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Microbial Volatile Compounds and Their Role in Growth, Development and Resistance in Plants

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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Abstract

Microbial Volatile Compounds (MVCs) are low molecular weight and low boiling point, high vapour pressure biochemical compounds, produced by a wide array of microorganisms ranging from bacteria to fungi. MVC are forms an interface for below and above soil interaction between microorganisms and plants. Global agricultural systems are under increasing pressure to deliver sufficient, healthy food for a growing population. MVCs can be of great benefit to plants and their use in agriculture thanks to their ability to inhibit the growth and development of plant pathogens, induce the activation of plant defense, or promote plant growth and development. Owing to their natural origin, MVCs have potential as possible alternatives to synthetic pesticides, fungicides, and bactericides as well as genetic modification. Recent studies have yielded mixed results regarding

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the application of MVCs. Hence, there is an urgent need to explore MVCs in more detail, including dose standardization, compatibility, method of application, and cost-effectiveness to integrate them into mainstream agriculture.

Keywords: MVCs; plants; defence; growth; modulation; agriculture.

1. Background

"Organisms differ from each other in various aspects, say genetically, morphologically, anatomically, structural complexity at cellular and sub-cellular level, habitat and many more. Chemical taxonomy, exemplified by biochemical compounds produced at various levels by organisms, plays a significant role in taxonomic classification. These biochemical compounds plays major role in adaptation, defence mechanisms, evolutionary processes etc; specifically in microorganisms like fungi, bacteria, protists. Microbial Volatile Compounds (MVCs) are of low molecular weight and boiling points" (Veselova et al., 2019), simple or complex compounds like sulphides, alcohols, benzoids, terpenes, alkenes, acids, esters, ketones and similar one (Gautam et al., 2021, Schmidt et al., 2015 and Morath et al., 2012). "Though lately, it was discovered that these MVCs can be very useful for the human being in one or other way like mediators of airborne interactions (Ryu et al., 2020), foods and beverages" (Dahunsi et al., 2020), plant vaccines (Rodriguez et al., 2018) and many more. "MVCs derived from fungi and bacteria are responsible for the aroma of particular food stuffs like wine, cheese as well as odour from degrading food materials" (Veselova et al., 2019; Li et al., 2011; Rajer et al., 2017).

"Off late, as the interest towards MVCs grown and studies were made, it also revealed that these compounds play an important role in the plant's growth and development in one or more ways in different stages of life cycle. Most noteworthy examples include modulation of plant growth, development of systemic resistance against pathogens, insects and pests, nematodes and a range of other organisms; where MVCs plays role of repellent or attractants" (Veselova et al., 2019).

Here in this review, attempt is made to in-depth study of the role of Microbial Volatile Compounds in the development of plants as well as resistance against pathogens/pests and insects.

