

Volatile Organic Compounds

Subjects: **Plant Sciences**

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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.

defense

plant

volatiles

1. General Aspects of Volatile Organic Compounds and Possible Biotechnological Applications

In nature, volatile organic compounds (VOCs) are emitted by all living organisms and occur as a complex mixture called “volatilome” ^[1]. 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 ^[2]. VOCs typically occur as a complex mixture produced by four major metabolic pathways, namely the shikimate/phenylalanine, the mevalonic acid (MVA), the methylerythritol phosphate (MEP), and lipoxygenase (LOX) pathways ^{[3][4]} (Figure 1).

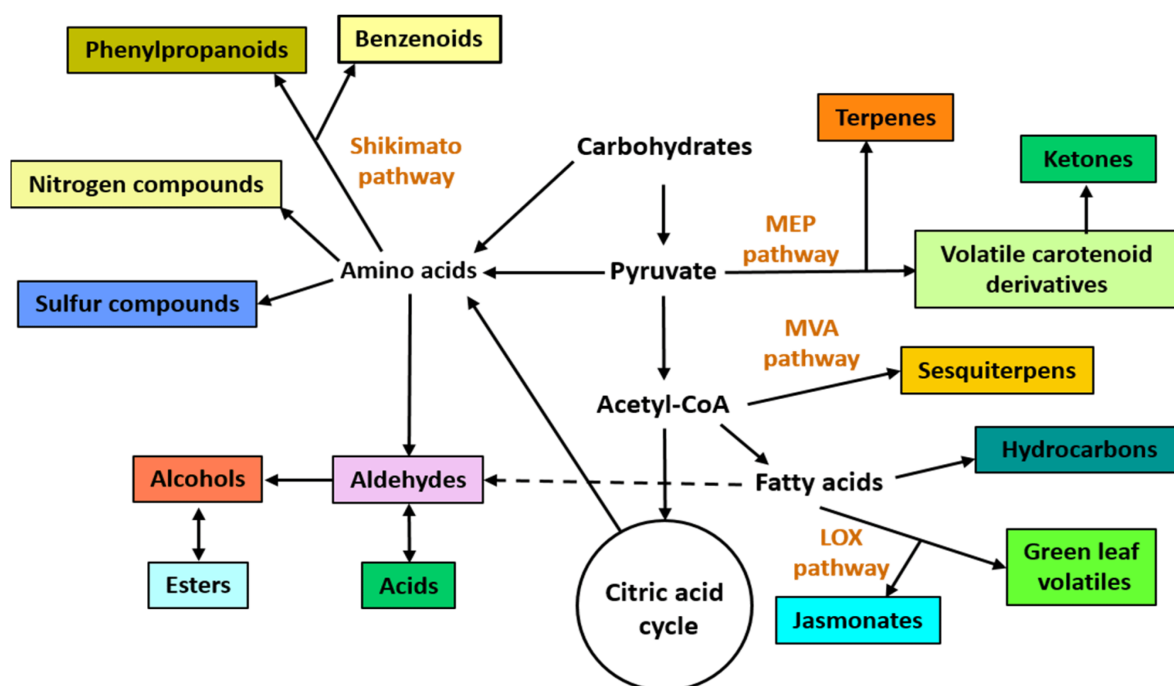


Figure 1. Overview of main biosynthetic pathways to produce plant and microbial volatile organic compounds. Different chemical classes of VOCs are depicted in colored rectangles. The four principal biosynthetic pathways are: the shikimate, the methylerythritol phosphate (MEP), the mevalonic acid (MVA), and the lipoxygenase (LOX) pathways.

Different studies demonstrated that VOCs modulate (suppress or stimulate) microbial and plant growth [5][6], induce systemic resistance in plants against biotic and abiotic stresses [7], and act as attractants or repellents of insects [2]. 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 [8]. However, researchers 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 [9]. For plants, high temperatures, high light intensities, and herbivore attacks increase VOC emissions [10]. 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 [11]. 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 [12].

