



## Review

# Volatile Organic Compounds: A Review of Their Current Applications as Pest Biocontrol and Disease Management

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**Abstract:** Sustainable agriculture is the most desired solution to ensure food security for the growing world population and to face climate change. Furthermore, sustainable agriculture seeks alternatives to harmful pesticides and chemical fertilizers. This review presents an overview of recent scientific research and potential applications of volatile organic compounds (VOCs) as pest biocontrol and disease management during pre- and postharvest, along with possible limitations in scalability at the agricultural level. According to the information reviewed, bacteria, fungi, yeast, and plants are the principal organisms that produce VOCs with biotechnological potential. The main applications reported for VOCs are enhanced resistance/tolerance to abiotic stressors, such as drought, cold, and salinity, and an enhanced defense response against biotic stressors, such as viruses, bacteria, fungi, nematodes, and insects. Some VOCs in particular present an antimicrobial effect on a wide range of plant and human pathogens. Therefore, VOCs are considered a promising, sustainable biocontrol strategy that can replace pesticides and fertilizers. However, future research needs to promote collaboration with farmers and the development of applications for VOCs at the industrial level.

**Keywords:** induced resistance; defense priming; parasitoids; intercropping; microbial volatiles; plant volatiles; biofumigant; stress tolerance



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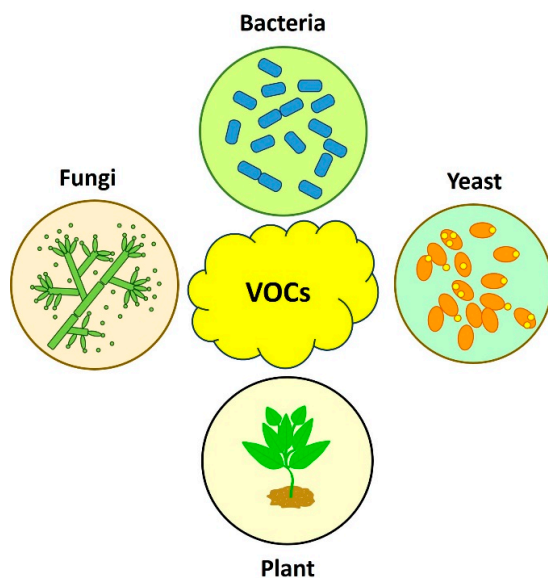
## 1. Introduction

The growing world population demands a significant increase in agricultural production. By 2050, the world population is estimated to reach 9.7 billion people [1]. According to the United Nations Food and Agriculture Organization (FAO), an increase of 70% in food production is necessary to supply future food demands [2]. Under this scenario, crop protection against abiotic stress, diseases, and infestations is essential for maintaining and improving crop yields [3]. Over the last few decades, pesticides have been and still are a significant tool for agricultural intensification, contributing enormously to increased food production [4]. However, the effectiveness and availability of pesticides are limited and insufficient to counteract the increased resistance observed in pathogens, insects, and weeds [5,6]. Furthermore, pesticides play a significant role in many human health problems and have other adverse side effects, such as soil and water contamination, toxicity to non-target species, and pesticide residues in food [7–9].

On the other hand, climate change affects crop production and pest and pathogen resistance because it promotes extreme weather events, reduces the adaptation time, and increases the ecosystem's vulnerability [10]. Some extreme climate events, such as drought, cause soil degradation and fertility loss, reducing agricultural area availability [11,12]. In addition, high temperatures are directly associated with increases in the spreading of plant pathogens, which favors the infection of new hosts [10,11]. In the past few decades,

there has been an increased interest in sustainable alternative agricultural techniques that improve crop yields while reducing losses [13].

Volatile organic compounds (VOCs) are promising alternatives to synthetic pesticides in pest and disease management. VOCs are gaining interest due to the various advantages of their application, such as the reduction in residuals in the environment and their ease of application in different agricultural systems [14]. Therefore, this review explores the potential applications of VOCs emitted by fungi, bacteria, yeasts, and plants (Figure 1) as sustainable alternatives that increase plant protection and productivity and the feasibility of their use. To achieve this goal, we defined appropriate keywords to form a search string (for example, sustainable agriculture, food security, pesticides, diseases management, pest management, biocontrol and preharvest, biocontrol and postharvest, preharvest diseases, postharvest diseases, fungal volatiles, bacterial volatiles, plant volatiles, yeast volatiles, biotic stress, abiotic stress, induction resistance and drought, induction resistance and cold, induction resistance and salinity, antimicrobial effect, climate change effect, herbivore-induced plant volatiles (HIPVs), microbial volatile organic compounds (MVOCs), metabolic pathways, volatile induction, phytohormone signaling pathway, defense priming, plant defense, natural enemies, terpenoids, attract and reward, green leaf volatiles, parasitoids, beneficial insects, predatory arthropods, induction mechanisms, intercropping, push–pull system, genetically modified crops, biofumigant, biofumigation, stress tolerance). The abbreviations of some keywords were also considered (for example, VOCs, HIPVs, and MVOCs). Relevant articles were found in Scopus, Google Scholar, PubMed, ScienceDirect, and Web of Science. A total of two hundred and ten articles were selected in the preliminary search; forty-eight articles were excluded, and a total of one hundred and sixty-two articles were used to build this review. The articles were selected in English, and the period selected was from 2013–2022; however, we did not discard relevant articles published before this period.

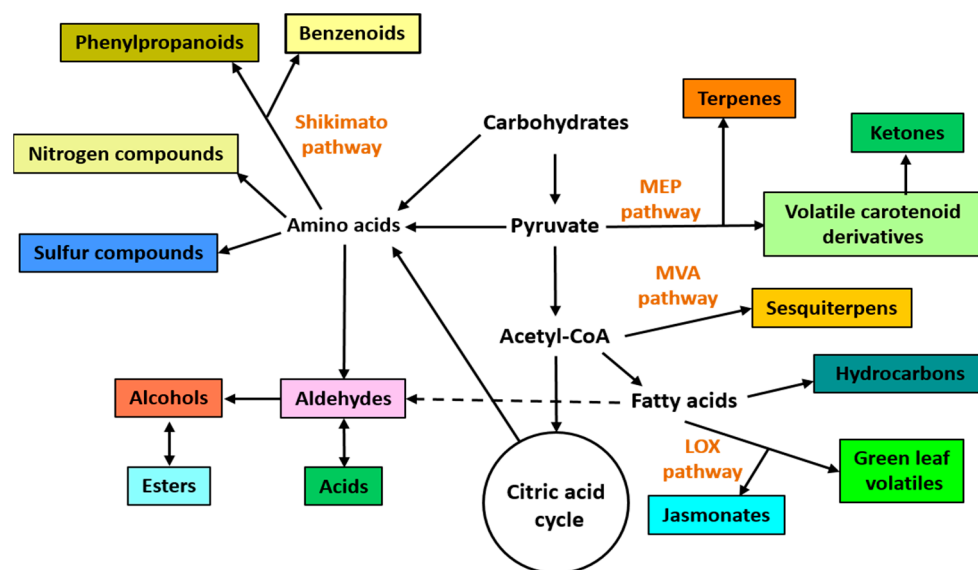


**Figure 1.** Organism producers of volatile organic compounds with biocontrol applications.

## 2. General Aspects of VOCs and Possible Biotechnological Applications

In nature, VOCs are emitted by all living organisms and occur as a complex mixture called “volatilome” [15]. For years, VOCs were considered non-essential to the functioning of the organisms that produced them. However, in the last decades, the scientific community has elucidated the important role of VOCs at the ecosystem level because they mediate intra- and interspecific interactions among all organisms [16]. VOCs typically occur as a complex mixture produced by four major metabolic pathways, namely the shiki-

mate/phenylalanine, the mevalonic acid (MVA), the methylerythritol phosphate (MEP), and lipoxygenase (LOX) pathways [17,18] (Figure 2).