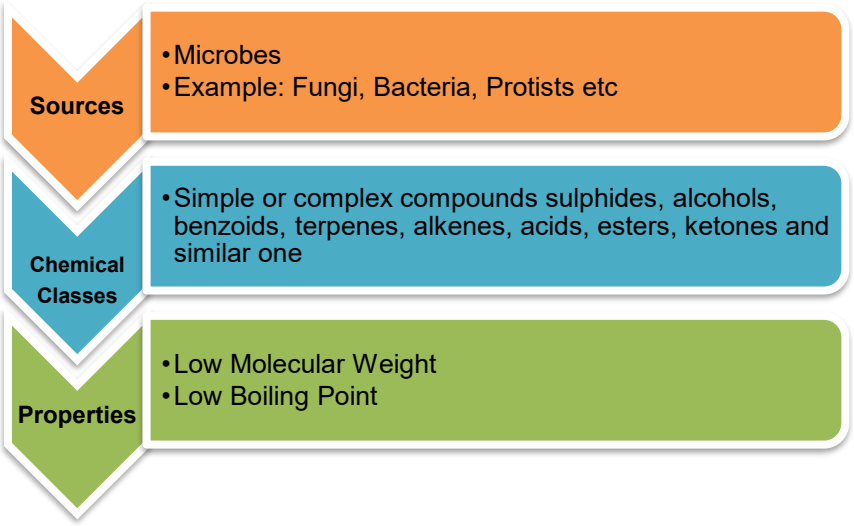

Fig. 1. Microbial volatile organic compounds at a glance

2. Plants and Role of MVCs

"Microbial volatile compounds are highly active owing to their chemical structure and character. They play an active role in ecological functions, which are highly competitive in nature like increased growth in plants, development of antibiosis process, reinvigoration of defense response as well as key

morphological and structural variation for the purpose of defense" (Poveda, 2021, Gautam et al. 2016). Though there have been understandings about MVCs and their roles in different domain of ecology, further investigation are needed to delve deeper and gain more insight."

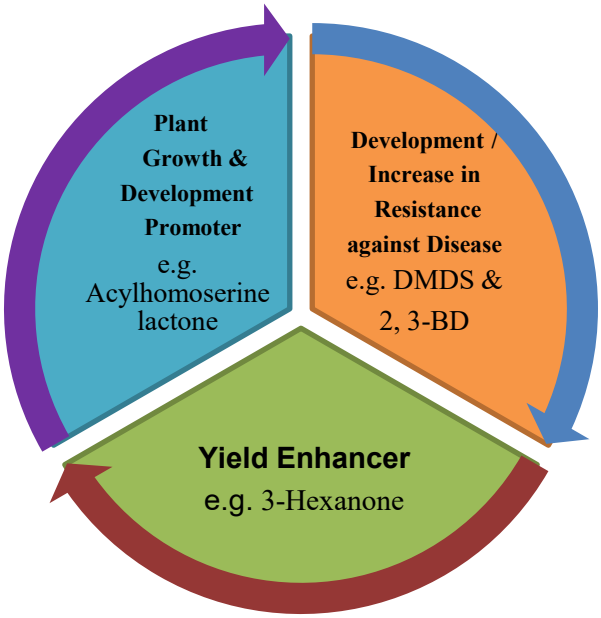

Fig. 2. MVCs and their potential roles in agriculture

Studies in last decade have shown that MVCs have wide range of involvement in crop biology, like a precursor elicitors of plant immunity, improving the plant health through antifungal and antibacterial actions, nematicidal actions etc. (Bitas et al., 2013 and Schalchli et al., 2016). Apart of this Sharifi and Ryu (2018) and Tyagi et al. (2018) also reported MVCs role in increase of yield and biomass by virtue of modulation of hormonal and physiological pathways, change in the bulk volumes of leaves like in form of leaf number, leaf size and similarly in root.

Kanchiswamy et al. (2015), Chung et al. (2016) have shown "a different aspect of MVCs, where they reported for their noteworthy potential to act as bio-stimulants and bio-protectants; and their capability to modulate metabolic activities of an organisms, as well as proteome and genome with equal efficiency".

2.1 MVCs in Plant-Microbe Interactions and Plant Development

"There has been a wide range of MVCs identified in bacteria and studied for their role in rhizosphere and soil ecology" (Kai et al., 2009). "Numerous bacteria, particularly rhizobacteria, have a strong affinity for soil and close association with the rhizosphere, where they play an important role in plant growth through the exploiting the rich nutrient exudates" (Bhattacharyya and Jha, 2012). "*Pseudomonas* is a very well known and extensively explored rhizobacteria which is widely used in agriculture in one or other way for crop production and protection and have been reported for its roles in the protections of crop from pathogens and maintenance of soil health" (Hol et al., 2013). "Volatile Organic Compounds (VOCs) released by rhizobacteria have been well known for their involvement in plant-pathogen interaction, plant-microbiome interaction and antimicrobial properties" (Vespermann et al., 2007; Goswami et al., 2013). While working on *Arabidosis thaliana*, Gutierrez et al. (2010) showed that "extensive communication occurs between plants and microorganisms during different stages of plant development in which signaling molecules from the two partners play an important role. They found that certain rhizospehric bacterial strains like L263, L266, L272a, L254, L265a and L265b; can modulate the plant growth and development as well as the architecture of root system like stimulation of primary root growth and lateral root development, promotion of lateral root formation etc. through the differential emission of volatile organic compounds".