2. Volatile Organic Compounds as Inductors of Resistance in Plants against Abiotic and Biotic Stress

Biotic and abiotic stresses are the two main factors that affect crop production [13], causing losses to approximately 25% and 50% of the world's crop production, respectively [14][15][16]. 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 [14][15]. 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 [17]. 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 [18]. 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 [18][19]. Different trials have demonstrated that specific single VOCs and mixtures of VOCs can induce a defense response in plants against pathogens [20][21][22], nematodes [23], insects [20], and viruses [24][25][26], which allows preparations to start beforehand and be present when at risk of attack [27]. 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 [28] (**Figure 2**). Indeed, various studies demonstrated the efficacy of VOCs in attracting beneficial insects such as parasitoids wasps [29][30][31], lady beetles [32], hoverflies, predatory mites [33], and

lacewing larvae [32], among others. Similarly, VOCs are capable of inducing systemic resistance/tolerance to different abiotic stresses such as drought [34][35][36], cold [36][37], and salinity [38] (Table 1).

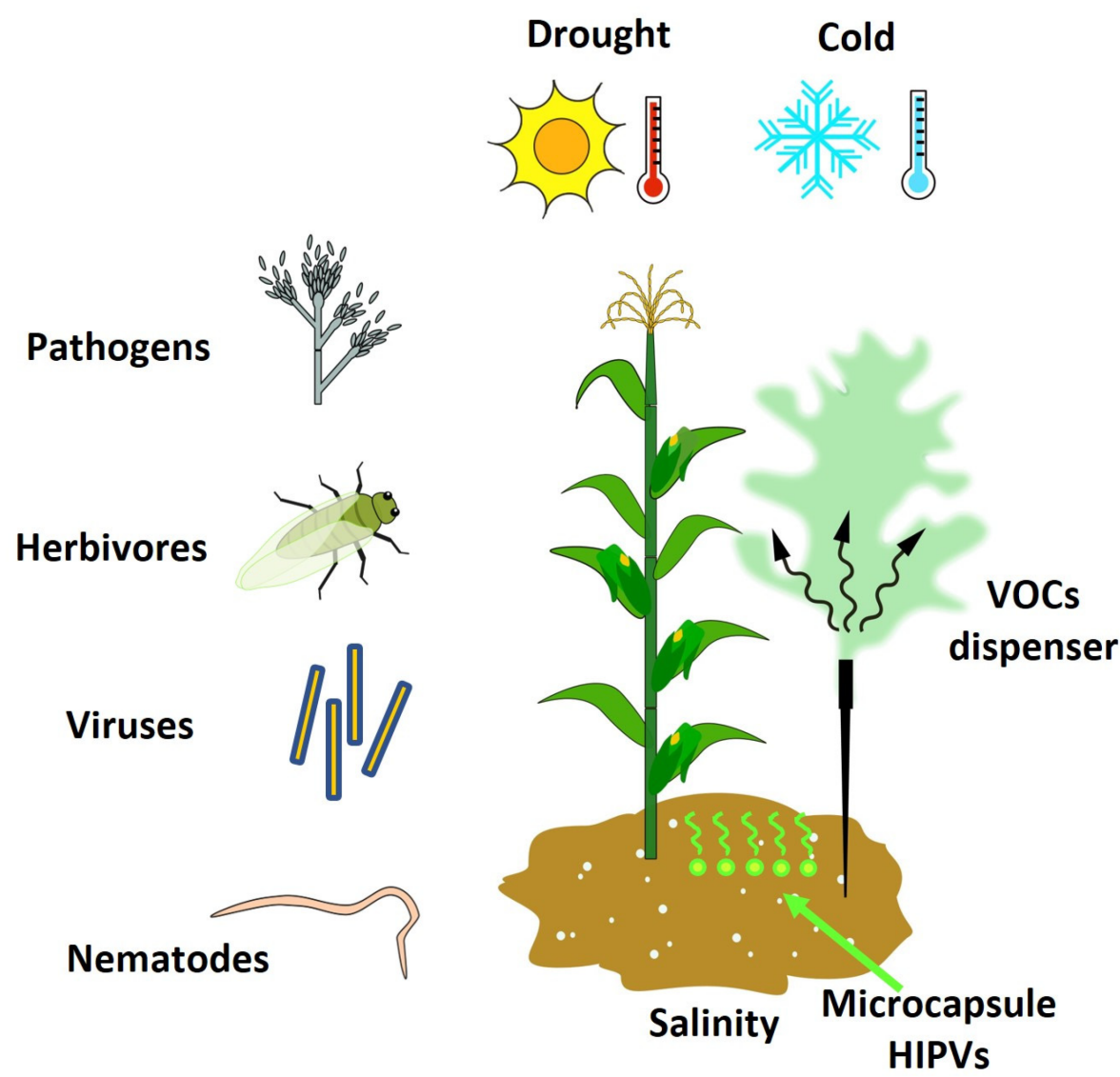


Figure 2. The herbivore-induced plant volatiles (HIPVs) as inducers of resistance against biotic and abiotic stresses.

