is less common [3,6,7], although wild plants express multiple traits to resist herbivory. Therefore, '**rewilding**' has become a new trend in crop breeding that opens exciting opportunities for **biological control** and organic farming. However, multiple regulatory and political issues currently impede the use of most genetic techniques to provide cultivars with specific resistance traits, particularly when these cultivars are to be used in organic farming [3].

Many resistance-related traits are inducible [8,9] or can be primed for a faster and stronger induction once damage occurs [10,11]. This phenotypic plasticity helps to balance costs and benefits of defense expression because it assures that costly defenses are only expressed when they are actually required [12,13]. Among the inducible traits, seemingly all plants respond to herbivore-inflicted damage with the enhanced emission of volatile organic compounds (VOCs), and plants in numerous taxa also respond with the secretion of **extrafloral nectar** (EFN) [14–17]. Both VOCs and EFN attract adult **parasitoids** and **predators** (hereinafter collectively termed 'carnivores'), an effect that can significantly reduce herbivore pressure on wild plants [18,19]. Nevertheless, relatively few attempts have made conscious use of VOCs or EFN for biological pest control [20–26] and, to the best of our knowledge, classical breeding has never aimed to improve anti-herbivore defense via VOCs or EFN [1,27] (but see [28] for the first attempt

Trends

Hundreds of studies convincingly demonstrate functioning indirect defenses in wild plants, but breeding approaches have never considered the underlying traits (e.g., food rewards or shelter for carnivores, and volatiles that mediate information-based interactions) as desirable targets.

We argue that induced plant volatiles, owing to their multiple roles as signals, repellents, and antimicrobial compounds, bear an as-yet underused potential for biological control, and that future breeding efforts should enhance the capacity of crops to engage in tritrophic interactions.

We also present ecological and evolutionary considerations that can explain why the constitutive release of volatile compounds that have evolved as inducible defenses is not likely to work, and why extrafloral nectar is likely to represent a better food reward for carnivores than floral nectar.

¹Swedish University of Agricultural Sciences, Department of Plant Protection Biology, PO Box 102, 23053 Alnarp, Sweden

²Departamento de Ingeniería Genética, CINVESTAV-Irapuato, Km 9.6 Libramiento Norte, Irapuato, Guanajuato, 36670 México

³Swedish University of Agricultural Sciences, Department of Plant Breeding, PO Box 101, 23053 Alnarp, Sweden

⁴Swedish University of Agricultural Sciences, Department of Ecology, PO Box 7044, 75007 Uppsala, Sweden

*Correspondence: mheil@ira.cinvestav.mx (M. Heil).

to genetically engineer wheat (*Triticum aestivum*) for the emission of an aphid alarm pheromone as a means to enhance repellence of aphids and attract aphid carnivores). We highlight the major defensive functions of VOCs and EFN, discuss why VOCs and EFN are rarely included in breeding programs, and propose how and to what degree these traits can be optimized to allow better biological control of pests and crop diseases.

Plant VOCs, EFN, and Biological Control

Plants express multiple traits that provide resistance to the majority of potential herbivores and pathogens [29]. Many traits act directly against these enemies via their toxic, repellent, or antimicrobial effects or function as mechanical barriers, but other resistance strategies work indirectly [18]. For example, plants release an array of VOCs when damaged [30–32], and the particular blends depend on the type of wound and even the type of attacker [33,34]. Because such induced VOCs frequently indicate the presence of a herbivore, they are utilized by many carnivores as cues to find their prey, a behavior that can reduce herbivore loads and thus cause ‘indirect’ defense of the plants [35]. Studies searching for beneficial effects of VOCs have reported multiple promising observations (Table 1), including enhanced recruitment of predators, parasitoids, or entomopathogenic nematodes to VOC-releasing plants [30,31,35–37], enhanced parasitization rates in caterpillars that were reared close to VOC-emitting plants [38], the successful use of intercropping with plant neighbors that mimic the emission of herbivore-induced VOCs [39] or with repellent crops to ‘push’ pests out of maize fields and ‘pull’ them into surrounding trap plants [20,40] (Figure 1), and enhanced density of parasitoids close to dispensers emitting, for example, the VOC methyl salicylate (MeSA) [24,41–44].

In addition to VOCs, plants commonly attract and maintain carnivores by offering shelter (such as domatia in the form of cavities or trichome tufts for ants and mites) or food rewards [such as pollen, floral nectar (FN), extrafloral nectar (EFN), and plant sap] [18]. These rewards contain carbohydrates and amino acids, and are consumed by a diverse range of carnivores [18], most frequently during the adult stage [19,45–47]. In particular, the ingestion of nectar enhances the longevity and predatory efficiency of carnivores or reduces intraguild predation [48–50]. These food rewards affect the performance, behavior, and voracity of carnivores [19,45,47–49], an effect that can be used to optimize the efficacy of biological control by using plant genotypes of a desired quality [51]. In particular, the secretion of EFN usually reduces herbivory on the respective plants [52–54]. In the horticultural context, there are reports of enhanced protection from herbivores in plants that secrete EFN [22,55,56], produce large amounts of pollen [57], or provide additional shelter to ants or predatory mites [58]. The availability of carbohydrates is a common bottleneck for carnivores, whereas herbivores are usually limited by the supply of

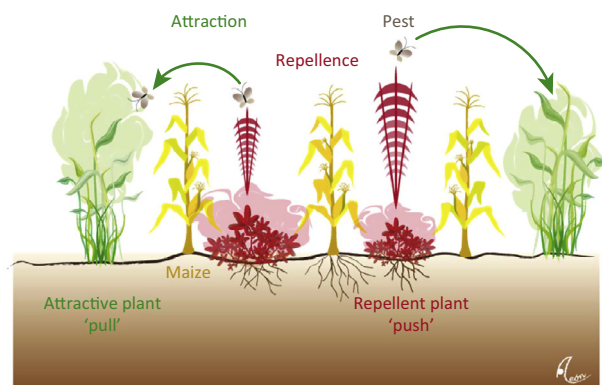


Figure 1. The Push–Pull System. The push–pull system mainly consists of intercropping the crop of interest (here maize) with a plant species that emits volatile organic compounds (VOCs) that repel the major pest. Planting an attractive (pull) plant around the field further enhances directional movements of the pest insect out of the field. Ideally, the pull plant does not allow the pest to reproduce, and both push and pull plants also serve other functions, for example, as ornamental plants, vegetables, spices, or as food for livestock (see [39,40] for details).

Glossary

Biological control: for the purposes of this review, ‘biological control’ comprises all strategies in which animals, plants, or plant-derived compounds are used to control pests and diseases in crops.

Domestication: the artificial selection of plants or animals to cultivate traits that are desirable to the cultivator (i.e., humans).

Extrafloral nectar (EFN): nectar that is secreted on the vegetative and in some cases also on the reproductive parts of plants and that serves to attract carnivorous arthropods as means of indirect defense.

Green leaf volatiles (GLVs): small C_6 molecules that are immediately released from damaged plant tissues and that form part of the general wound response of plants.

Parasitoids: arthropods that as larvae develop within a living host and kill this host before the emergence of the adult stage.

Predators: animals that feed on other animals and usually kill their prey.

Rewilding: the reintroduction of properties from the wild relatives of crops, for example, to re-establish resistance traits that were lost during domestication.