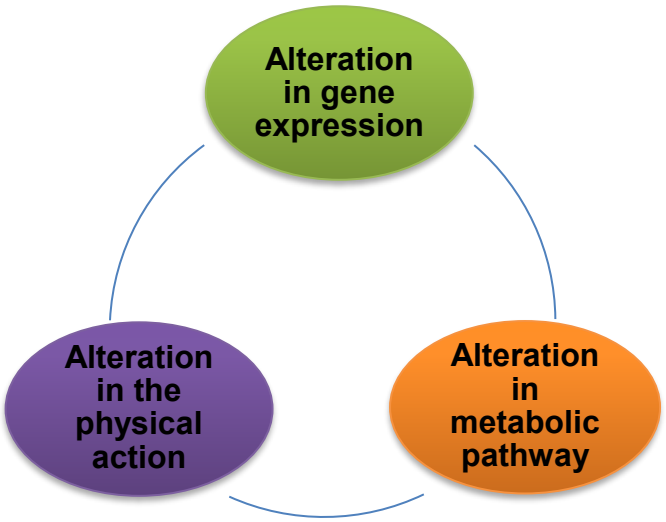

Fig. 3. Mode of action of microbial volatile organic compounds

Microbes release a wide range of volatile organic compounds with different mode and degree of action. Blom et al. (2011) screened "forty two strains of soil borne bacterial strains to study the effects of released VOCs on the growth of *Arabidosis thaliana* and sorted out thirty six compounds which had high degree of penetration to stimulate plant growth such as 1-hexanol, indole and pentadecane". Among the screened compounds, Dimethyl disulfide (DMDS) and ammonia were found to be among the most bioactive (Kai et al., 2010); and "DMDS is known to protect the tobacco and maize plants against the infection of *Botrytis cinerea* and *Cochliobolus heterostrophus* respectively" (Huang et al., 2012). "DMDS is also reported to have the property to alter the gene expression, more specifically to reduce the level of expression e.g. methionine biosynthesis and recycling and sulfur-assimilation genes in tobacco (*Nicotiana attenuata*)" (Meldau et al., 2013). Gautam et al. (2016) have shown "a wide range of volatile oils and oleoresins in small cardamom, that play an active role in plant development and quality of capsule".

Ryu et al. (2003) and Rudrappa (2010) identified "3-hydroxy-2-butanone also known as acetoin and 2, 3- butanediol (2, 3-BD); which are released from were released consistently from strains of *Bacillus subtilis* and *B. Amyloliquefaciens* and responsible for inducing the systemic resistance and enhancing the total leaf surface area in *A. thaliana".* "2, 3-BD, produced by *Enterobacter aerogenes* is also reported to induce the resistance against Northern corn leaf blight in corn" (D'Alessandro et al., 2014). "An important VOC 3-Hexanone, produced by *Burkholderia ambifaria* is known to significantly increase the biomass of *Arabidosis thaliana*; which is very similar in the action of two other VOCs namely acetophenone and DMDS" (Groenhagen et al., 2013).

2.2 MVCs and their Role in Inducing Phenotypic Plant Responses

"Owing to their wide range of activities and properties like enhancing biomass, modulation of gene action, inducing plant defence, alteration in root architecture, modulation of plant-microbe interaction and many more, Microbial volatile organic compounds have been subject of constant interest for researcher; and considerable progress has been made in recent toward these compounds. MVCs play critical roles in multitrophic interactions during different stages of plant development in form of communication between soil microorganisms and plants as well as plant-pathogen interactions. MVCs through their multifaceted inter and intra-specific interactions; are responsible for many genetic, phenotypic and morphologic alteration of the interacting organisms" (Penuelas et al., 2014 and Effmert et al., 2012).