**Figure 2.** Overview of main biosynthetic pathways to produce plant and microbial volatile organic compounds. Different chemical classes of VOCs are depicted in colored rectangles. The four principal biosynthetic pathways are: the shikimate, the methylerythritol phosphate (MEP), the mevalonic acid (MVA), and the lipoxygenase (LOX) pathways.

Different studies demonstrated that VOCs modulate (suppress or stimulate) microbial and plant growth [13,19], induce systemic resistance in plants against biotic and abiotic stresses [20], and act as attractants or repellents of insects [16]. For these reasons, developing effective VOCs formulations for their biotechnological application in the field could facilitate the emergence of strategies for sustainable plant disease and pest control and productivity improvement [21]. However, we must consider that VOC emissions' composition and quantity can be affected by different factors. For example, VOC emissions in bacteria and fungi depend on microbial taxa, life stage, growth phase, substrate type, and temperature [22]. For plants, high temperatures, high light intensities, and herbivore attacks increase VOC emissions [23]. This issue could be solved by using pure volatiles, thus improving reproducibility. However, the high vapor pressure at which VOCs would have to be stored and their high diffusion rate make them unstable, shortening their helpful half-life under normal conditions [24]. These characteristics, as well as the long-term exposure needed to obtain the beneficial effects of VOCs, are the main challenges for the production of VOC formulations [25].

### 3. Microbial Volatile Organic Compounds as Biocontrol Alternatives for Postharvest Diseases

Postharvest diseases result in considerable spoilage, lowering the quality and nutrient composition of fruits and vegetables, which leads to losses of about 40–60% of global production [26–29]. The most important pathogens causing postharvest losses are usually bacteria and fungi, with fungi predominantly responsible for spoilage and losses in postharvest products [30]. MVOs are produced by various microorganisms such as fungi, bacteria, and yeast and have essential roles in distant interactions and communication. Recent evidence shows that MVOs are an eco-friendly, sustainable strategy that enhances productivity and disease resistance and can be implemented in agricultural systems. Therefore, in recent decades, the use of MVOs with antimicrobial effects to control postharvest diseases has received much attention [28,31]. MVOs produced by different fungal species, such as *Muscodor* spp. [32–38], *Trichoderma* spp. [19,39–45], *Aspergillus* spp. [46], *Oxyporus* spp. [47],

and *Daldinia cf. concentrica* [48]; bacterial species of the genus *Bacillus* spp. [49–54], *Pseudomonas* spp. [54–57], and *Streptomyces* spp. [58,59]; and yeast of the genus *Pichia* spp. [60], *Hanseniaspora* spp. [61], *Candida* spp. [62], and *Clavispora* spp. [63] have been widely studied for their potential as biocontrols of postharvest diseases that affect mainly fruits, such as bananas, muskmelons, apples, peaches, strawberries, citrus fruits, grapes, apricots, litchi, among others, and also vegetables, such as lettuce, chilis, and potatoes, and seeds such as rice, wheat, and barley.

Different trials have demonstrated that biofumigation (Figure 3) with MVOCs produced by these organisms, both naturally-produced and synthetic and as mixtures or a single MVOC, contributes to controlling important plant pathogen species responsible for losses in postharvest, such as *Fusarium* spp., *Tilletia* spp., *Pythium* spp., *Phytophthora* spp., *Sclerotinia* spp., *Penicillium* spp., *Colletotrichum* spp., *Rhizoctonia* spp., *Aspergillus* spp., *Alternaria* spp., *Botrytis* spp., *Monilinia* spp., *Verticillium* spp., among others. MVOCs produced by *Muscodor crispans* demonstrated effectiveness against plant pathogens such as *Xanthomonas* spp. and human bacterial pathogens with medical importance, such as *Yersinia pestis* and *Staphylococcus aureus*, including drug-resistant strains of *Mycobacterium tuberculosis* (Table 1) [34]. In addition, MVOCs produced by different strains of *Bacillus* spp., *Pseudomonas* spp., *Streptomyces* spp., *Pichia* spp. and *Candida* spp. have demonstrated the capacity to inhibit the production of the mycotoxins that are significant contaminants of the agricultural and food industries, produced mainly by species of *Aspergillus* spp., *Penicillium* spp. and *Fusarium* spp. For example, *Aspergillus flavus* LA1, a non-aflatoxigenic strain, emitted 3-octanone and trans-2-methyl-2- butenal. These MVOCs can reduce the aflatoxins B1, G1, and cyclopiazonic acid (CPA) levels in *A. flavus* LA2, LA3, and *Aspergillus parasiticus* LA4 aflatoxigenic strains. Another two compounds emitted by this strain, 2,3-dihydrofuran and decane, can reduce aflatoxin levels and completely inhibit CPA production in *A. flavus* in LA3 by interfering with fatty acid synthases or polyketide synthases in aflatoxin biosynthesis [46]. Another example is the volatilome of *Bacillus megaterium*, which can inhibit the aflatoxins (B1, G1, and G2) produced by *A. flavus* as well as other mycotoxins such as ochratoxin A produced by *Penicillium verrucosum* and Fumonisin B1 produced by *Fusarium verticillioides* [53]. On the other hand, volatilome emitted by *Trichoderma koningiopsis* PSU3-2 inhibits the fungal growth of *Colletotrichum gloeosporioides*, responsible for postharvest anthracnose in chili pepper, by increasing the activity of cell-wall degrading enzymes (CWDEs) chitinase and  $\beta$ -1,3-glucanase [43]. Similar results show MVOCs emitted by *Trichoderma asperellum* T1 strain on leaf spot fungi *Corynespora cassiicola* and *Curvularia aeria* by inducing a defense response in lettuce through the increase of activity of CWDEs, chitinase, and  $\beta$ -1,3-glucanase [40]. One example of synthetic MVOCs used as a biocontrol is phenylethyl alcohol (PEA), which demonstrated in in vivo assays its ability to effectively control *Fusarium incarnatum*, a causal agent of a destructive postharvest disease of muskmelon that causes abnormal changes in the fungal mycelia [39]. Moreover, PEA is effective in controlling *Botrytis cinerea* by slowing down its growth, and it can also maintain the fresh aroma in a strawberry after being stored for 15 days, demonstrating this fruit's prolonged shelf-life and quality [64]. Biofumigation with MVOCs has advantages in comparison with traditional disease control; for example, MVOCs are effective at low concentrations and easily dispersed in closed spaces due to their high vapor pressure and low molecular weight. In addition, the inhibitory activity of MVOCs does not require direct physical contact with the product; therefore, they do not leave toxic residues in the products [18,65–68]. These characteristics turn MVOCs into potential biofumigant candidates for biocontrol in postharvest agricultural products, such as fruits, vegetables, and seeds.