Table 1. 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> Kofoid and White)	Induce defense response and growth promotion	Tomato (<i>Solanum lycopersicum</i> L.)	[23]
(E)-nerolidol	Leafhopper (<i>Empoasca onukii</i> Matsuda), Fungus	Induce defense response	Tea plant (<i>Camellia sinensis</i> L.)	[20]

Volatile Compound	Organism Target	Effect	Crop	Reference
	(Colletotrichum fructicola Prihast et al.)			
Z-3-hexenol	Tomato yellow leaf curl virus	Induces defense response	Tomato (Solanum lycopersicum L.)	[24]
2R,3R-butanediol, 2R,3S- butanediol	Cucumber mosaic virus, Tobacco mosaic virus	Induce defense response	Pepper (Capsicum annum L. cv. Bukwang)	[25]
6-pentyl-α-pyrone (6PP)	Tobacco mosaic virus	Induces systemic resistance	Tobacco (Nicotiana tabacum cv. White Burley)	[26]
Dimethyl disulfide (DMDS)	Fungus (Sclerotinia minor Jagger)	Induces systemic resistance	Tomato (Solanum lycopersicum L.)	[21]
Nonanal, limonene	Fungus (Colletotrichum lindemuthianum Sacc. and Magnus)	Induce systemic resistance	Common bean (Phaseolus vulgaris L. Sp. Pl.)	[22]
Dimethyl disulfide, 2,3-butanediol, 2-pentylfuran		Induces systemic drought tolerance	Maize (Zea mays L.)	[34]
(Z)-3-hexen-1-yl acetate		Induces tolerance against cold stress	Maize (Zea mays L.)	[37]
		Induces drought resistance	Wheat (Triticum spp. L.)	[35]
		Protects against salinity stress	Peanut Arachis hypogaea L.)	[38]
Eugenol		Induces cold and drought tolerance	Tea plant (Camellia sinensis L.)	[36]

modulated phytohormones, such as JA, MeJA, SA, MeSA, and EI, 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 [20][39]. 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 [39][40], and confers resistance against phloem-sap-sucking insects and chewing herbivores, as well as necrotrophic pathogens. Moreover, SA and hydrogen peroxide (H₂O₂) induce resistance against biotrophic pathogens and sucking/piercing insects [41][42]. Some of the most studied HIPVs involved in resistance induction are GLVs, which are produced and emitted by plants in response to stress [37][43]. GLVs consist of C6 compounds, including aldehydes, alcohols, and esters [43][44]. 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 [43][44]. 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 [37], enhance drought resistance in wheat, mainly through antioxidant and osmoregulation systems [35], and enhance salinity stress tolerance in peanuts through modifications in the photosynthetic apparatus, antioxidant systems, osmoregulation, and root morphology [38]. 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 [24]. 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 H₂O₂ burst, as well as the induction of jasmonic acid and abscisic acid signaling [20]. Another terpene is β -ocimene, which is emitted by tea plants when treated with an exogenous application of individual HIPVs (Z)-3-hexenol, linalool, α -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 [45]. In addition, MeJA primes the plant defenses through epigenetic modifications in wounding-inducible genes in rice, enhancing the response of rice to wounding [46]. Compared with direct defenses, priming does not represent an energetically costly activation of metabolic pathways [47]. Therefore, priming represents a sustainable strategy to implement in agriculture systems as a crop biocontrol.

3. Application of Volatile Organic Compounds 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 [48]. Another case is the use of HIPV (sabinene, n-heptanal, α -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 [49]. Similar results were shown with the dispenser application of β -caryophyllene and β -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 [50]. 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 [51]. On the other hand, the use of genetically modified (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 [52]. 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* [53]. In addition, the overexpression of the caryophyllene synthase gene GhTPS1 in cotton enhanced the emission of (E)- β -caryophyllene, which reduces pests, such as *Apolygu slucorum*, *Aphis gossypii*, and *Helicoverpa armigera*, through the attraction of parasitoids, such as *Peristenus spretus* and *Aphidius gifuensis* [54]. 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 [55].

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 [56]. 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 [57][58].

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