"Recent studies revealed that a class of MVCs, acyl-homoserine lactone (AHL) are important intercellular signaling molecules used by many bacteria to monitor their population density in

quorum-sensing control of gene expression. AHLs are known to play important roles in signalling of plant-microbe interactions, such as biofilm formation, bacterial motility, expression of pathogenicity genes, plasmid transfer, production of antibiotics etc. can be recognized by plants. AHLs can activate the bacterial cells to regulate gene expression depending on population density and they can also alter gene expression in roots and shoots and modulate the defense and cell growth responses. In *Arabidosis*, AHLs have showed a dose dependent effect on the root architecture, initiation of lateral roots and development of root hairs, and modify the growth of primary roots" (Ortiz Castro et al., 2009 and von Rad et al., 2008). Nehvi et al. (2022, 2024) have showed that volatile oils in saffron tends to change with the impact of varying climate

"Studies in recent past unravelled the puzzles of induced systemic resistance (ISR) by the bacteria, and it was showed that majority of bacteria that activate ISR are known to do so by virtue of a salicylic acid (SA) independent pathway which involves involving jasmonate (JA) and ethylene signals" (Kanchiswamy et al., 2015). Ryu et al. (2004) showed that "VOCs released from *Bacillus subtilis* strain GB03 activates systemic resistance through an ethylene dependent pathway, which is independent of the SA or JA signalling pathways; on the other hand MVCs of Bacillus amyloliquefaciens strain IN937a triggers the ISR through an ethylene independent signalling pathway".

These studies provided new information about the role of MVOCs as initiators of defence responses in plants, and revealed that when compared with water control or treatment with the *Escherichia coli* strain DH5α; inoculation with bacterial strains GB03 and IN937a contribute in a very significant manner to promote the growth of *Arabidopsis* and the compounds involved were identified as acetoin and 2, 3- butanediol (2, 3-BD). It is noteworthy that when applied exogenously, acetoin and 2, 3- butanediol result in the dose dependent stimulation of plant growth.

"During the activation of ISR, different defensive cascades are elicited in response to different pathogens, as evident from a study; where the application of 2, 3-BD resulted the ISR response against *Pseudomonas carotovora* sub sp. *Carotovora* but failed to do same in case of *Pseudomonas syringae* pv. *tabaci*. Interestingly, acetosin, the precursor of 2, 3-BD successfully triggered the ISR in *Arabidopsis* against the *Pseudomonas syringae*. MVCs like 3-pentanol and 2-butanone when applied on cucumber seedlings consistently, can trigger the plant systemic defense responses against *Pseudomonas syringae* pv. *lachrymans*; through the activation of gene expression of plant green leaf volatile signalling pathway".