Table 1. Examples of Direct and Indirect Resistance Effects for Application in Biocontrol

Plant Species	Environment	Treatment	Response Observed	Refs
Barley (<i>Hordeum vulgare</i>)	Laboratory	Plants infested by aphid (<i>Rhopalosiphum padi</i>)	Attraction of the predatory beetle, <i>Coccinella septempunctata</i>	[121]
Birch (<i>Betula pubescens</i>)	Field	Presence of herbivore- damaged leaves or methyl jasmonate (MeJA) treatment	Attraction of insectivorous birds	[122,123]
Bean (<i>Phaseolus vulgaris</i>)	Field	Exposure to inoculated or Benzothiadiazole (BTH)-treated emitter plant	Enhanced resistance to the fungal pathogen, <i>Colletotrichum</i> <i>lindemuthianum</i> , priming of PR-1, 2, and 4, and direct inhibition of fungal spore germination on the leaf surface	[62]
Cotton (<i>Gossypium hirsutum</i>)	Field and Cage	Herbivore-damaged plants	Repellence of adult females of the herbivore, <i>Spodoptera littoralis</i>	[124]
Maize (<i>Zea mays</i>)	Laboratory	Application of caterpillar oral secretion to wounded leaf tissue	Females of parasitic wasp <i>Cotesia</i> <i>marginiventris</i> learn to respond to the released VOCs	[31]
Maize (<i>Zea mays</i>)	Field	Damage by root- feeding <i>Diabrotica</i> larvae	Attraction of entomopathogenic nematodes	[36]
Maize (<i>Zea mays</i>)	Field	Intercropping with the grass, <i>Melinis</i> <i>minutiflora</i>	Increased levels of infestation by stem-borers and enhanced parasitization rates of these	[39]
Lima bean (<i>Phaseolus lunatus</i>)	Laboratory	Damage inflicted by the spider mite, <i>Tetranychus urticae</i>	Enhanced attraction of the predatory mite, <i>Phytoseiulus</i> <i>persimilis</i>	[30]
Lima bean (<i>Phaseolus lunatus</i>)	Field	Supplementation of EFN	Enhanced number of ants, decreased rates of herbivory, and enhanced seed set	[125]
Lima bean (<i>Phaseolus lunatus</i>)	Laboratory	Treatment with jasmonic acid (JA)	Adult females of the herbivorous beetles, <i>Gynandrobrotica</i> <i>guerreroensi</i> and <i>Ceratomya</i> <i>ruficornis</i> , preferred controls over induced plants	[77]
Lima bean (<i>Phaseolus lunatus</i>)	Laboratory	Exposure to conspecific plants treated with BTH or to the pure VOC, nonanal	Enhanced resistance to pathogenic bacterium, <i>Pseudomonas syringae</i> , and priming of PR-2	[70]
Wild tobacco (<i>Nicotiana attenuata</i>)		Release of <i>cis</i> -3-hexen- 1-ol, linalool, and <i>cis</i> - α - bergamotene	Increased herbivore egg predation rates by a generalist predator (<i>Geocoris pallens</i>)	[35]
Wild tobacco (<i>Nicotiana attenuata</i>)		Linalool and the complete blend of MeJA-treated plant	Decreased lepidopteran (<i>Manduca quinquemaculata</i>) oviposition rates	[35]
Tomato (<i>Lycopersicon</i> <i>esculentum</i>)	Field	Exogenous application of JA	Higher parasitization rates of caged caterpillars	[38]
Tobacco (<i>Nicotiana tabacum</i>)	Field	Damage by different herbivores	Females of the specialist parasitoid (<i>Cardiochiles nigriceps</i>) distinguish plants damaged by hosts vs non-host caterpillars	[37]
Tobacco plants (<i>Nicotiana tabacum</i>)	Greenhouse	Damage by <i>Heliothis</i> <i>virescens</i> caterpillars	Repellence of conspecific females	[126]

proteins. Therefore, carbohydrate-based rewards can shift the balance in favor of the third trophic level [19], even when a specific reward happens to be used by herbivores as well. Similarly, domatia are usually occupied by predators rather than herbivores [18,58,59], and thus should favor predators more than herbivores.

Finally, several **green leaf volatiles** (GLVs) [60,61] and other VOCs, that are quickly released in response to injury, have direct antimicrobial effects and thereby contribute to an immediate resistance to disease, both in the damaged plant and in its neighbors [15,60,62]. For example, MeSA represents the volatile form of salicylic acid (SA), a central regulator of induced plant resistance to biotrophic pathogens [63]. (*Z*)-3-hexenal and its isomer, (*E*)-2-hexenal, inhibit the growth of several strains of bacteria and the pathogenic fungus *Botrytis cinerea* (see [60] for review), and monoterpenes such as linalool and limonene at natural concentrations can inhibit the germination of conidia of the pathogenic fungus, *Colletotrichum lindemuthianum*, on bean plants [62].

In addition to their direct antimicrobial properties, such VOCs are known to trigger resistance responses in remote parts of the same plant or in neighboring plants [64–66] and, frequently, they prime resistance traits that are directed against herbivores [67–69] or pathogens [60,62,70]. The multiple functions of GLVs and other plant VOCs as plant hormones, direct antimicrobial agents, and cues for host-searching carnivores break with the common trade-off between (direct) resistance traits against pathogens and herbivores [71] and make these compounds particularly attractive targets for integrated breeding efforts and other applications in biocontrol.

Putative Functions of VOCs in Biological Control

In most cases, biological control makes use of native or alien natural enemies of herbivores such as predators and parasitoids. Common strategies to enhance the populations of these carnivores in agricultural or horticultural environments aim at conserving the natural populations of these animals, attracting them from adjacent natural areas, or via the active release of commercially reared animals. Although biological pest control represents an environmentally-friendly strategy that has had tremendous success in particular systems, its wider success is frequently limited by various intrinsic problems. First, carnivores that are released in open areas often disperse to adjacent, more natural ecosystems (see examples in [72]). Second, carnivore populations will crash as soon as they have eradicated the target pest if no alternative food sources are provided. Third, beneficial carnivores in most systems cannot be released in a preventive manner because they need to prey on herbivores for their own survival and reproduction.

The discovery of the above-mentioned VOCs seemed to open new possibilities for biological control [42]. These ‘semiochemicals’ or ‘infochemicals’ can be used by carnivores as host-finding cues [18,32], and can be released artificially [41,42,44,73], or crops can be bred or transformed for their enhanced emission [27,28,74–76], to attract beneficial organisms from wild populations, maintain commercially released biocontrol agents in an agricultural field, or simply repel herbivores from the target crop. However, VOC-based indirect resistance to herbivores has not been adopted in traditional plant breeding [1,27] and, despite the above-mentioned examples of successful biocontrol via plant VOCs, there are also examples of the opposite: VOCs can be used by herbivores to localize their host plants [77,78], a situation which can lead to highly counterproductive effects [26,77,79,80]. We argue that these seemingly contradictory results are likely to be caused by the following factors.

- (i) Plant VOCs play multiple roles in direct resistance to herbivores and pathogens, which makes it unlikely that strategies that focus on one single mechanism can be successful. Apparently for historic reasons, most work has focused on VOC-mediated tritrophic interactions [15].

- (ii) The emission of plant volatiles depends on multiple environmental factors, including abiotic ones such as heat, drought stress, and soil nutrient content [81–83]. After their release, the compounds are directly exposed to the environment and, unfortunately, we know very little on how air temperature, UV irradiation, and other variable environmental factors affect the stability of individual VOCs [84,85]. Therefore, the release of VOCs and their biological effects are strongly context-dependent.
- (iii) Herbivore-induced (HI-) VOCs that are used by carnivores as ‘infochemicals’ solely represent information rather than providing a resource *per se* [86]. Thus, responding to HI-VOCs in the absence of herbivores can negatively affect the fitness of carnivores in general and, in particular, reduce the survival rates of adult parasitoids. These animals will rapidly learn – or be selected – to ignore the misleading information that is transmitted when VOCs are released in a preventive manner. A recent study by Toby Bruce and colleagues [28] shows that insects can even change the response to their own alarm pheromones if they are exposed to the respective selective pressure. In an attempt to genetically engineer wheat (*Triticum aestivum*) for constitutive release of the aphid alarm pheromone, (*E*)- β -farnesene, transformed plants successfully repelled aphids in the laboratory. However, aphids that were reared on (*E*)- β -farnesene emitting plants showed strongly reduced repellence responses after only five generations [28].
- (iv) Finally, disregarding the effects of domestication on the interactions between crops and the natural enemies of pest insects (see [72] for recent review), and the multiple interactions among the various defensive traits of plants, could lead to missed opportunities [87,88] and unwanted repercussions. Tritrophic interactions are never ruled by HI-VOCs alone, and apparently were rarely considered in the breeding process. In particular, plant surface structures such as trichomes and plant-derived food rewards are important complements of VOC-mediated attraction effects that are essential for stable and long-term indirect defense via tritrophic interactions [18]. If domestication has negatively affected only one of the underlying traits, biological control might be significantly impaired [72].