**Table 1.** Microbial volatile organic compounds with application in postharvest diseases control.

Organism Emitter	Organism Target	Emitted Volatile	Activity	Crop	Reference
<i>Muscodor albus</i> Worapong et al.	<i>Fusarium sambucinum</i> Fukel, <i>Helminthosporium solani</i> Durieu and Mont, <i>Pectobacterium atrosepticum</i> van Hail, <i>Tilletia horrida</i> Padwick and A. Khan, <i>Tilletia indica</i> Mitra, <i>Tilletia tritici</i> (DC.) Tul. and C. Tul	Volatilome	Fungal growth inhibition	Potato ( <i>Solanum tuberosum</i> L.), Rice ( <i>Oryza sativa</i> L.), Wheat ( <i>Triticum aestivum</i> L.)	[32,33]
<i>Muscodor crispens</i> . Mitchell et al.	<i>Pythium ultimum</i> Trow, <i>Phytophthora cinnamomic</i> Rands, <i>Sclerotinia sclerotiorum</i> (Lib.) de Bary, <i>Mycosphaerella fijiensis</i> Morelet, <i>Xanthomonas axonopodis</i> pv. Citri Hasse, <i>Yersinia pestis</i> Lehmann & Neumann, <i>Mycobacterium tuberculosis</i> Zopf, <i>Staphylococcus aureus</i> Rosenbach	Volatilome	Fungal and bacterial growth inhibition	Banana ( <i>Musa × paradisiaca</i> L.)	[34]
<i>Muscodor brasiliensis</i> Pena et al.	<i>Penicillium digitatum</i> Pers	Volatilome	Fungal growth inhibition	Orange ( <i>Citrus × sinensis</i> L.)	[35]
<i>Muscodor sutura</i> Kudalkar et al.	<i>Phyllosticta citricarpa</i> McAlpine	Volatilome	Fungal growth inhibition	Citrus	[36]
<i>Muscodor albus</i> Worapong et al.	<i>Phthorimaea operculella</i> Zeller	Volatilome	Insecticidal effect	Potato ( <i>Solanum tuberosum</i> L.)	[37]
<i>Muscodor heveae</i> Siri-udom et al.	<i>Rigidoporus microporus</i> Swartz	Volatilome	Fungal growth inhibition	Rubber trees ( <i>Hevea brasiliensis</i> Müll. Arg.)	[38]
<i>Trichoderma asperellum</i> Samuels et al.	<i>Fusarium incarnatum</i> Desm., <i>Corynespora cassiicola</i> Berk. and M.A. Curtis, <i>Curvularia aeria</i> Bat et al.	Phenylethyl alcohol	Fungal growth inhibition	Muskmelon ( <i>Cucumis melo</i> L.), Lettuce ( <i>Lactuca sativa</i> L.)	[39,40]

Table 1. Cont.

Organism Emitter	Organism Target	Emitted Volatile	Activity	Crop	Reference
<i>Trichoderma harzianum</i> Rifai	<i>Pyrenophora teres</i> Drechsles, <i>Fusarium moniliforme</i> Sheldon	6-pentyl-alpha-pyrone (6PAP)	Fungal growth inhibition	Barley ( <i>Hordeum vulgare</i> L.)	[41,42]
<i>Trichoderma</i> spp. Persoon <i>Longibrachiatum</i> Rifai	<i>Sclerotium rolfsii</i> Curzi, <i>Macrophomina phaseolina</i> Tassi	Volatilome	Fungal growth inhibition	Generalist	[44]
<i>Trichoderma koningiopsis</i> Samuels et al.	<i>Colletotrichum gloeosporioides</i> Penz	Volatilome	Fungal growth inhibition	Chili pepper ( <i>Capsicum annuum</i> L.)	[43]
<i>Trichoderma atroviride</i> Bissett	<i>Phytophthora infestans</i> Mont.	6-pentyl-2-pyrone (6-PP), isoamyl alcohol, isobutyl alcohol	Fungal growth inhibition	Potato ( <i>Solanum tuberosum</i> L.)	[19]
<i>Trichoderma viridens</i> Pers.	<i>Rhizoctonia solani</i> J.G.Kühn	Volatilome	Fungal growth inhibition	Generalist	[45]
<i>Aspergillus flavus</i> Link	<i>Aspergillus flavus</i> Link <i>Aspergillus parasiticus</i> Speare	3-octanone, trans-2-methyl-2- butenal, 2,3- dihydrofuran, decane	Mycotoxin inhibition		[46]
<i>Daldinia cf. concentrica</i> Bolton	<i>Aspergillus niger</i> P.E.L. van Tieghem, <i>Alternaria alternata</i> Fr., <i>Botrytis cinerea</i> Whetzel, <i>Colletotrichum</i> sp. Corda, <i>Coniella</i> sp. Höhnel, <i>Fusarium euwallaceae</i> Freeman et al., <i>Fusarium mangiferae</i> Britz et al., <i>Fusarium oxysporum</i> Schltdl, <i>Lasiodiplodia theobromae</i> Pat., <i>Penicillium digitatum</i> Pers., <i>Phoma tracheiphila</i> Petri, <i>Pythium ultimum</i> Trow, <i>Pythium aphanidermatum</i> Edson, <i>Rhizoctonia solani</i> J.G.Kühn, <i>Sclerotinia sclerotiorum</i> (Lib.) de Bary	Volatilome; mixture of 4-heptanone and trans-2-octenal	Fungal growth inhibition	Dried fruits, Peanuts ( <i>Arachis hypogaea</i> L.)	[48]



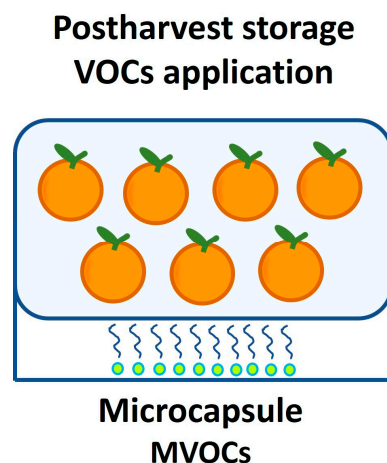
Table 1. Cont.

Organism Emitter	Organism Target	Emitted Volatile	Activity	Crop	Reference
<i>Oxyporus latemarginatus</i> Durieu & Mont.	<i>Botrytis cinerea</i> Whetzel, <i>Rhizoctonia solani</i> J.G.Kühn	5-pentyl-2-furaldehyde	Fungal growth inhibition	Apple ( <i>Malus domestica</i> Borkh)	[47]
<i>Bacillus subtilis</i> Ehrenberg	<i>Botrytis cinerea</i> Whetzel, <i>Colletotrichum gloeosporioides</i> Penz, <i>Penicillium expansum</i> Link, <i>Monilinia fructicola</i> Winter, <i>Alternaria alternata</i> (Fr.) Keissl, <i>Fusarium oxysporum</i> Schltdl	Volatilome; individual compounds 2,4-di-tert-butylphenol, benzothiazole	Fungal growth inhibition	Peach ( <i>Prunus cv.</i> DaJiubao), Litchi ( <i>Litchi chinensis</i> Sonn.)	[52]
<i>Bacillus amyloliquefaciens</i> Priest et al.	<i>Fusarium solani</i> Mart.	Volatilome	Fungal growth inhibition		[49]
<i>Bacillus velezensis</i> Ruiz-García et.al.	<i>Verticillium dahlia</i> Kleb, <i>Fusarium oxysporum</i> Schltdl, <i>Botrytis cinerea</i> Whetzel, <i>Monilinia fructicola</i> Winter, <i>Monilinia laxa</i> Honey, <i>Penicillium italicum</i> Wehmer, <i>Penicillium expansum</i> Link	Decanal, 3-undecanone, 2-undecanone, 2-undecanol, undecanal, 2,4-dimethyl-6-tert-butylphenol, benzothiazole, benzaldehyde, diacetyl, 1,3-butadiene, N, N-dimethyldodecylamine	Fungal growth inhibition	Strawberry ( <i>Fragaria</i> × <i>ananassa</i> Duch.), Apricot ( <i>Prunus persica</i> L.), Grape ( <i>Vitis vinifera</i> L.), Mandarin ( <i>Citrus reticulata</i> L.)	[50,51]
<i>Bacillus megaterium</i> de Bary	<i>Aspergillus flavus</i> Link, <i>Penicillium verrucosum</i> Dierckx, <i>Fusarium verticillioides</i> Sacc.	Volatilome	Mycotoxin inhibition		[53,54]
<i>Pseudomonas fluorescens</i> Migula	<i>Penicillium italicum</i> Wehmer	Dimethyl disulfide (DMDS), dimethyl trisulfide (DMTS)	Fungal growth inhibition	Citrus fruits	[55]

Table 1. Cont.