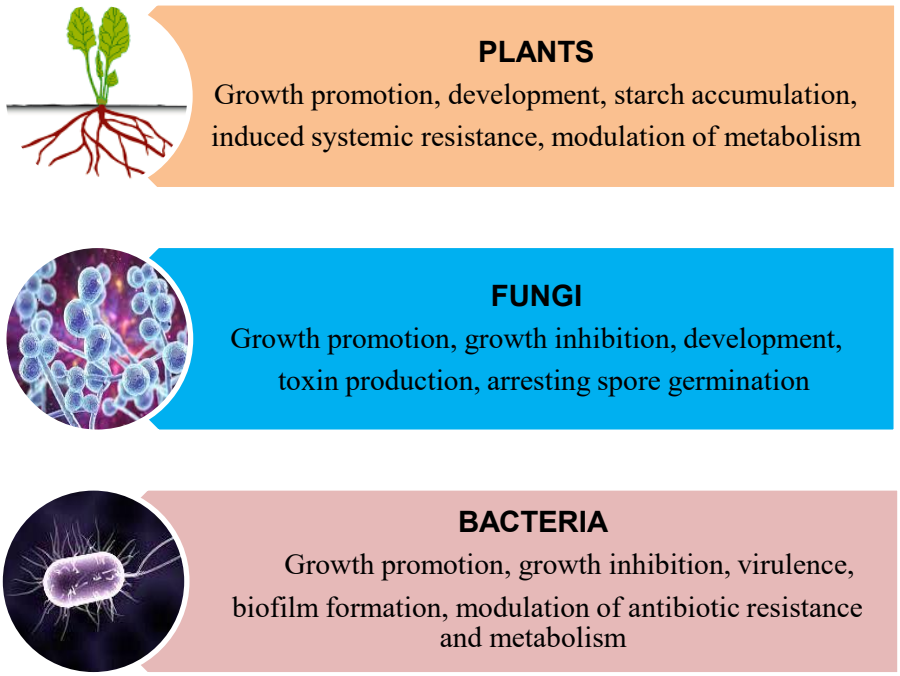

Fig. 4. Effects caused by MVCs in plants, fungi and bacteria

Song and Ryu (2013) showed that "these compounds led to an increase in crop yield but have not had any effect on plant growth".

An interesting outcome from the studies by Ezquer et al. (2010) revealed that "microbial species known for MVOC emission strongly promoted starch accumulation in leaves of both mono- and dicotyledonous plants. The leaves of two days treatment of plants with these MVCs, showed a starch content comparable to potato tuber and in some cases even in higher side. To some extents, this explains the course of action of MVCs towards an enhanced yield of a crop".

While investigating the starch content in the leaves of MVCs treated plants, Li et al. (2011) found that "MVOC induced starch accumulation process (MVOCISAP) is subjected to photoreceptor-mediated control; as evident from the starch level in the illuminated leaves of MVOCs treated *hy1/c*ry1, hy1/cry2, and hy1/cry1/cry2 mutants of Arabidopsis. Molecular studies of enzymatic and transcriptome level activities of potato leaves treated with the MVCs released by *Alternaria alternate*; showed that the phenomenon of starch accumulation due to exposure to MVCs is accompanied by multiple factors, viz. up-regulation of sucrose synthase invertase inhibitors, starch synthase (SS) class III and IV, starch branching enzyme and glucose-6-phosphate transporter".

3. Harnessing the MVCs Crop Protection and Production and Challenges

In the rapidly changing climatic conditions and emergence of new races of insect-pests and pathogens, there is a constant threat to food production around the globe. Owing to the drastic effects on human and environment health, there has been a constant debate over the use of synthetic pesticides and fertilizers over the last two decades.

"This has paved the way for formulation and applications of bio-pesticides, bio-fertilizers, and bio-control agents derived from living microbes are becoming suitable in a larger scale as a replacement of synthetic inputs. However, the high costs, inconsistent results and field performance and reduced efficiency have been a serious concern for these replacement inputs" (Glare et al., 2012).

"In such scenario, MVCs offer an alternative for a cost effective, result oriented and sustainable crop production and protection system for food security. Since past two decades, extensive research on MVCs and their roles in soil-plant, plant-microbes, plant-plant have provided new insights and conceptual understanding of the extremely complex and dynamic nature of these compounds and their potential role for a sustainable crop production and protection system. As discussed earlier, a wide range of MVCs have been reported and tested for their action against different pathogens, their ability to modulate the developmental process of a plant e.g. root architecture and total leaf area, and enhancing the production of biomass and economic yield e.g. enhanced starch accumulation etc. through different metabolic, physiological and transcriptional changes. It has been very well established that plants have the ability to perceive and respond to MVCs; this means MVCs have a very good prospects of application in crop production and protection. It won't be an exaggeration if we say that researchers are tapping a new era of MVCs and their potential application for a better tomorrow".