However, identifying the traits that currently limit the successful engagement of many crops in successful tritrophic interactions will help to breed future cultivars for the capacity to express the traits in question. Therefore, it is our ambition to inspire plant breeders to consider tritrophic interactions and inducible resistance to a greater extent [27,89]. We present some of the plant traits that are promising candidates for enhancing biocontrol, and discuss whether and how these traits have been affected by domestication. Finally, we highlight resistance-related traits that breeding should focus on, and experiments that still are needed for, enhancing the potential of domesticated plants to engage successfully in tritrophic interactions (Figure 2 and Figure 3, Key Figure). We focus here on the effects of plant-derived VOCs and food rewards because the potential of microbial VOCs in sustainable agriculture has been reviewed recently [90].

Domestication Affects the Quality of Plants for Friends and Foes

Many of the traits that confer direct resistance to pests have been counter-selected during domestication, either because they depend on undesirable properties such as bitterness, hairiness, toughness, or toxicity, and thus reduce the quality of the consumed parts, or because they cause a yield penalty as a consequence of the metabolic costs of resistance expression [91]. Apart from the consequences of monocultures on the population dynamics of pests and pathogens, this reduction in the natural levels of direct resistance is one of the major reasons why most crops are more prone to infestation than are their wild ancestors.

Unfortunately, we know rather little on how domestication has affected the indirect defense of crops via tritrophic interactions [72]. On the one hand, the higher food quality of domesticated plants for herbivores can translate into a better quality of the herbivores as hosts for parasitoids

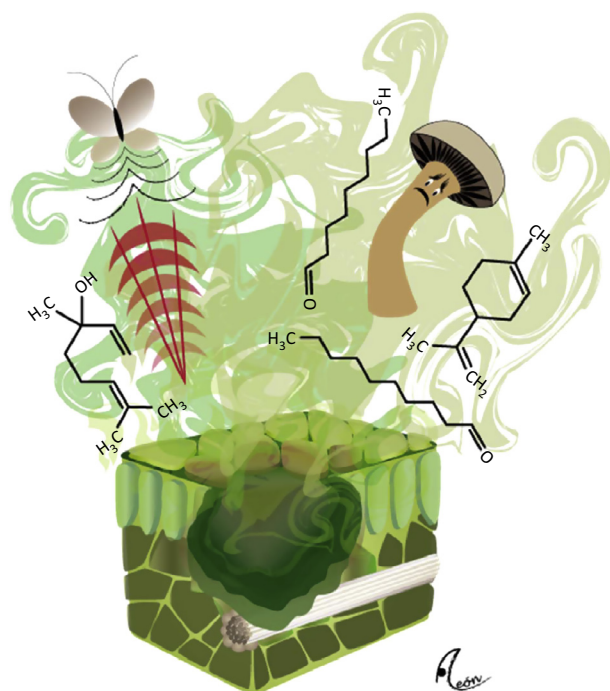


Figure 2. Direct Resistance-Related Effects of Volatile Organic Compounds (VOCs). Multiple plant VOCs that are released from damaged tissue or from intact tissue in response to damage in other tissue, such as linalool, can repel herbivores [35,126], and compounds such as nonanal, decanal, and limonene have antimicrobial properties [62]. Owing to their direct nature, these effects should be less context-dependent than the more indirect mechanisms.

Trends in Plant Science

[92], an effect that would enhance the opportunities for biocontrol. On the other hand, enhanced vigor of herbivores on crops can also enhance their capacity to perform immune responses, such as the encapsulation of parasitoid eggs [93]. Domestication might even create 'enemy-free spaces' for specific pests, and larger fruits or seeds of cultivated olive (*Olea europaea*) trees or sunflowers (*Helianthus annuus*) allow herbivorous larvae to physically escape from parasitization [94,95].

For some cases, breeding efforts against particular traits are likely to explain why attempts to control pests by releasing biocontrol agents have failed [96]. For example, 50% of maize (*Zea mays*) landraces tested responded to stemborer oviposition with the emission of HI-VOCs that attracted parasitoids, whereas only two of 30 hybrid cultivars retained this capacity [7]. Tamiru and colleagues conclude that 'there is a steady decline in the prevalence of the trait from wild ancestors to landraces to higher yielding hybrid varieties favored by breeders' [7]. Similarly, the ability to release aboveground (or, in the case of maize, also belowground) HI-VOCs has been reduced or lost during the breeding of cotton, maize, and cranberry (*Vaccinium macrocarpon*) [36,87,88,97]. Peach cultivars without extrafloral nectaries have been produced inadvertently [55], and cotton (*Gossypium hirsutum*) lines without extrafloral nectaries were consciously preferred by breeders and governmental agencies in the first half of the last century, because the enhanced presence of insects on EFN-secreting plants was considered undesirable, and did not discriminate among different feeding guilds [98].

By contrast, cultivated genotypes of bean (*Phaseolus coccineus*) and cabbage (*Brassica oleracea*) were more attractive to parasitoids than related wild species [99], some cultivated accessions of lima bean (*Phaseolus lunatus*) emitted more HI-VOCs than related wild accessions, although they showed strongly impaired direct resistance via cyanogenesis [100], and the overall quantities of HI-VOCs emitted from the aboveground parts of maize tended to be higher in cultivated lines as compared to the ancestor, teosinte [101]. In summary, the few existing

Key Figure

The Attract and Reward Concept

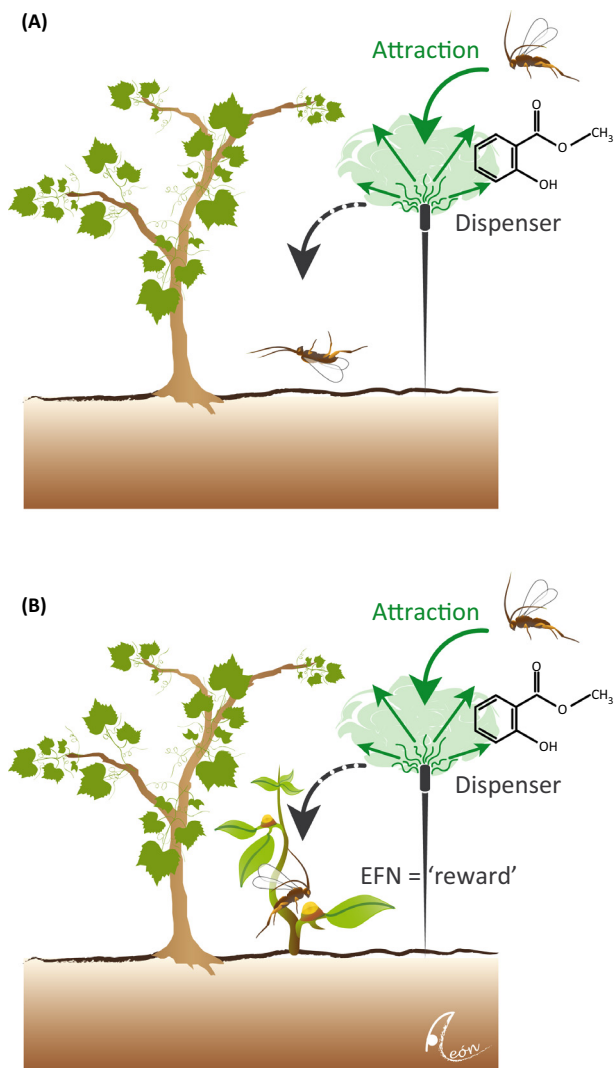


Figure 3. (A) The emission of HI-VOCs from non-infested plants, or luring parasitoids and predators by artificially dispensing attractive compounds such as MeSA, represent erroneous information that negatively affects the fitness of the attracted biocontrol organisms. Therefore, the additional provision of a reward such as floral or extrafloral nectar, EFN in panel (B), can enhance the survival and efficiency of parasitoids and predators, and thus allow the establishment of more stable populations of these biocontrol organisms ([25,103] for details). Abbreviations: EFN, extrafloral nectar; HI-VOC, herbivore-induced VOC; MeSA, methyl salicylate; VOC, volatile organic compound.

Trends in Plant Science

reports do not allow us to draw general conclusions concerning how domestication has affected the capacity of crops to engage in tritrophic interactions or other indirect defense mechanisms [72]. In particular, these seemingly opposite results concerning the capacity of maize to engage in VOC-mediated interactions with biocontrol organisms [7,101] show that generalizations are difficult, even when we consider the same crop, likely because the observed responses are affected by various factors such as plant genotype, species and developmental stage of the herbivore, type of 'readout' (i.e., performing chemical analyses of emitted VOCs versus observing the behavioral response of an animal), and environmental conditions. However, all these studies also show that traits for tritrophic interactions have not been generally and irreversibly reduced or eliminated in crops.