Organism Emitter	Organism Target	Emitted Volatile	Activity	Crop	Reference
<i>Pseudomonas protegens</i> Flügge	<i>Aspergillus flavus</i> Link	Volatilome	Mycotoxin Inhibition	Rice ( <i>Oryza sativa</i> L.)	[54]
<i>Pseudomonas chlororaphis</i> subsp. <i>aureofaciens</i> Kluver	<i>Ceratocystis fimbriata</i> Ellis and Halst	3-methyl-1-butanol, phenylethyl alcohol, 2-methyl-1-butanol	Fungal growth inhibition	Sweet potato ( <i>Ipomoea batatas</i> L. Lam.)	[57]
<i>Streptomyces alboflavus</i> Waksman and Curtis	<i>Aspergillus flavus</i> Link	Dimethyl trisulfide, benzenamine	Mycotoxin Inhibition		[58]
<i>Streptomyces philanthi</i>	<i>Colletotrichum gloeosporioides</i> Penz	Volatilome	Fungal growth inhibition	Chili ( <i>Capsicum annuum</i> L.)	[59]
<i>Pichia anomala</i> Hansen	<i>Aspergillus flavus</i> Link	2-phenylethyl ethanol	Mycotoxin Inhibition	Tree nuts	[60]
<i>Hanseniaspora uvarum</i> Niehaus	<i>Botrytis cinerea</i> Whetzel	Volatilome	Fungal growth inhibition	Strawberry ( <i>Fragaria × ananassa</i> Duch.), Cherries ( <i>Prunus</i> subsp. <i>cerasus</i> L.)	[61]
<i>Candida nivariensis</i> Alcoba-Florez	<i>Aspergillus flavus</i> Link	Volatilome	Fungal growth inhibition, Mycotoxin inhibition		[62]
<i>Clavispora lusitaniae</i> Uden & Carmo Souza	<i>Penicillium digitatum</i> Pers.	Volatilome	Fungal growth inhibition	Lemon ( <i>Citrus × limon</i> L.)	[63]





**Figure 3.** Biofumigation with MVOs strategy for biocontrol of postharvest disease can enhance the shelf-life and quality of food.

#### 4. Herbivore-Induced Plant Volatiles (HIPVs) as Biocontrol Alternatives in Agriculture

Plants' response to herbivore attacks is to synthesize different defensive VOCs, so-called HIPVs. HIPVs are complex mixtures shaped basically by green leaf volatiles (GLVs), terpenoids, aromatics, and amino acid volatile derivatives, and they vary according to the plant and herbivore species, as well as the development stage and condition of them [66,69,70]. The induction of HIPVs occurs for different reasons (herbivores feeding on leaves, the deposition of insect eggs on plant parts, and feeding by insect larvae on roots [71]), and they are emitted from infested and non-infested leaves, flowers, fruits, and roots [69,72]. Different plant hormones are involved in the regulation of the emission of HIPVs, particularly jasmonate (JA), salicylic acid (SA), and ethylene (ET), and crosstalk among these phytohormones' signaling pathways is necessary for adjusting the plant responses. These phytohormone signaling pathways are the octadecanoic pathway (JA biosynthesis), the shikimate pathway (SA biosynthesis), and the ethylene pathway (ET biosynthesis). The activation of these pathways depends on the herbivore's nature [73–76]. For example, when plants are damaged by sucking arthropods, such as aphids and spider mites, the regulation of HIPV emission from infested leaves is given through antagonistic crosstalk between SA and JA [77,78]. Another example is when mechanical damage is applied to lima bean leaves that mimics the damage caused by chewing arthropods: JA accumulates locally in response to damage, immediately activating the up-regulation of the  $\beta$ -ocimene synthase gene (PIOS) [79].

HIPVs can act as an indirect form of plant defense in different ways, for example, by directly or indirectly affecting herbivore performance [70], inducing defense responses in the undamaged parts of the plant (interplant), alerting neighboring undamaged plants to the forthcoming danger (intraplant), a phenomenon called “priming” [70,80–83], and acting as oviposition and feeding deterrents to herbivores [66,69]. In addition, some HIPVs can attract natural enemies, such as predators and parasitoids (an organism whose larvae feed and develop inside or on the body surface of another organism), that serve as a defense against herbivores and weeds [71]. Recognition of the importance of HIPVs in natural communities has turned them into a sustainable alternative for pest management in agriculture in different ways: (I) the recruitment of natural enemies to plantations mediated using synthetic HIPVs; (II) the release of synthetic HIPVs to repel or attract herbivores; (III) the use of synthetic HIPVs that elicit resistance in plants; (IV) the use of plant varieties that emit HIPVs that induce resistance in neighboring plants.

##### *HIPVs as a Tool for Recruitment of Natural Enemies as a Biocontrol of Pests*

The use of HIPVs for the attraction of natural enemies of herbivores, such as carnivorous arthropods (parasitoids and predators) and entomopathogenic agents (nematodes and

fungi), has been widely documented [84,85] (Figure 4). Numerous studies have demonstrated the efficiency of HIPVs as reliable indicators of suitable hosts for parasitoids (Table 2). Therefore, manipulating the foraging behavior of predatory insects can be an effective method to enhance their effectiveness as biocontrol agents in pest management [86]. Among HIPVs, terpenoids are the largest and most representative group; therefore, it is normal that terpenes dominate the HIPV mixtures [87,88]. Several studies have tested synthetic terpenes for recruiting natural enemies in agricultural systems. For example,  $\beta$ -ocimene, which is one of the terpenes most studied and most important of the HIPVs [80,89–91], demonstrated that it is efficient in the attraction of different predators, such as parasitic wasps *Aphytis melinus* [92] and *Aphidius gifuensis* and the lady beetle, and green lacewing larvae (*Chrysoperla carnea*) favored the biocontrol of important pests, such as the California red scale (*Aonidiella aurantii*) and the aphid (*Myzus persicae*) that cause significant production losses in citrus [92], peach [93], and cabbage [91]. Other important HIPVs is the methyl salicylate (MeSA), which attracts natural enemies in different agroecosystems, such as the Linyphiid spider (*Erigonidium graminicolum*), bug (*Orius similis*), mite (*Neoseiulus californicus*), Geocorid (*Geocoris pallens*), hoverflies (*Syrphidae*) (*Toxomerus marginatus*), and coccinellid (*Stethorus punctum picipes*). In addition, behavioral assays show that the release of  $\beta$ -myrcene and  $\beta$ -caryophyllene volatiles from dispensers enhances the efficacy of *Encarsia formosa* as a biological agent against *Bemisia tabaci* whiteflies in glasshouse production systems [94]. MeSA favored the attraction of these natural enemies of an important pest, the spider mite (*Tetranychus urticae*), which is a potentially harmful pest because it can affect many types of crops, including vegetables, fruits, and flowers [86], as well as the corn borer (*Ostrinia nubilalis*), which affects corn, apple, strawberry, and pepper [95] (Table 2). However, to achieve the success of this strategy, it is necessary to consider the synchronicity of crop pests and their natural enemies. “Attract and reward” is a pest control strategy that combines the “attraction” effects of synthetic HIPVs with companion plants (non-crop plants) that provide a “reward” such as nectar and/or pollen that could enhance the survival periods of parasitoids and predators without host or prey [96–99] (Figure 4). Different laboratory and field studies have demonstrated the potential of this pest control strategy; for example, they used a dispenser of MeSA and methyl jasmonate (MeJA) as the “attractants” of predators of the sweetcorn pest *Helicoverpa* spp. and buckwheat (*Fagopyrum esculentum*) as a companion plant that provides nectar as a “reward”. It was demonstrated that the application of this pest control strategy increased the abundance and residence of natural enemies, which resulted in an efficient regulation of *Helicoverpa* spp., reducing damage in different crops (sweet corn, broccoli, and wine grapes) [99]. Similar results were found by applying synthetic MeSA in the dispenser as an attractant of predatory ladybird *Propylea japonica* in apple orchards using the companion plant *Calendula officinalis* as a reward, resulting in the regulation of the aphid population in the short-term [100].