"Application of MVCs is still in its tender stage with a limited practical and commercial availability. As of now merely 400 bacteria and fungi and 1000 MVCs released by them are identified and documented released by have been described in the literature". "Though MVCs have shown potential for a wide range of application in agriculture system, but most of the results are from lab studies rather than the data from open field conditions. However, there have been few studies in open field condition in recent past and showed the promising results" (Cortes Barco et al., 2010a). These results back up the assumptions and idea of the application of MVCs in open field conditions for protection against herbivores, to increase pathogen resistance, and bio-control agents in general.

"There have been considerable differences in the results in lab and field conditions; also there have been ample reports which showed that MVCs may modulate growth/defense in a species-dependent manner and may be specific to conditions. One such example is 2, 3-butanediol, which in an open field condition has shown to exert its effect only as a modulator of defense but no effect as growth modulator. This makes it a pre-requisite to demonstrate and evaluate a single MVC or mixtures of MVCs on different crop species both at lab and field conditions, before generalization of the MVCs as growth or defence modulators" (Cortes Barco et al., 2010a).

Table 1. Some microbial volatile organic compounds, their source and effects

Microbe group	MVCs	Source	Effects	Reference
Bacteria	Benzaldehyde	*Bacillus amyloliquefaciens* strain FZB42	Resistance against *Ralstonia solanacearum*	Tahir et al., (2017a)
	Dimethylhexadecylamine	*Arthrobacter agilis*	Growth promotion in *Medicago sativa*	Velazquez Becerra et al., (2011)
	2,5-Dimethyl pyrazine	*Bacillus amyloliquefaciens*	Antifungal activity against *Fusarium* sp. and *Colletotrichum gloeosporioides*	Guevara Avenda˜no et al., (2019)
	Nonanal		Resistance against *Clavibacter michiganensis*	
	Benzothiazole			
	Acetophenone	*Bacillus subtilis FA26*		Rajer et al., (2017)
	Decyl alcohol		Resistance against *Xanthomonas oryzae*	
	3,5,5-Trimethylhexanol			
	Chloroacetic acid	*Bacillus* strain D13	Antifungal activity against *Colletotrichum gloeosporioides*	Xie et al., (2018)
	Octadecane			
	Hexadecanoic acid	*Bacillus atrophaeus HAB-5*		Rajaofera et al., (2019)
	2-Undecanone		Antibacterial activity against *Ralstonia solanacearum*	
	2-Tridecanone			
	Heptadecane			Raza et al., (2016d)
	Undecanal	*Bacillus amyloliquefaciens SQR-9*		
	2-Ethyl-1-hexanol			
	2-Undecanone		Antifungal activity against *Colletotrichum acutatum*	Che et al., (2017)
	1-undecene			
		Lysinibacillus sp. *P. brassicacearum*	Antifungal activity against *Rosellinia necatrix, F. oxysporum, F. solani, R. solani, S. Sclerotiourm, Macrophomina phaseolina, B. cinerea, Fusarum equiseti,* and *Verticillium dahliae*	
	Hydrogen cyanide			
	Dimethyl sulfide		Oomyceticidal activity against *Phytophthora cactorum*	Ossowicki et al., (2017)
	S-Methyl thioacetate			
	Methyl thiocyanate	*Pseudomonas donghuensis*	Antifungal activity against *Ralstonia. solani, Fusarium culmorum* and *Verticillium dahliae*	
	Dimethyl trisulfide			
	1-undecane		Oomyceticidal activity against *Pythium ultimum*	
Fungi	2-Methyl-1-butanol	*Hypoxylon anthochroum*	Antifungal activity against *Fusarium oxysporum*	Macías Rubalcava et al., (2018)
	3-Methyl-1-butanol			