Biological Control as a Goal in Plant Breeding: Opportunities

It seems that breeding never aimed consciously to modify tritrophic interactions [89], although several reviews have described how pest control could be enhanced by considering biocontrol already in the breeding programs [27,102,103]. Fortunately, crop wild relatives, landraces, and commercial varieties of many crops retain genetic diversity with respect to indirect defense traits [27,88,100,101,104,105], and these represent a genetic resource that could be utilized in breeding for improved biocontrol. For example, some African and Latin American landraces of maize produce HI-VOCs that attract *Cotesia* parasitoids [88]. Further examples of cultivated plants for which genetic diversity in resistance-related VOCs has been reported are compiled in Table 2. The genetic variation available for traits that provide food rewards, such as extrafloral nectar, remains to be investigated for essentially all commercial plants and their wild relatives. However, extrafloral nectar traits in wild cotton (*Gossypium thurberi*) [106] and aspen (*Populus tremuloides*) [107] exhibit heritable genetic variation, and varieties that retain high EFN production exist in peach [55]. Genetic variation in other rewarding traits has also been reported, for example, in pepper varieties that support omnivorous mites leading to stronger top-down suppression of thrips [57], and some European willow clones that support omnivorous predatory bugs through high-quality plant sap [48]. This phenomenon found in European willow is already being utilized in breeding for improved biocontrol [108].

Plants transformed or mutated in a single gene exhibited changes in GLVs, terpenoids, or glucosinolate-related compounds, with subsequent effect on both herbivores and their natural enemies (see [27] for overview), and plants can even be transformed to emit insect alarm pheromones, an approach that might enhance direct resistance via repellence [28]. EFN is restricted to specific plant taxa and is secreted by specific structures, properties that make it more demanding to breed a specific crop for this type of reward. However, breeders could make use of existing genetic variation in crops such as cotton, salicaceous trees, and all the fruiting shrubs and trees in the Rosaceae that bear extrafloral nectaries (<http://biosci-labs.unl.edu/Emeriti/keeler/extrafloral/worldlistfamilies.htm>). Finally, the chemical composition of plant saps that can be used as favorable rewards for omnivores is less known, and should be explored further for breeding purposes. In summary, genetic variability exists in traits that underlie indirect defense, but deeper knowledge will be required before directed genetic improvements become feasible.

Biological Control as a Goal in Plant Breeding: Obstacles and Risks

All the examples in Table 2 represent crops in which genetic variation suggests that breeding for improved biocontrol would be possible. Why, then, have these traits not been considered in classical breeding programs? There are three possible reasons: (i) despite forming the topic of an ever-increasing number of publications, herbivore-induced plant VOCs have a short history in science [15]; the 30 years since the first description of the role of VOCs in tritrophic interactions [30,31] might simply not have been sufficient to create the level of consciousness of VOC-based interactions that would be required to be considered in larger breeding programs. (ii) As exemplified elsewhere [27,89], improving a crop, for example, by crossing, mutation or transformation, or by QTL-based breeding, requires stable phenotypes that can easily be monitored and quantified. Whereas disease resistance is frequently based on gene-for-gene resistance, and thus depends on the presence of a single and usually dominant gene, the blends of VOCs that exert biological functions are complex and are subject to strong phenotypic plasticity [32,34,109]. Moreover, the synthesis of VOCs is controlled by a network of hormonal pathways, and requires the involvement of multiple biosynthetic pathways; the same appears to be true for the formation of an extrafloral nectary and the synthesis and secretion of nectar. Therefore, it seems unlikely that classical breeding strategies or targeted transformation could form suitable tools to enhance VOC- or EFN-based tritrophic interactions. (iii) The physiological and ecological costs of a resistance trait need to be considered. It is often assumed that VOCs are relatively cheap to produce in comparison to direct defenses [110,111], but no data exist to support this assumption.

Table 2. Selected Examples of Cultivated Plant Species with Reported Genetic Variability in VOC Emission

Species	Material Investigated	Observation	Refs
Bean (<i>Phaseolus vulgaris</i>)	Four cultivars with different levels of resistance to spider mite (<i>Tetranychus urticae</i>)	Resistant cultivars respond to spider mite infestation with the emission of quantitatively and qualitatively more VOCs than susceptible ones	[127]
Cabbage (<i>Brassica oleracea</i> L. var. <i>alba</i>)	Four cultivars with different attractiveness to <i>Cotesia</i> sp. parasitoids	Amounts of terpenoids and methyl salicylate emitted after caterpillar feeding differ among the cultivars	[128]
Carrot (<i>Daucus carota</i>)	Two cultivars	Cultivars differed significantly in the amount of sabinene, myrcene, limonene, and methylisoeugenol emitted after psyllid (<i>Trioza apicalis</i>) feeding	[129]
Cotton (<i>Gossypium hirsutum</i>)	Five cultivars and a naturalized variety	The naturalized variety emitted significantly more mono- and sesquiterpenes and VOCs derived from the LOX pathway	[97]
Cranberry (<i>Vaccinium macrocarpon</i>)	Five varieties spanning a wild ancestor and old and recent cultivars	The varieties differed significantly in released sesquiterpenes and resistance-related phytohormones	[87]
Gerbera (<i>Gerbera jamesonii</i>)	Four cultivars with different levels of resistance to spider mite (<i>Tetranychus urticae</i>)	Striking differences among cultivars in the emission of <i>cis</i> - α -bergamotene, <i>trans</i> - α -bergamotene, and <i>trans</i> - β -bergamotene	[130]
Lima bean (<i>Phaseolus lunatus</i>)	Sixteen accessions, covering wild forms, landraces, and cultivars	Up to 50-fold difference among varieties in overall amounts of VOCs released from JA-treated plants, with no detectable overall effect of domestication	[100]
Maize (<i>Zea mays</i>)	Eleven maize cultivars and five teosinte species	Total amounts and composition of volatiles differed among maize cultivars and among teosintes	[101]
Maize (<i>Zea mays</i>)	Twenty-five landraces, 30 hybrids, and 22 inbred lines	Stemborer oviposition elicited attraction of parasitoids in 13 landraces but only two hybrids	[7]
Pear (<i>Pyrus</i> spp.)	Four cultivars with different levels of resistance to psyllids (<i>Cacopsylla pyricola</i>)	Up to fivefold difference among cultivars varieties in overall amounts of VOCs emitted from fully psyllid-infested plants	[131]
Rice (<i>Oryza sativa</i>)	Six cultivars	Significant quantitative and qualitative differences in the VOCs emitted from JA-treated plants	[132]
Soybean (<i>Glycine max</i>)	Three cultivars	Specific VOCs [(<i>Z</i>)-2-octen-1-ol, (<i>E</i>)-2-octen-1-ol, (<i>E</i>)-2-hexenyl acetate, indole, and DMNT] were only emitted from one of the tested cultivars	[133]
Strawberry (<i>Fragaria</i> \times <i>ananassa</i>)	Two cultivars	Significant quantitative and qualitative differences in the VOCs emitted from cyclamen mite-damaged plants	[134]
Willow (<i>Salix</i> spp.)	Three clones: <i>S. viminalis</i> and <i>S. dasyclados</i> cultivars, and a native <i>S. cinerea</i>	Females of the omnivorous predator, <i>Anthocoris nemorum</i> , distinguished between intact and damaged plants of the three clones in an olfactometer set-up	[135]

Box 1. Combining Breeding-Dependent and Cultivation-Based Strategies for Enhanced Biological Control of Pests and Diseases

Plants VOCs and EFN represent notoriously difficult targets for directed breeding: few crops naturally secrete EFN, and blends of VOCs and EFN secretion are phenotypically-plastic traits that are encoded by multiple genes. Thus, breeding-dependent and cultivation-based strategies must be combined for optimized use of these traits.

Honest Signals

Breeding should aim at more efficient priming rather than constitutively upregulating the emission of VOCs that function in tritrophic interactions.

Direct Effects

Breeding for enhanced emission should focus on specific VOCs with direct repellent or antimicrobial properties. Plant VOCs that directly interfere with more than one central metabolic process of the targeted pest or pathogen are less likely to facilitate the rapid evolution of counter-resistance phenomena.