**Table 2.** Herbivore-induced plant volatiles with attraction capacity of natural enemies.

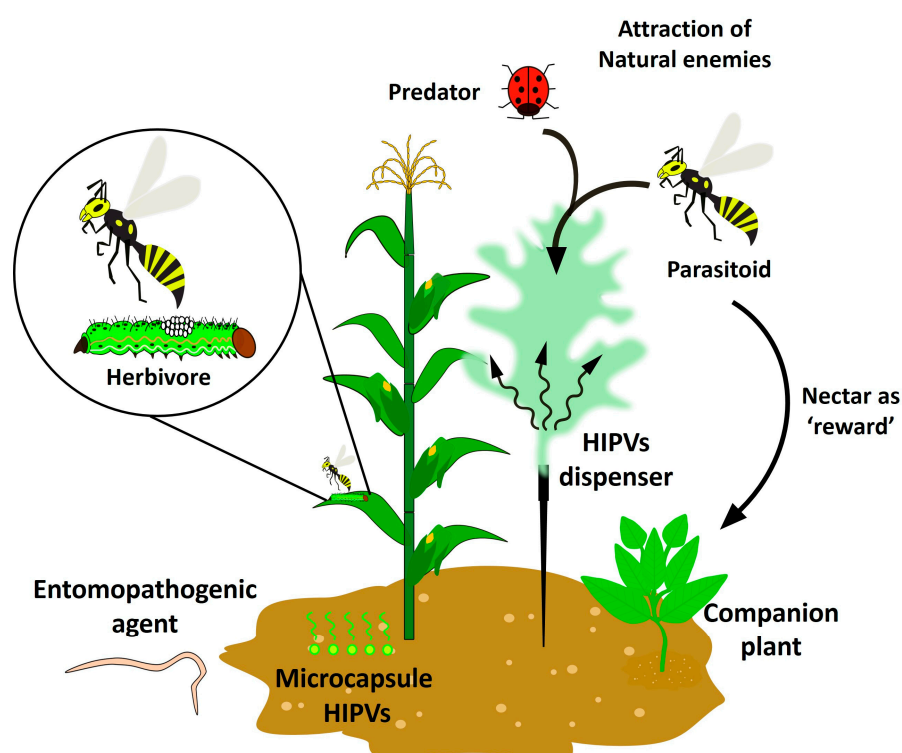
Volatile Compound	Beneficial Insect	Pest Insect	Crop	Reference
$\beta$ -myrcene, $\beta$ -caryophyllene	Wasp ( <i>Encarsia formosa</i> Gahan)	Whitefly ( <i>Bemisia tabaci</i> Gennadius)	Tomato ( <i>Solanum lycopersicum</i> L.)	[94]
D-limonene, $\beta$ -ocimene	Wasp ( <i>Aphytis melinus</i> DeBach)	California red scale ( <i>Aonidiella aurantii</i> Maskell)	Mandarin ( <i>Citrus reticulata</i> L.), Orange ( <i>Citrus × sinensis</i> L.), Lemon ( <i>Citrus × limon</i> L.)	[101]
$\beta$ -ocimene	Wasp ( <i>Aphidius gifuensis</i> Ashmaed)	Aphid ( <i>Myzus persicae</i> Sulzer)	Chinese cabbage [ <i>Brassica rapa</i> L. subsp <i>pekinensis</i> (Lour) Hanelt]	[91]

Table 2. Cont.

Volatile Compound	Beneficial Insect	Pest Insect	Crop	Reference
(E)- $\beta$ -ocimene	Lady beetle ( <i>Adalia bipunctata</i> L.), Green lacewing larvae ( <i>Chrysoperla carnea</i> Stephens)		Peach ( <i>Prunus persica</i> L.)	[93]
$\alpha$ -pinene	Wasp ( <i>Aphelinus varipes</i> Foerster)	Aphid ( <i>Myzus persicae</i> Sulzer)	Chili pepper ( <i>Capsicum annuum</i> L.), Eggplant ( <i>Solanum melongena</i> L.), Crown daisy ( <i>Glebionis coronaria</i> L.), Chinese cabbage [ <i>Brassica rapa</i> L. subsp <i>pekinensis</i> (Lour) Hanelt], Cabbage ( <i>Brassica oleracea</i> var. <i>capitata</i> L.)	[102]
Mixture ( $\beta$ -pinene, $\beta$ -phellandrene, 3-carene, $\beta$ -ocimene)	Mirid ( <i>Nesidiocoris tenuis</i> Reuter)	Tomato moth ( <i>Tuta absoluta</i> Meyrick), Whitefly ( <i>Trialeurodes vaporariorum</i> Westwood)	Tomato ( <i>Solanum lycopersicum</i> L.)	[103]
(E)-3-hexenyl acetate	Mirid ( <i>Deraeocoris brevis</i> Uhler), Anthocorid ( <i>Orius tristicolor</i> White), Coccinellid ( <i>Stethorus punctum picipes</i> Casey)			[104]
(Z)-3-hexenyl acetate	Ladybird beetle ( <i>Coccinella septempunctata</i> L.)			
Nonanal, (Z)-3-hexenyl acetate, methyl salicylate	Linyphiid spider ( <i>Erigonidium graminicolum</i> Sundevall)			
Octanal	Bug ( <i>Deraeocoris punctulatus</i> Fallen)			
Dimethyl octatriene, nonanal + (Z)-3-hexen-1-ol, octanal	Syrphid fly ( <i>Paragus quadrifasciatus</i> Meigen)		Cotton ( <i>Gossypium</i> L.)	[105]
3,7-dimethyl,1,3,6- octatriene, nonanal, (Z)-3-hexenyl acetate, nonanal + (Z)-3-hexen-1-ol, methyl salicylate	Bug ( <i>Orius similis</i> Zheng)			
Pregeijerene	Nematodes <i>Steinernema diaprepesi</i> Nguyen and Duncan, <i>Steinernema</i> sp. <i>glaseri</i> Glaser and Fox, <i>Steinernema riobrave</i> Cabanillas, Poinar and Raulston, <i>Steinernema carpocapsae</i> Weiser, <i>Steinernema feltiae</i> Filipjev, <i>Steinernema kraussei</i> Nikdel and Niknam, <i>Steinernema scapterisci</i> Nguyen and Smart, <i>Heterorhabditis indica</i> Poinar, Karunakar and David, <i>Heterorhabditis zealandica</i> Poinar, <i>Heterorhabditis bacteriophora</i> Poinar	Beetle larvae ( <i>Diaprepes abbreviatus</i> L.) Wax moth ( <i>Galleria mellonella</i> L.) Beetle ( <i>Anomala orientalis</i> Waterhouse)	Citrus	[106]

Table 2. Cont.

