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REVIEW ARTICLE

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Antagonistic fungal volatiles as potential biocontrol countermeasure for microbial postharvest fruit diseases

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Abstract

Background Fruits are the main important agricultural commodity, but very susceptible in terms of postharvest losses (PHL) due to diseases by microbial pathogens. Recently, there has been increased interest in countermeasure efforts to reduce PHL. As an alternative to chemical pesticides, fungal volatile organic compounds (FVOCs) are potential countermeasures because they are considered more environmentally friendly with less toxicity to human health.

Main body

FVOCs include wide diverse of organic chemical functional groups, but with low molecular weight (< C20) which possesses sufficient chemical, physical, and biological properties that can be clearly perceived by other organisms through intra- or inter-kingdom interactions, either mutualistic or antagonistic. Based on the antagonistic function, some beneficial FVOCs can be utilized as a biological control agent and biofumigant to combat microbial pathogens in postharvest fruit. Proposed mechanisms of the antagonistic effect of FVOCs toward their cell counterpart include alteration of the morphology of cell wall and cell membrane, influencing intracellular redox balance, elevating reactive oxygen species (ROS) level, and also possibly damaging DNA target. All these conditions potentially disrupt cell contents and then lead to cell death. In order to achieve this purpose, the suitable formulation of FVOC-loaded biofumigant is very crucial.

Conclusion FVOCs have potential application as biofumigant to control microbial pathogens in postharvest fruits. However, for the development of a product, the formulation of FVOC-loaded biofumigant should consider the compatibility of the formula with fruits, toxicity effect to humans, and cost production to ensure the effectiveness of the formula.

Keywords Biological control, Biofumigant, Food losses, Fungal interaction, VOC

Background

The increasing growth of the world population affects the demand for food availability. It is estimated that the world population will reach a peak at 9.7 billion in 2064 (Vollset et al. 2020); thus, increasing agricultural production is inevitable in order to fulfill the world food demand. Under this projection, the protection of crops from both abiotic and biotic stresses during cultivation is necessary for supporting crop yield demand. Moreover, the management of postharvest agriculture is complementary to preharvest to prevent irreducible yield losses in terms of the quality and shelf life of harvested products (Arah et al. 2015). For centuries, synthetic pesticides have been successfully utilized to overcome biotic stresses and intensify agricultural yields in order to increase

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food production and maintain postharvest quality and quantity. Regarding the availability and effectiveness of synthetic pesticides, their constant applications face various limitations that are considerably a threat to sustainable agricultural practices. Cases of microbial resistance have been reported for long-term during continuous use of synthetic pesticides (Xing et al. 2020). Moreover, synthetic pesticides such as xenobiotics have potential harm to human health through direct exposure (Kim et al. 2017) or via food chains (Zia et al. 2009).

Meanwhile, climate change deteriorated the production of crops by increasing pathogen resistance and weakening ecosystem susceptibility and vulnerability (Santini and Ghelardini 2015). As an example, continuous exposure to drought and high temperature contributed to decreasing plant productivity as a response to physiological, biochemical, and physical damages (Fahad et al. 2017), expanding the spreading and resistance of plant pathogens (Prasch and Sonnewald 2013) and increasing soil degradation thus directly affected loss of fertility (Lal 2012). Not only during cultivation but climate change also contributed to increasing incidents of postharvest losses (PHL) mainly by altering the quality of products due to elevated temperature during storage (Moretti et al. 2010) and escalating activity of postharvest pathogens (Dixon 2012). Recently, there has been increased interest in countermeasure efforts to provide sustainable agricultural practices in order to improve crop yield and reduce PHL (Díaz et al. 2020).

Among various agricultural products, fruits are the main important agricultural commodities, but very susceptible in terms of PHL (Conrad et al. 2018). Depending on the region, the losses of fruits are in the range of 5 to 20% of total production volume in developed countries, and between 20 and 50% in developing countries (Dwiastuti et al. 2021). Regarding the climatic condition, tropical fruits have a relatively higher susceptibility to loss than subtropical or temperate fruits, due to their inherent biological trait (Bantayehu et al. 2017). Related to the handling and supply chain processes, massive loss is obtained during handling, storage, packing, and transportation, compared to the farmer level (Olayemi et al. 2012), due to physiological, mechanical, as well as microbial causes. The fruit decay caused by microbial obstruction is a consequence of phytopathogen proliferation, mostly bacteria and fungi, on the edible part of the fruits. For example, *Fusarium* spp. along with *Colletotrichum musae* were major causative fungal agents that were responsible for crown rot postharvest disease in bananas (Lassois et al. 2010). The source of inoculum can be from flower or dried leaves and transferred to the banana bunches during harvest or postharvest cleaning with contaminated water (Kamel et al. 2016). During storage, the fungal pathogens caused early ripening on the contaminated banana bunches, thus undesirably shorting their shelf life (Kuyu and Tola 2018). Further implication leads to softening and blackening of the fruit tissue (Lassois et al. 2010).