Synergies

Breeding can also improve those anatomical and physiological traits that are known to favor indirect defense in the wild species.

Breeding-Independent Strategies

Agricultural practices such as 'push-pull' and 'attract and reward' are successful and should receive more attention in efforts for an integrated pest management.

Extrafloral nectar (EFN)

EFN is likely to represent a better reward for carnivores than FN because EFN has evolved for indirect defense and is secreted over the entire vegetation period.

Above and beyond physiological costs, potential ecological costs warrant consideration. Plant volatiles have multiple functions as direct resistance agents and as signals in plant–plant, plant–herbivore, and plant–pollinator interactions [15]. Furthermore, dispensing artificial volatiles in maize fields can lead to enhanced attraction of herbivores to the VOC-exposed plants [26], herbivorous thrips were attracted to MeSA [103], and transgenic maize plants that constitutively released (*E*)-caryophyllene and humulene also became more apparent to a specialist herbivore [112]. This multifunctionality needs to be considered to avoid counterproductive results. Finally, indirect defenses can interact with direct defenses in multiple ways. For example, attracting carnivores with MeSA and rewarding them with floral nectar of intercropped buckwheat (*Fagopyrum esculentum*) in vineyards did not benefit yield, and actually decreased the quality of the grapes owing to enhanced levels of infection with a pathogenic fungus [103]; moreover, parasitoids are exposed to direct plant defense compounds as they develop inside herbivores [113–115]. In other cases, however, direct and indirect defense traits operate in synergy [116]. For example, phenolic glycoside-producing *Salix*, which reduces herbivore fitness, provides high-quality plant sap to particular predators [48,117].

Biological Control as a Goal in Plant Breeding: Recommendations

We present a list of recommendations for how best to integrate tritrophic interactions in breeding efforts and crop management (see Box 1 for a short overview). Based on the reports on beneficial effects of plant VOCs and reward-based indirect defenses (Table 1), and on the shortcomings of merely information-based tritrophic interactions [86], we suggest that research and breeding could focus on the following biocontrol strategies:

- (i) We should investigate the wild ancestor of the crop of interest to understand its strategies for indirect defense, and compare the underlying traits in wild plants, landraces, and modern cultivars. Provided that genetic variation still exists (Table 2), these traits can be reinforced in contemporary high-yield cultivars. In this context, we must always consider that successful tritrophic interactions frequently depend on synergies among several, seemingly independent traits, for example, the combination of volatile infochemicals with food rewards or physical shelter. Furthermore, care must be taken to avoid over-costly defense strategies as well as strategies that negatively affect the quantity or quality of the product (fruit, grain, fiber etc.). Much more research will be necessary to separate defensive traits that have inadvertently been lost during the breeding process from those traits that have been actively (although in many cases unconsciously) counter-selected during breeding because their

reduction or complete elimination had positive consequences on the traits of the plant as a crop.

- (ii) An unexplored potential for integrated crop protection is represented by the triple function of many VOCs as antimicrobial agents, resistance-inducing hormones, and cues for carnivores [60,62,75,118]. Direct VOC-mediated resistance to herbivores and microorganisms (Figure 2) does not require the presence and action of any further organisms, and thus might be less context-dependent than tritrophic interactions. Transforming plants for enhanced emission of GLVs has been suggested explicitly ‘for improving plant resistance against both herbivores and pathogens’ [75]. However, by analogy with HI-VOCs that are ‘dishonest’ signals in the absence of prey or rewards, VOCs that only reduce herbivore attraction and not subsequent herbivore performance may not be a durable strategy owing to herbivore proximate and ultimate adaptations. In the aforementioned study by Bruce and colleagues, wheat that was genetically engineered to emit the (*E*)- β -farnesene exhibited significant repellent effects on aphids in the laboratory, whereas field trials revealed no reduction in aphid infestation [28].
- (iii) Any attempt to enhance the potential of crops for classical (tritrophic) biocontrol strategies should breed for a continuously primed stage, rather than for constitutive expression, to avoid constitutive emission of HI-VOCs in the absence of herbivores.
- (iv) Information-based and reward-based defenses should be combined. Information-based interactions are unlikely to function in isolation because VOCs can attract unwanted insects [26] and because attracting carnivores to herbivore-free plants deprives them of any benefit. A strategy known as ‘attract and reward’ (Figure 3) has already been successfully applied in several systems [25,103]. In this approach, synthetically produced VOCs are combined with intercropped floral resources. The ‘attract’ and the ‘reward’ parts independently improved biocontrol in the studied systems, and their combination provided synergistic effects on the target pest [103]. In this context, schemes relying on the attraction of naturally-occurring parasitoids and predators should be compared to the consequences of the artificial release of such biocontrol agents.
- (v) In all attempts that employ rewards for carnivores, extrafloral nectar might represent an as-yet underexplored possibility in biocontrol. Ultimately, EFN, rather than FN, represents the type of nectar that serves to attract predators and parasitoids in natural systems, and EFN is usually secreted over the entire lifespan of a plant whereas FN secretion is restricted to the flowering phase [119]. Therefore, we should investigate the protective effects of EFN in agronomic setups, both with and without the additional release of carnivores.
- (vi) Breeding could aim at returning attracting and rewarding traits to the crops themselves and reduce the need for intercropping. However, intercropping could also represent an interesting option, particularly for organic farming and in regions where manual maintenance and harvesting techniques still dominate. Alternatively, both VOCs and energy-rich resources can be applied artificially to those crops that cannot express these traits or in more technological agricultural systems.
- (vii) We must consider carefully unwanted side effects, such as the induction of one resistance type at the cost of another, the attraction of herbivores, and so on. Finally, we must measure the effects that are relevant for the farmer. In the end, factors that are ultimately of interest for the grower are crop yield and the quality of the resulting product (fruits, grains, vegetables) obtained under realistic agronomic or horticultural conditions.

Concluding Remarks

Biological control of pests usually works best for perennial cropping systems and forest systems, where carnivores have time to build up high populations [51], and in closed environments, such as greenhouses, where biological control agents can be released and confined. The potential for utilizing carnivores in annual field crops and large monocultures appears to be more limited. However, deploying VOCs as agents for biological control of plant disease [62] and

Outstanding Questions

How has breeding affected the capacity of crops to engage in tritrophic interactions? Among the few crop species investigated so far for the emission of herbivore-induced volatiles, both higher and lower emission rates than their wild relatives have been reported. Even less information is available on the effects of breeding on food rewards or shelter for carnivores.

Can plant volatiles be used for biological control of both pests and crop disease? Volatile organic plant compounds are usually investigated in the context of herbivory, and biological control generally concerns pests, not pathogens. However, recent reports on multiple inhibitory effects of plant volatiles on pathogenic fungi indicate that volatiles might bear an as-yet underused potential for biological control of crop diseases.

What are the limits for breeding crops with biological control? The secretion of extrafloral nectar is likely to depend on hundreds of genes, which makes it seemingly impossible to breed this trait into a crop that does not naturally possess extrafloral nectaries. Similarly, most herbivorous insects respond to overall blends of plant volatiles rather than to single compounds.

adding rewards and shelter for predators [58] are two strategies that can enhance biocontrol even in monoculture crops.

Tritrophic interactions are often complex, and plant traits that provide information and resources may sometimes have unforeseen effects on ecological food webs. These and other interacting effects might overwhelm and discourage plant breeders who traditionally consider direct bitrophic interactions, which are unconsciously complemented with biocontrol in plant breeding nurseries where an essential part of the selection for resistance is taking place. In addition, there may be problems of acceptance by farmers because these more natural strategies usually do not completely eliminate pests and pathogens from the systems. Finally, genetic engineering is not accepted in several countries, and particularly not as a tool in organic farming [3], a situation which is likely to limit the optimization of crops for biological control.

However, new regulations and changing consumer demands are gradually improving the prospects for more sustainable agriculture. For example, European Parliament directive 2009/128/EG made the implementation of integrated pest management obligatory within the EU from 2014. Thus, there are several trends towards increased acceptance of 'good enough' solutions to pest problems. Indeed, two breeding projects already target natural enemies of pests. In the SAMBA project (www.samba-webb.se), plant breeders collaborated with insect ecologists to identify willow traits that attract and reward natural enemies of detrimental leaf beetles [108]. The major natural enemies of the leaf beetles are omnivorous bugs (mirids and anthocorids), which can maintain high densities even during periods of low prey availability. A second promising breeding project involves the restoration of indirect defense traits in maize, utilizing traits that are still available in some landraces [7, 120].