Volatile Compound	Beneficial Insect	Pest Insect	Crop	Reference
Methyl salicylate	Mite ( <i>Neoseiulus californicus</i> McGregor)	Spider mite ( <i>Tetranychus urticae</i> C. L. Koch)		[86]
	Geocorid ( <i>Geocoris pallens</i> Stål.) Hoverflies ( <i>Syrphidae</i> Latreille), Coccinellid ( <i>Stethorus punctum picipes</i> Casey) Hoverflies ( <i>Toxomerus marginatus</i> Say)	Corn borer ( <i>Ostrinia nubilalis</i> Hübner)		[95]



**Figure 4.** The “attract and reward” method is a pest control strategy that enhances the efficiency and survival periods of natural enemies (parasitoids and predators), which allows the establishment of stable populations.

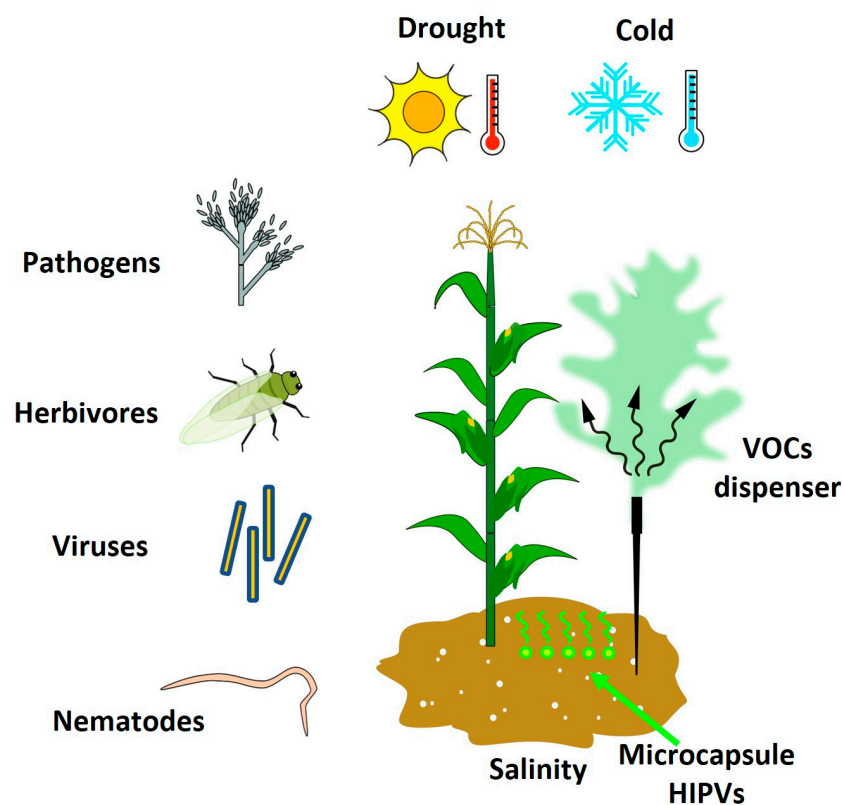
### 5. VOCs as Inductors of Resistance in Plants against Abiotic and Biotic Stress

Biotic and abiotic stresses are the two main factors that affect crop production [107], causing losses to approximately 25% and 50% of the world’s crop production, respectively [108–110]. The various biotic agents (viruses, bacteria, fungi, nematodes, weeds, insects, and arachnids) and abiotic factors (extreme temperatures, drought, salinity, and heavy metals) can deprive the plants of nutrients, limit growth, and lead to their death, thus reducing and limiting crop productivity and agriculture sustainability worldwide [108,109]. Moreover, factors such as pests’ resistance to pesticides, the emergence of new insect pests and diseases, and the loss of soil fertility, among others, improve the severity of crop loss and favor pest infestations and diseases [111]. To defend against these stresses, plants synthesize secondary metabolites that act directly by acting on the pathogen or indirectly by inducing the necessary defensive or resistance/tolerance response of the plant [112]. These secondary metabolites include VOCs, which play different roles in the defense against biotic stresses and the resistance/tolerance to abiotic stresses; therefore, they have received particular attention because they constitute one of the most promising alternatives for pest

and disease management preharvest [112,113]. Different trials have demonstrated that specific single VOCs and mixtures of VOCs can induce a defense response in plants against pathogens [114–116], nematodes [117], insects [114], and viruses [118–120], which allows preparations to start beforehand and be present when at risk of attack [121]. In addition, some VOCs can attract beneficial insects, such as predatory arthropods and parasitoids (an organism whose larvae feed and develop inside or on the body surface of another organism), that serve as a defense against herbivores and weeds [71] (Figure 5). Indeed, various studies demonstrated the efficacy of VOCs in attracting beneficial insects such as parasitoids wasps [91,94,101], lady beetles [93], hoverflies, predatory mites [95], and lacewing larvae [93], among others. Similarly, VOCs are capable of inducing systemic resistance/tolerance to different abiotic stresses such as drought [122–124], cold [124,125], and salinity [126] (Table 3).

**Table 3.** Volatile organic compounds with application in biocontrol against biotic and abiotic stress.

Volatile Compound	Organism Target	Effect	Crop	Reference
Dimethyl disulfide, methyl isovalerate, 2-undecanone	Nematode ( <i>Meloidogyne incognita</i> Kofoed and White)	Induce defense response and growth promotion	Tomato ( <i>Solanum lycopersicum</i> L.)	[117]
(E)-nerolidol	Leafhopper ( <i>Empoasca onukii</i> Matsuda), Fungus ( <i>Colletotrichum fruticicola</i> Prihast et al.)	Induce defense response	Tea plant ( <i>Camellia sinensis</i> L.)	[114]
Z-3-hexenol	Tomato yellow leaf curl virus	Induces defense response	Tomato ( <i>Solanum lycopersicum</i> L.)	[118]
2R,3R-butanediol, 2R,3S- butanediol	Cucumber mosaic virus, Tobacco mosaic virus	Induce defense response	Pepper ( <i>Capsicum annum</i> L. cv. Bukwang)	[119]
6-pentyl- $\alpha$ -pyrone (6PP)	Tobacco mosaic virus	Induces systemic resistance	Tobacco ( <i>Nicotiana tabacum</i> cv. White Burley)	[120]
Dimethyl disulfide (DMDS)	Fungus ( <i>Sclerotinia minor</i> Jagger)	Induces systemic resistance	Tomato ( <i>Solanum lycopersicum</i> L.)	[115]
Nonanal, limonene	Fungus ( <i>Colletotrichum lindemuthianum</i> Sacc. and Magnus)	Induce systemic resistance	Common bean ( <i>Phaseolus vulgaris</i> L. Sp. Pl.)	[116]
Dimethyl disulfide, 2,3-butanediol, 2-pentylfuran		Induces systemic drought tolerance	Maize ( <i>Zea mays</i> L.)	[122]
		Induces tolerance against cold stress	Maize ( <i>Zea mays</i> L.)	[125]
(Z)-3-hexen-1-yl acetate		Induces drought resistance	Wheat ( <i>Triticum</i> spp. L.)	[123]
		Protects against salinity stress	Peanut <i>Arachis hypogaea</i> L.)	[126]
Eugenol		Induces cold and drought tolerance	Tea plant ( <i>Camellia sinensis</i> L.)	[124]