Microbe group	MVCs	Source	Effects	Reference
	Eucalyptol Ocimene Terpinolene			
	1-Butanol 3-Methyl-phenylethyl alcohol Acetic acid 2-Phenylethyl ester	*Gliocladium sp.*	Antifungal activity against *Verticillium dahliae* Oomyceticidal activity against *Pythium ultimum*	Stinson et al., (2003)
	1,8 Cineole 1-Butanol 2-Methyl Phenylethanol alcohol	*Nodulisporium sp.*	Antifungal activity against *Ralstonia solani* and *Sclerotinia sclerotiorum* Oomyceticidal activity against *Phytophthora palmivora* and *Phytophthora cinnamomi*	Hassan et al., (2013)
	3-Octanone 3-Octanol 7-Octen-4-ol	*Myrothecium inundatum*	Antifungal activity against *Sclerotinia sclerotiorum* Oomyceticidal activity against *Pythium ultimum*	
	Methyl-propanol 3-Methyl-butanol	*Phoma sp.*	Growth promotion in tobacco	Naznin et al., (2013)
	1-Butanol 3-Methyl Benzeneethanol	*Phomopsis sp.*	Oomyceticidal activity against *Pythium* sp. and *Phytophthora* sp.	Singh et al., (2011)
	1-Propanol 2-Methyl 2-Propanone		Antifungal activity against S*clerotinia* sp., *Rhizoctonia* sp., *Fusarium* sp., Botrytis sp., *Verticillium* sp. and *Colletotrichum* sp.	
	3-Octanone Acetic acid 1-Octen-3-ol	*Trichoderma spp.*	Antifungal activity against *Fusarium oxysporum*	Li et al., (2018a)
	4-Heptanone Nonane 2-Octanone Limonene	*Trichoderma spp.*	Growth promotion in *Arabidopsis thaliana*	Nieto Jacobo et al., (2017)
	3-Methyl-1-butanol 2-Methyl-1-butanol 2-Methyl-1-propanol Thujopsene	*Xylaria sp.*	Oomyceticidal activity against *Pythium aphanidermatum* and *Phytophthora capsici* Antifungal activity against *Alternaria solani* and *Fusarium oxysporum*	Sanchez Ortiz et al., (2016)
	3-Methyl-1-butanol 2-Methyl-1-butanol	*Saccharomyces cerevisiae*	Resistance against *Colletotrichum gloeosporoides* Resistance against *Colletotrichum acutatum*	Rezende et al., (2015)

Microbes emits a plethora of MVCs, and there are very chances that a particular microbial compound or a mixture of such compounds has a synergistic effect on plant resistance to diseases; and at same time it may have a positive effect on plant growth and development. This can offer an abundance of blends of MVCs and their effective application to modulate the growth and development and disease resistance of crop plants.

"Another concern with the application of MVCs in crop production is manner of application of and their exploitation in open field conditions and their side effects. Most of the MVCs are known for their rapid evaporation rates, therefore the protocols for their application are needed to standardize at greater scale. Similarly, many MVCs are known to have inhibitory effects and some point of concentration they may be toxic also. Therefore an extensive assessment of the dose-response effect on specific crops, characterization of bioactive molecules are required before their use can be safely managed" (Cortes Barco et al., 2010a).

4. Conclusion

Microbial volatile organic compounds form an interface of microbial interaction at above and below ground level. These are very complex and dynamic in nature and a better understanding about their mode of action at molecular level, ecology and evolution can pave the way for effective use towards the crop protection and production for sustainable agriculture perspective. MVCs offer a most desirable alternative of synthetic pesticides or fertilizers; as they are biodegradable and can be applied in low concentration, they are in synergy with nature and no serious hazardous effects as in the case of synthetic pesticides or fertilizers.

To understand the roles, efficacy and suitability of MVCs; more open field studies coupled with physiological and molecular studies, are required to use the microbial volatile organic compounds in a cost effective, eco-friendly and sustainable manner to realise their potential in a sustainable crop production and protection.

Disclaimer (Artificial Intelligence)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

Competing Interests

Authors have declared that no competing interests exist.

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