Based on the considerations outlined in this paper, we stress the importance of including both information-based and reward-based plant traits to achieve functioning tritrophic defense, and of exploring the direct resistance-related functions of VOCs, which could allow biocontrol of pests and pathogens independently of the third trophic level. The 'attract-and-reward' concept and the direct defensive effects of plants VOCs provide a useful framework for the design of biocontrol strategies that can allow sustainable and cost-efficient protection of our crops. The resulting benefits are potentially very large, and data on the net-outcomes of specific strategies in realistic agronomic and horticultural environments can be obtained quickly.

Acknowledgments

We apologize to authors whose work could not be cited owing to space constraints. We thank Toby J.A. Bruce, Ian Kaplan, and two anonymous referees for multiple helpful comments on an earlier version of this manuscript. J.A.S. is funded by the Swedish research council Formas; M.H. is funded by CONACyT (grants 129678 and 212715); C.B. is funded by the Swedish Energy Agency, the SAMBA project, the Future Forests Project, and the Swedish University of Agricultural Sciences (SLU). I.Å. is funded by Formas and SLU.

References

1. Evans, L.T. (1996) *Crop Evolution, Adaptation and Yield*, Cambridge University Press
2. Hammer, K. (1984) Das Domestikationssyndrom. *Kulturpflanze* 32, 11–34
3. Andersen, M.M. *et al.* (2015) Feasibility of new breeding techniques for organic farming. *Trends Plant Sci.* 20, 426–434
4. Dangl, J.L. *et al.* (2013) Pivoting the plant immune system from dissection to deployment. *Science* 341, 746–751
5. Hammond-Kosack, K.E. and Parker, J.E. (2003) Deciphering plant–pathogen communication: fresh perspectives for molecular resistance breeding. *Curr. Opin. Biotechnol.* 14, 177–193
6. Godfray, H.C.J. *et al.* (2010) Food security: the challenge of feeding 9 billion people. *Science* 327, 812–818
7. Tamiru, A. *et al.* (2015) New directions for improving crop resistance to insects by breeding for egg induced defence. *Curr. Opin. Insect Sci.* Published online February 28, 2015. <http://dx.doi.org/10.1016/j.cois.2015.02.011>
8. Arimura, G. *et al.* (2005) Herbivore-induced, indirect plant defences. *Biochim. Biophys. Acta Mol. Cell Biol. Lipids* 1734, 91–111
9. Welling, L.L. (2000) The myriad plant responses to herbivores. *J. Plant Growth Regul.* 19, 195–216
10. Conrath, U. *et al.* (2006) Priming: getting ready for battle. *Mol. Plant Microbe Interact.* 19, 1062–1071
11. Frost, C. *et al.* (2008) Plant defense priming against herbivores: getting ready for a different battle. *Plant Physiol.* 146, 818–824
12. Karban, R. and Baldwin, I.T. (1997) *Induced Responses to Herbivory*, University of Chicago Press

13. Heil, M. (2010) Plastic defence expression in plants. *Evol. Ecol.* 24, 555–569
14. Karban, R. (2011) The ecology and evolution of induced resistance against herbivores. *Funct. Ecol.* 25, 339–347
15. Heil, M. (2014) Herbivore-induced plant volatiles: targets, perception and unanswered questions. *New Phytol.* 204, 297–306
16. Unsicker, S.B. *et al.* (2009) Protective perfumes: the role of vegetative volatiles in plant defense against herbivores. *Curr. Opin. Plant Biol.* 12, 479–485
17. Dudareva, N. *et al.* (2006) Plant volatiles: recent advances and future perspectives. *Crit. Rev. Plant Sci.* 25, 417–440
18. Heil, M. (2008) Indirect defence via tritrophic interactions. *New Phytol.* 178, 41–61
19. Heil, M. (2015) Extrafloral nectar at the plant–insect interface: a spotlight on chemical ecology, phenotypic plasticity, and food webs. *Annu. Rev. Entomol.* 60, 213–232
20. Khan, Z.R. *et al.* (2014) Achieving food security for one million sub-Saharan African poor through push-pull innovation by 2020. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 369 0120284
21. Atanassov, A. and Shearer, P. (2005) Peach extrafloral nectar impacts life span and reproduction of adult *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae). *J. Agric. Urban Entomol.* 22, 41–47
22. Brown, M.W. *et al.* (2010) Extrafloral nectar in an apple ecosystem to enhance biological control. *J. Econ. Entomol.* 103, 1657–1664
23. Mathews, C.R. *et al.* (2011) Interactions between extrafloral nectaries, ants (Hymenoptera: Formicidae), and other natural enemies affect biological control of *Grapholita molesta* (Lepidoptera: Tortricidae) on Peach (Rosales: Rosaceae). *Environ. Entomol.* 40, 42–51
24. James, D.G. and Price, T.S. (2004) Field-testing of methyl salicylate for recruitment and retention of beneficial insects in grapes and hops. *J. Chem. Ecol.* 30, 1613–1628
25. Orre-Gordon, G.U.S. *et al.* (2013) 'Attract and reward': combining a herbivore-induced plant volatile with floral resource supplementation – multi-trophic level effects. *Biol. Contr.* 64, 106–115
26. Mérey, G.V. *et al.* (2011) Dispensing synthetic green leaf volatiles in maize fields increases the release of sesquiterpenes by the plants, but has little effect on the attraction of pest and beneficial insects. *Phytochemistry* 72, 1838–1847
27. Åhman, I. *et al.* (2010) The potential for modifying plant volatile composition to enhance resistance to arthropod pests. *CAB Rev. Perspect. Agric. Vet. Sci., Nutr. Nat. Res.* 5, 006
28. Bruce, T.J.A. *et al.* (2015) The first crop plant genetically engineered to release an insect pheromone for defence. *Sci. Rep.* 5, 11183
29. Barrett, L.G. and Heil, M. (2012) Unifying concepts and mechanisms in the specificity of plant–enemy interactions. *Trends Plant Sci.* 17, 282–292
30. Dicke, M. and Sabelis, M.W. (1988) How plants obtain predatory mites as bodyguards. *Netherlands J. Zool.* 38, 148–165
31. Turlings, T.C.J. *et al.* (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250, 1251–1253
32. Dicke, M. and Baldwin, I.T. (2010) The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. *Trends Plant Sci.* 15, 167–175
33. Clavijo McCormick, A. *et al.* (2012) The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. *Trends Plant Sci.* 17, 303–310
34. Dicke, M. *et al.* (2009) Chemical complexity of volatiles from plants induced by multiple attack. *Nat. Chem. Biol.* 5, 317–324
35. Kessler, A. and Baldwin, I.T. (2001) Defensive function of herbivore-induced plant volatile emissions in nature. *Science* 291, 2141–2144
36. Rasmann, S. *et al.* (2005) Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* 434, 732–737
37. de Moraes, C.M. *et al.* (1998) Herbivore-infested plants selectively attract parasitoids. *Nature* 393, 570–573
38. Thaler, J.S. (1999) Jasmonate-inducible plant defences cause increased parasitism of herbivores. *Nature* 399, 686–688
39. Khan, Z.R. *et al.* (1997) Intercropping increases parasitism of pests. *Nature* 388, 631–632
40. Hassanali, A. *et al.* (2008) Integrated pest management: the push-pull approach for controlling insect pests and weeds of cereals, and its potential for other agricultural systems including animal husbandry. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 363, 611–621
41. Braasch, J. and Kaplan, I. (2012) Over what distance are plant volatiles bioactive? Estimating the spatial dimensions of attraction in an arthropod assemblage. *Entomol. Exp. Appl.* 145, 115–123
42. Kaplan, I. (2012) Attracting carnivorous arthropods with plant volatiles: the future of biocontrol or playing with fire? *Biol. Contr.* 60, 77–89
43. Turlings, T.C.J. and Ton, J. (2006) Exploiting scents of distress: the prospect of manipulating herbivore-induced plant odours to enhance the control of agricultural pests. *Curr. Opin. Plant Biol.* 9, 421–427
44. Kelly, J.L. *et al.* (2014) Semiochemical lures reduce emigration and enhance pest control services in open-field predator augmentation. *Biol. Contr.* 71, 70–77
45. Lundgren, J.G. (2009) *Relationships of Natural Enemies and Non-Prey Foods*, Springer
46. Narvaez, A. *et al.* (2012) Effect of different dietary resources on longevity, carbohydrate metabolism, and ovarian dynamics in two fruit fly parasitoids. *Arthropod Plant Interact.* 6, 361–374
47. Wäckers, F.L. *et al.* (2005) *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*, Cambridge University Press
48. Stenberg, J.A. *et al.* (2010) Uncoupling direct and indirect plant defences: novel opportunities for improving crop security in willow plantations. *Agricul. Ecosyst. Environ.* 139, 528–533
49. Stenberg, J.A. *et al.* (2011) Host-plant genotype mediates supply and demand of animal food in an omnivorous insect. *Ecol. Entomol.* 36, 442–449
50. Ferreira, J.A.M. *et al.* (2011) Leaf domatia reduce intraguild predation among predatory mites. *Ecol. Entomol.* 36, 435–441
51. Ågren, G.I. *et al.* (2012) Omnivores as plant bodyguards – a model of the importance of plant quality. *Basic Appl. Ecol.* 13, 441–448
52. Chamberlain, S.A. and Holland, J.N. (2009) Quantitative synthesis of context dependency in ant-plant protection mutualisms. *Ecology* 90, 2384–2392
53. Romero, G.Q. and Koricheva, J. (2011) Contrasting cascade effects of carnivores on plant fitness: a meta-analysis. *J. Anim. Ecol.* 80, 696–704
54. Rosumek, F.B. *et al.* (2009) Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia* 160, 537–549
55. Mathews, C.R. *et al.* (2009) Extrafloral nectaries alter arthropod community structure and mediate peach (*Prunus persica*) plant defense. *Ecol. Appl.* 19, 722–730
56. Mathews, C.R. *et al.* (2007) Leaf extrafloral nectaries enhance biological control of a key economic pest, *Grapholita molesta* (Lepidoptera: Tortricidae), in peach (Rosales: Rosaceae). *Environ. Entomol.* 36, 383–389
57. Abdala-Roberts, L. *et al.* (2014) Plant traits mediate effects of predators across pepper (*Capsicum annuum*) varieties. *Ecol. Entomol.* 39, 361–370
58. Agrawal, A.A. and Karban, R. (1997) Domatia mediate plant–arthropod mutualism. *Nature* 387, 562–563
59. Agrawal, A.A. *et al.* (2000) How leaf domatia and induced plant resistance affect herbivores, natural enemies and plant performance. *Oikos* 89, 70–80
60. Scala, A. *et al.* (2013) Green leaf volatiles: a plant's multifunctional weapon against herbivores and pathogens. *Int. J. Mol. Sci.* 14, 17781–17811
61. Turlings, T.C.J. *et al.* (1998) Timing of induced volatile emissions in maize seedlings. *Planta* 207, 146–152
62. Quintana-Rodriguez, E. *et al.* (2015) Plant volatiles cause direct, induced and associational resistance in common bean to the