**Figure 5.** The HIPVs as inducers of resistance against biotic and abiotic stresses.

The mechanisms involved in the induction of defense are associated with different signaling-modulated phytohormones, such as JA, MeJA, SA, MeSA, and ET, which trigger the induction of defense responses after insect damage. JA is one of the most important elicitors, as it induces resistance in plants against herbivores and accumulates rapidly in plant tissue after wounding or insect damage [69,114]. The exogenous application of JA induces defense-related responses, such as the activation of oxidative enzymes, proteinase inhibitors, alkaloids, and the production of volatile compounds [69,127], and confers resistance against phloem-sap-sucking insects and chewing herbivores, as well as necrotrophic pathogens. Moreover, SA and hydrogen peroxide ( $H_2O_2$ ) induce resistance against biotrophic pathogens and sucking/piercing insects [128,129]. Some of the most studied HIPVs involved in resistance induction are GLVs, which are produced and emitted by plants in response to stress [125,130]. GLVs consist of C6 compounds, including aldehydes, alcohols, and esters [130,131]. GLVs can induce resistance “priming”, the capacity of the plant to respond to future stress. Usually, GLVs are immediately released from damaged plant tissues, which induces defense-related genes contributing to immediate resistance to stress in the damaged plant and its neighbors [130,131]. Therefore, GLVs are crucial for plant resistance to biotic and abiotic stresses. One example is (Z)-3-hexenyl acetate, whose exogenous application in seedlings can induce resistance against cold stress in maize [125], enhance drought resistance in wheat, mainly through antioxidant and osmoregulation systems [123], and enhance salinity stress tolerance in peanuts through modifications in the photosynthetic apparatus, antioxidant systems, osmoregulation, and root morphology [126]. Another example is (Z)-3-hexen-1-ol, whose exogenous application enhanced defense against the *Tomato yellow leaf curl virus* (TYLCV), resulting in improved flavonoid levels and defense gene transcripts as well as increased transcripts of JA biosynthetic genes and increased whitefly-induced transcripts of SA biosynthetic genes in plants [118]. Terpenes also are involved in the induction of defense responses; one example is (E)-nerolidol, which elicits a strong defense response in tea plants against *Colletotrichum fructicola* by the activation of a mitogen-activated protein kinase (MAPK),

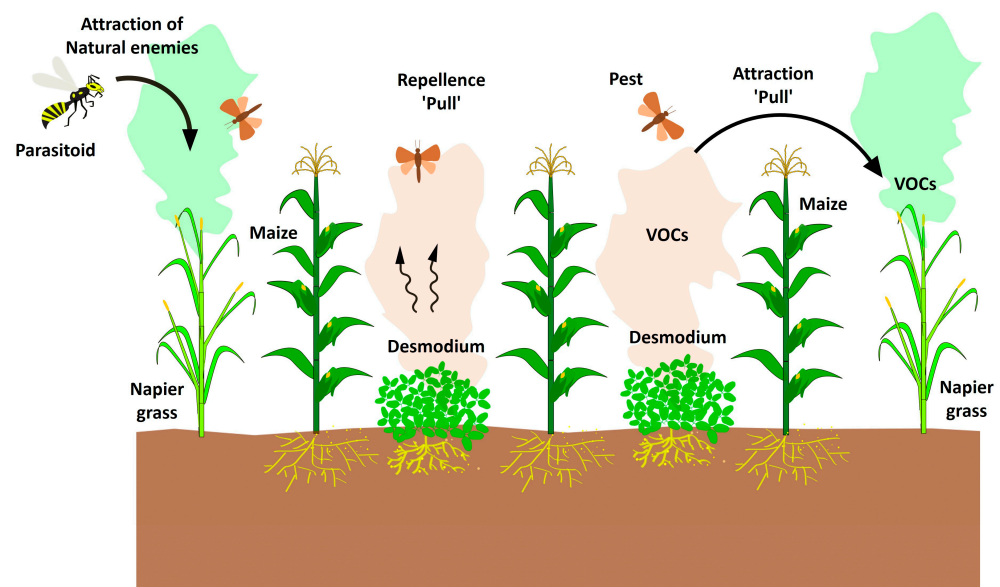


the WRKY transcription factor plant defense, and H<sub>2</sub>O<sub>2</sub> burst, as well as the induction of jasmonic acid and abscisic acid signaling [114]. Another terpene is  $\beta$ -ocimene, which is emitted by tea plants when treated with an exogenous application of individual HIPVs (Z)-3-hexenol, linalool,  $\alpha$ -farnesene, and (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and is a powerful repellent of mated *Ectropis obliqua* females, which is one of the most devastating leaf-feeding pests of tea plants [132]. In addition, MeJA primes the plant defenses through epigenetic modifications in wounding-inducible genes in rice, enhancing the response of rice to wounding [133]. Compared with direct defenses, priming does not represent an energetically costly activation of metabolic pathways [134]. Therefore, priming represents a sustainable strategy to implement in agriculture systems as a crop biocontrol.

## 6. Intercropping ‘Push–Pull’ system

Intercropping is an ancient agricultural practice of cultivating multiple crop species in the same space [135,136]. The advantages of this system are the optimization of resources, the improvement in soil fertility due to the incorporation of legumes in the mixture, and the more extensive area coverage, which allows for better soil conservation, reduces the incidence of pests and diseases as well as the weed population, and minimizes the use of pesticides. Therefore, the intercropping system has shown enormous potential for agricultural implementation as a biocontrol of pests and diseases [136,137]. The push–pull system is a stimulus–deterrent cropping strategy that consists of intercropping cereals with legumes and surrounding fodder grasses. It is based on a mechanism that consists of two functional groups, trap plants and repellent plants, which have characteristics that make them attractive or repellent to a specific insect [138]. For example, taking the intercropping crop of interest as maize (*Zea mays*), a legume species such as Desmodium (*Desmodium uncinatum*) emits volatiles that repel stemborers moths (the ‘push’ effect) and a border of a trap crop, such as Napier grass (*Pennisetum purpureum*), attracts stemborers moths (the ‘pull’ effect) (Figure 6) [139–142]. This system enhances soil fertility through Desmodium’s N-fixation and decreases the presence of the parasitic weed, Striga [139]. In addition, fodder crops make the crop habitat more attractive to natural enemies of stemborers, such as ants, earwigs, and spiders, increasing the parasitism of this herbivore [143]. On the other hand, the implementation of the push–pull system may be improved by replacing Desmodium with other legumes that serve as food, such as the common bean, which is widely consumed worldwide and is an important source of protein. Recent studies demonstrated that the common bean is as efficient as Desmodium in repelling stemborers and increasing the abundance of predators; therefore, the common bean can replace Desmodium in areas with a low abundance of the parasitic weed Striga [140]. The success of this system has been attributed to repellent (‘push’) and attractive (‘pull’) VOCs that are released by the companion plants [138]. The volatiles emitted by Desmodium and Brachiaria companion plants (E)-2-hexenal, (Z)-3-hexenyl acetate, (E)- $\beta$ -ocimene, (S)-linalool, DMNT, MeSA, indole,  $\beta$ -caryophyllene, (E)- $\beta$ -farnesene, and (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT), serve as inducers of HIPVs in maize, repel herbivores and attract natural enemies, and affect the germination of the parasitic Striga weed [144–147]. DMNT and TMTT are very attractive for braconid parasitoids. In addition, (E)-2-hexenal, (Z)-3-hexenyl acetate, (E)- $\beta$ -ocimene, 1-octen-3-ol, (S)-linalool, MeSA, indole, and  $\beta$ -caryophyllene induced responses to caterpillar herbivory and egg laying, and are attractants of parasitic wasps [148,149]. The push–pull system is widely considered a potential strategy for pest control due to its abilities in improving crop yields and helping to avoid the use of chemical pesticides, favoring the environment’s care. It also has a significant impact on food security due to its assistance in producing more food on less land.