- fungal pathogen *Colletotrichum lindemuthianum*. *J. Ecol.* 103, 250–260
63. Park, S.W. *et al.* (2007) Methyl salicylate is a critical mobile signal for plant systemic acquired resistance. *Science* 318, 113–116
 64. Arimura, G.-I. *et al.* (2000) Herbivory-induced volatiles elicit defence genes in lima bean leaves. *Nature* 406, 512–515
 65. Frost, C. *et al.* (2007) Within-plant signalling by volatiles overcomes vascular constraints on systemic signalling and primes responses against herbivores. *Ecol. Lett.* 10, 490–498
 66. Heil, M. and Silva Bueno, J.C. (2007) Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *Proc. Natl. Acad. Sci. U.S.A.* 104, 5467–5472
 67. Engelberth, J. *et al.* (2004) Airborne signals prime plants against insect herbivore attack. *Proc. Natl. Acad. Sci. U.S.A.* 101, 1781–1785
 68. Heil, M. and Kost, C. (2006) Priming of indirect defences. *Ecol. Lett.* 9, 813–817
 69. Kessler, A. *et al.* (2006) Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata*. *Oecologia* 148, 280–292
 70. Yi, H.-S. *et al.* (2009) Airborne induction and priming of plant resistance to a bacterial pathogen. *Plant Physiol.* 151, 2152–2161
 71. Thaler, J.S. *et al.* (2012) Evolution of jasmonate and salicylate signal crosstalk. *Trends Plant Sci.* 17, 260–270
 72. Chen, Y.H. *et al.* (2015) Crop domestication and its impact on naturally selected trophic interactions. *Annu. Rev. Entomol.* 60, 35–58
 73. Rodríguez-Saona, C. *et al.* (2011) Field responses of predaceous arthropods to methyl salicylate: A meta-analysis and case study in cranberries. *Biol. Contr.* 59, 294–303
 74. Brillada, C. *et al.* (2013) Metabolic engineering of the C₁₆ homoterpene TMTT in *Lotus japonicus* through overexpression of (E, E)-geranylinalool synthase attracts generalist and specialist predators in different manners. *New Phytol.* 200, 1200–1211
 75. Shiojiri, K. *et al.* (2006) Changing green leaf volatile biosynthesis in plants: An approach for improving plant resistance against both herbivores and pathogens. *Proc. Natl. Acad. Sci. U.S.A.* 103, 16672–16676
 76. Birkett, M.A. and Pickett, J.A. (2014) Prospects of genetic engineering for robust insect resistance. *Curr. Opin. Plant Biol.* 19, 59–67
 77. Ballhorn, D.J. *et al.* (2013) Distance and sex determine host plant choice by herbivorous beetles. *PLoS ONE* 8, e55602
 78. Bruce, T.J.A. and Pickett, J.A. (2011) Perception of plant volatile blends by herbivorous insects – finding the right mix. *Phytochemistry* 72, 1605–1611
 79. Halitschke, R. *et al.* (2008) Shared signals – ‘alarm calls’ from plants increase apparency to herbivores and their enemies in nature. *Ecol. Lett.* 11, 24–34
 80. von Meroy, G.E. *et al.* (2012) Minor effects of two elicitors of insect and pathogen resistance on volatile emissions and parasitism of *Spodoptera frugiperda* in Mexican maize fields. *Biol. Contr.* 60, 7–15
 81. Gouinguéné, S.P. and Turlings, T.C.J. (2002) The effects of abiotic factors on induced volatile emissions in corn plants. *Plant Physiol.* 129, 1296–1307
 82. Pichersky, E. *et al.* (2006) Biosynthesis of plant volatiles: Nature’s diversity and ingenuity. *Science* 311, 808–811
 83. Holopainen, J.K. and Gershenzon, J. (2010) Multiple stress factors and the emission of plant VOCs. *Trends Plant Sci.* 15, 176–184
 84. Gish, M. *et al.* (2015) Herbivore-induced plant volatiles in natural and agricultural ecosystems: open questions and future prospects. *Curr. Opin. Insect Sci.* 9, 1–6
 85. Loreto, F. *et al.* (2014) Plant volatiles and the environment. *Plant Cell Environ.* 37, 1905–1908
 86. Kessler, A. and Heil, M. (2011) The multiple faces of indirect defences and their agents of natural selection. *Funct. Ecol.* 25, 348–357
 87. Rodríguez-Saona, C. *et al.* (2011) Tracing the history of plant traits under domestication in cranberries: potential consequences on anti-herbivore defences. *J. Exp. Bot.* 62, 2633–2644
 88. Tamiru, A. *et al.* (2011) Maize landraces recruit egg and larval parasitoids in response to egg deposition by a herbivore. *Ecol. Lett.* 14, 1075–1083
 89. Åhman, I. (2013) Breeding for inducible resistance. *IOBC WPRS Bulletin* 89, 311–317
 90. Kanchiswamy, C.N. *et al.* (2015) Bioprospecting bacterial and fungal volatiles for sustainable agriculture. *Trends Plant Sci.* 20, 206–211
 91. Heil, M. and Baldwin, I.T. (2002) Fitness costs of induced resistance: emerging experimental support for a slippery concept. *Trends Plant Sci.* 7, 61–67
 92. Gols, R. *et al.* (2008) Performance of generalist and specialist herbivores and their endoparasitoids differs on cultivated and wild *Brassica* populations. *J. Chem. Ecol.* 34, 132–143
 93. Bukovinszky, T. *et al.* (2009) Consequences of constitutive and induced variation in plant nutritional quality for immune defence of a herbivore against parasitism. *Oecologia* 160, 299–308
 94. Chen, Y.H. and Welter, S.C. (2007) Crop domestication creates a refuge from parasitism for a native moth. *J. Appl. Ecol.* 44, 238–245
 95. Wang, X.-G. *et al.* (2009) Larger olive fruit size reduces the efficiency of *Psytalia concolor*, as a parasitoid of the olive fruit fly. *Biol. Contr.* 49, 45–51
 96. Collier, T. and Van Steenwyk, R. (2004) A critical evaluation of augmentative biological control. *Biol. Contr.* 31, 245–256
 97. Loughrin, J.H. *et al.* (1995) Volatiles emitted by different cotton varieties damaged by feeding beet armyworm larvae. *J. Chem. Ecol.* 21, 1217–1227
 98. Beach, R.M. *et al.* (1985) Nectaried and nectariless cotton cultivars as nectar sources for the adult soybean looper. *J. Entomol. Sci.* 20, 233–236
 99. Benrey, B. *et al.* (1998) The effects of domestication of *Brassica* and *Phaseolus* on the interaction between phytophagous insects and parasitoids. *Biol. Contr.* 11, 130–140
 100. Ballhorn, D.J. *et al.* (2008) Trade-offs between direct and indirect defences of lima bean (*Phaseolus lunatus* L.). *J. Ecol.* 96, 971–980
 101. Gouinguéné, S. *et al.* (2001) Variability in herbivore-induced odour emissions among maize cultivars and their wild ancestors (teosinte). *Chemoecology* 11, 9–16
 102. Cortesero, A.M. *et al.* (2000) Understanding and manipulating plant attributes to enhance biological control. *Biol. Contr.* 17, 35–49
 103. Simpson, M. *et al.* (2011) Field evaluation of the ‘attract and reward’ biological control approach in vineyards. *Ann. Appl. Biol.* 159, 69–78
 104. Hagenbucher, S. *et al.* (2013) Resistance mechanisms against arthropod herbivores in cotton and their interactions with natural enemies. *Crit. Rev. Plant Sci.* 32, 458–482
 105. Hare, J.D. (2011) Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annu. Rev. Entomol.* 56, 161–180
 106. Rudgers, J.A. (2004) Enemies of herbivores can shape plant traits: Selection in a facultative ant–plant mutualism. *Ecology* 85, 192–205
 107. Wooley, S.C. *et al.* (2007) Extrafloral nectaries in aspen (*Populus tremuloides*): heritable genetic variation and herbivore-induced expression. *Ann. Bot.* 100, 1337–1346
 108. Berlin Koim, S. *et al.* (2011) Nya salixsorter med modern växtförädlings teknik. *Fakta Jordbruk* 1, 1–6
 109. Hare, J.D. (2010) Ontogeny and season constrain the production of herbivore-inducible plant volatiles in the field. *J. Chem. Ecol.* 36, 1363–1374
 110. Hoballah, M.E. *et al.* (2004) Costs of induced volatile production in maize. *Oikos* 105, 168–180
 111. Dicke, M. and Sabelis, M.W. (1989) Does it pay plants to advertise for bodyguards? Towards a cost-benefit analysis of induced synomone production. In *Causes and Consequences of*