**Figure 6.** ‘Push–Pull’ system consists of intercropping cereals such as maize (*Zea mays*) with a legume such as Desmodium (*Desmodium uncinatum*), which emits volatiles that repels stemborers moths (‘push’ effect) and is bordered by a trap crop such as Napier grass (*Pennisetum purpureum*), which attracts stemborers moths (‘pull’ effect). In addition, Desmodium enhances soil quality through nitrogen fixation.

## 7. Application of VOCs in Agricultural Systems

Currently, alternatives that exploit the potential of VOCs in agricultural systems have been increasing, such as dispensers for the application of single or a mixture of VOCs, as well as the use of genetically modified (GM) crops with altered VOC emissions. Recent studies have demonstrated the success of HIPVs in the biocontrol of pests, for example, the continuous application of (Z)-3-hexenyl propanoate ((Z)-3-HP) by a polymeric dispenser in tomato plants in commercial greenhouse conditions. These dispensers maintained the defenses of commercial tomato plants activated for over two months, reducing the attack of economically significant tomato pests *Tetranychus urticae* and *Tuta absoluta* without lowering productivity. The induction of tomato plants with (Z)-3-HP increased the production of fatty acids, the activation of the lipoxygenase pathway, the accumulation of specific defense compounds, and the upregulation of genes involved in the antiherbivore defense [150]. Another case is the use of HIPV (sabinene, n-heptanal,  $\alpha$ -pinene, and (Z)-3-hexenyl acetate) dispensers to attract the *Cotesia vestalis* larval parasitoid to control the diamondback moth (DBM) (*Plutella xylostella*) larvae, which are an important pest of cruciferous crops in greenhouses. The dispensers successfully attracted *C. vestalis* and honey feeders, which reduced the presence of DBM in the greenhouse [151]. Similar results were shown with the dispenser application of  $\beta$ -caryophyllene and  $\beta$ -myrcene which enhanced the attraction of the parasitic wasp *Encarsia formosa*, resulting in the feeding of *Bemisia tabaci* adults. The use of dispensers enhanced the efficacy of *E. formosa* as a biological agent to control the *B. tabaci* pest in glasshouse production systems [152]. Limonene applied in the dispenser system acts as a repellent and plant defense elicitor to control the whitefly (*Trialeurodes vaporariorum*) pest on tomatoes in a commercial glasshouse. In addition, MeSA reduces whitefly population development, elevates peroxidase (POD) activity, and increases the thioredoxin peroxidase (TPX1) and pathogenesis-related protein 1 (PR1) transcripts and both volatiles [153]. On the other hand, the use of GM crops with altered VOC emissions provides enhanced resistance against pests and abiotic stress. The hypersensitive GM crops could be used as an attractant to trap and kill herbivores, as a repellent of herbivores, or as a lure to attract natural enemies [154]. For example, the overexpression of the protein OsCYP92C21, which is known to be responsible for homoterpene biosynthesis

in rice, enhanced the emission of DMNT and TMTT, which attract the parasitic wasp *Cotesia chilonis*, the natural enemy of the rice pest striped stemborer *Chilo suppressalis* [155]. In addition, the overexpression of the caryophyllene synthase gene GhTPS1 in cotton enhanced the emission of (E)- $\beta$ -caryophyllene, which reduces pests, such as *Apolygu sluorum*, *Aphis gossypii*, and *Helicoverpa armigera*, through the attraction of parasitoids, such as *Peristenus spretus* and *Aphidius gifuensis* [57]. The overexpression of enzymes responsible for the emission of specific volatiles could be an excellent tool to improve pest management. In agricultural systems, GM crops can favor the enhanced resistance to pests and abiotic stresses [85].

However, GM crops can also favor the presence of non-target species due to the reduction in chemical pesticides; for example, GM cotton that has been cultivated in China for more than two decades and that promotes the presence of mirid bugs, such as *Adelphocoris suturalis*, *Apolygus lucorum*, and *Lygus pratensis*. These bugs are pests that affect a broad range of important crops including cotton, jujube, and grape [156]. Recent studies demonstrated that VOCs obtained from plant extracts such as *Allium tuberosum* had a significantly higher attractive effect on *A. suturalis* and *A. lucorum*; among the volatiles responsible for this effect are diethyl phthalate and methyl levulinate. Therefore, applying these volatile as attractants has a potential to control mirid bugs in agriculture [157,158].

## 8. Future Trends and Conclusions

The multiple benefits of VOCs as novel eco-friendly alternatives provide sustainable solutions to different problems, such as controlling pathogen-associated diseases in pre- and postharvest, inducing plant resistance against biotic and abiotic stresses, and positive factors such as promoting plant growth. However, we must consider the factors that could limit the success of VOC exploitation in agricultural practices. For example, only a few studies have proven the efficacy of VOCs in open field conditions; most VOC-related experiments are performed in laboratory conditions using concentrations that are difficult to achieve in open field conditions. In addition, VOCs are unstable compounds that can react easily with highly reactive chemicals present in the environment, such as NO<sub>x</sub>, OH<sup>−</sup> radicals, and ozone [159,160]. Moreover, the high biodegradability of VOCs can reduce their effects and impacts on targets, limiting their persistence and activity [11,21,24]. However, these limitations can be resolved through modern technologies of micro- and nano-encapsulation in polymer shells or coats, which can increase the half-life and stability of VOCs, control their release into the environment, and protect them against oxidation, UV, and evaporation, thereby improving their effectiveness [11,21]. Another limitation of VOCs when used to attract beneficial insects is that the information transmitted is not selective, so they may attract many non-target species, including undesirable ones such as pests, disease vectors, etc., causing the opposite effect.

Additionally, the asynchronous crop colonization of pests and beneficial insects can limit the implementation of annual cropping system. Thus, providing a nurturing environment that allows for the establishment of stable populations of beneficial organisms by supplying food such as nectar or pollen that can enhance the survival periods of parasitoids and predators without a host or prey and can solve this issue [98,113]. Other factors to consider are the high processing costs and lengthy screening procedures required to research and develop an effective synthetic VOC formulation. Furthermore, some VOCs have nutritional and organoleptic side effects on the final agricultural product, which may necessitate further research to guarantee quality. All these limitations have delayed the use of VOCs in agriculture. Therefore, until now, an effective synthetic VOC formulation has yet to be developed for their agricultural application. Nevertheless, the increasing interest in sustainable solutions that enhance crop protection and productivity, and the promise of pesticide-free, healthy food could promote the investment and development of VOCs, driving them to become a part of the competitive agricultural industry.

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