- Variation in Growth Rate and Productivity of Higher Plants* (Lambert, H. et al., eds), pp. 341–358, SPB Publishing
112. Robert, C. et al. (2012) A specialist root herbivore exploits defensive metabolites to locate nutritious tissues. *Ecol. Lett.* 15, 55–64
 113. Gols, R. et al. (2008) Genetic variation in defense chemistry in wild cabbages affects herbivores and their endoparasitoids. *Ecology* 89, 1616–1626
 114. Harvey, J.A. et al. (2011) Tri-trophic effects of inter- and intra-population variation in defence chemistry of wild cabbage (*Brassica oleracea*). *Oecologia* 166, 421–431
 115. Stenberg, J.A. (2012) Plant-mediated effects of different *Salix* species on the performance of the braconid parasitoid *Perilitus brevicollis*. *Biol. Contr.* 60, 54–58
 116. Fatouros, N.E. et al. (2014) Synergistic effects of direct and indirect defences on herbivore egg survival in a wild crucifer. *Proc. Biol. Sci.* 281, 20141254
 117. Stenberg, J.A. et al. (2011) Plant defence: feeding your bodyguards can be counter-productive. *Basic Appl. Ecol.* 12, 629–633
 118. Engelberth, J. et al. (2007) Insect elicitors and exposure to green leafy volatiles differentially upregulate major octadecanoids and transcripts of 12-oxo phytodienoic acid reductases in *Zea mays*. *Mol. Plant Microbe Interact.* 20, 707–716
 119. Heil, M. (2011) Nectar: generation, regulation and ecological functions. *Trends Plant Sci.* 16, 191–200
 120. Tamiru, A. et al. (2012) Oviposition induced volatile emissions from African smallholder farmers' maize varieties. *J. Chem. Ecol.* 38, 231–234
 121. Ninkovic, V. et al. (2001) The influence of aphid-induced plant volatiles on ladybird beetle searching behavior. *Biol. Contr.* 21, 191–195
 122. Mäntylä, E. et al. (2008) From plants to birds: higher avian predation rates in trees responding to insect herbivory. *PLoS ONE* 3, e2832
 123. Mäntylä, E. et al. (2014) Does application of methyl jasmonate to birch mimic herbivory and attract insectivorous birds in nature? *Athrop. Plant Interact.* 8, 143–153
 124. Zakir, A. et al. (2013) Herbivore-induced plant volatiles provide associational resistance against an ovipositing herbivore. *J. Ecol.* 101, 410–417
 125. Kost, C. and Heil, M. (2008) The defensive role of volatile emission and extrafloral nectar secretion for Lima bean in nature. *J. Chem. Ecol.* 34, 2–13
 126. de Moraes, C.M. et al. (2001) Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410, 577–580
 127. Tahmasebi, Z. et al. (2014) Herbivore-induced indirect defense across bean cultivars is independent of their degree of direct resistance. *Exp. Appl. Acarol.* 63, 217–239
 128. Poelman, E.H. et al. (2009) Field parasitism rates of caterpillars on *Brassica oleracea* plants are reliably predicted by differential attraction of *Cotesia parasitoids*. *Funct. Ecol.* 23, 951–962
 129. Nissinen, A. et al. (2005) Influence of carrot psyllid (*Trioxa apicalis*) feeding or exogenous limonene or methyl jasmonate treatment on composition of carrot (*Daucus carota*) leaf essential oil and headspace volatiles. *J. Agric. Food Chem.* 53, 8631–8638
 130. Krips, O.E. et al. (2001) Comparison of cultivars of ornamental crop *Gerbera jamesonii* on production of spider mite-induced volatiles, and their attractiveness to the predator *Phytoseiulus persimilis*. *J. Chem. Ecol.* 27, 1355–1372
 131. Scutareanu, P. et al. (2003) Constitutive and herbivore-induced volatiles in pear, alder and hawthorn trees. *Chemoecology* 13, 63–74
 132. Lou, Y.G. et al. (2006) Differences in induced volatile emissions among rice varieties result in differential attraction and parasitism of *Nilaparvata lugens* eggs by the parasitoid *Anagrus nilaparvatae* in the field. *J. Chem. Ecol.* 32, 2375–2387
 133. Michereff, M.F.F. et al. (2011) Volatiles mediating a plant-herbivore-natural enemy interaction in resistant and susceptible soybean cultivars. *J. Chem. Ecol.* 37, 273–285
 134. Himanen, S. et al. (2005) Effects of cyclamen mite (*Phytonemus pallidus*) and leaf beetle (*Galerucella tenella*) damage on volatile emission from strawberry (*Fragaria × ananassa* Duch.) plants and orientation of predatory mites (*Neoseiulus cucumeris*, *N. californicus*, and *Euseius finlandicus*). *J. Agric. Food Chem.* 53, 8624–8630
 135. Lehman, A. et al. (2013) Constitutive and herbivore-induced systemic volatiles differentially attract an omnivorous biocontrol agent to contrasting *Salix* clones. *AoB Plants* 5, pii005