In common practices, fruits along with other agricultural products are protected from postharvest decay using chemical substances. Postharvest fruit control strategies carried out by chemical control must meet aspects that include biological safety (humans and the environment), effectively increase shelf time, limited sensory interaction with fruit, and no less important are economic aspects (cost and process). Currently, effective control is using synthetic chemical pesticides, but these methods can create resistance to fungal pathogens if used continuously alone (Hawkins et al. 2019). In addition, chemical pesticides have a high potential for toxicity to humans and the environment with their persistent and accumulative nature (Pathak et al. 2022). As an alternative, chemical pesticide agents derived from vegetable sources have been developed, such as *Nicolaia speciosa* flower extract (Pratomo et al. 2009), betel leaf extract (Madhumita et al. 2019), and cinnamon oil (Wang et al. 2023). However, this biocontrol method is still needing great improvement due to the limited use of crude extracts, changes in fruit sensory (aroma), unstable control results obtained, and formulas that have not been standardized.

In the past few decades, the development and utilization of volatile organic compounds (VOCs) from microbes has increased and attracted many studies in order to further investigate their diversity as well as biotechnological applications (Bui and Desaeger 2021). VOCs are a mixture of highly volatile carbon-based compounds as primary or secondary metabolites that are emitted as signals for intra- or inter-organism communication, both mutualistic and non-mutualistic. VOCs from several fungi and bacteria have been used as a biological control agent ("biofumigant") for plant diseases and pest management because they are considered more environmentally friendly and reduce the use of synthetic pesticide applications (Boukaew et al. 2019).

Main Body

Chemistry and analysis of fungal volatiles

Fungal volatile organic compounds (FVOCs) are carbon compounds emitted by fungi that have been vaporized to a gas phase with a low boiling point at a temperature of around 20 °C, high vapor pressure at the pressure of 0.01 kPa, and typically odorous (Pagans et al. 2006). Most FVOCs are lipophilic, thus having low solubility in water and other polar solvents. FVOCs include wide-diverse of organic chemical functional groups (< C20), but with

low molecular weight, generally in the range of 50–200 Daltons (Rowan 2011) which possess sufficient chemical, physical, and biological properties that can be clearly perceived by other organisms through intra- or inter-kingdom interactions.

FVOCs are belonged to various chemical classes (Table 1), from simple hydrocarbons to different functional group moieties including alcohols, aldehydes, ketones, phenols, thioalcohols, and thioesters. More than 300 distinct FVOCs have been identified and characterized (Hung et al. 2015), but most attention of research interest was focused on the terpenoid-related volatile compounds, particularly sesquiterpenoids (Kramer and Abraham 2012).

For the current time, gas chromatography mass spectrometry (GC–MS) is still the prominent method for FVOC detection because it is powerful capabilities of sensitive detection as well as high separation ability (Epping and Koch 2023). Identification of the compounds are done by using mass spectra database, a library, or by retention times and spectra comparison with known standards. In order to collect the FVOCs proceed the detection, headspace solid-phase microextraction (HS-SPME) provides one of the best techniques for preparation of samples, particularly for the profiling of volatiles derived from living fungal cultures (Lancioni et al. 2022). However, some alternative methods have been developed as well. Activated charcoal filters were able to adsorb various class of volatile compounds, but some of the compounds such as unsaturated hydrocarbons, phenols, aldehydes, and amines were tight stronger to the filters, made them difficult to recover for further analysis (Matysik et al. 2009). A more classic method involved simultaneous distillation extraction (SDE) that merges extraction of solvent and vapor distillation, as examined toward FVOCs of *Penicillium roqueforti* (Jeleń 2003).

Production and biosynthesis of FVOCs

Single fungal species produce and emit a cocktail of FVOCs (volatolome) to the surrounding atmospheric environment. However, the composition and concentration of the FVOC produced are highly influenced by various environmental factors, particularly available nutrients and oxygen, pH, and temperature. The amount and diversity of available macronutrients, specifically carbon and nitrogen, affect the fungal metabolism to produce certain FVOCs. For example, the shifting chemical composition of FVOCs produced by *F. verticillioides* was observed when the fungus was incubated in different simple sugars (Achimón et al. 2022). Similarly, variation of nitrogen supply ($(NH_4)_2SO_4$ or KNO_3) changed considerably the amount and type of FVOCs produced by *Trichoderma* spp. (Wheatley et al. 1997). Oxygen availability is a basic parameter that affects fungal respiration and thus significantly shapes FVOC production (McNeal and Herbert 2009). Under aerobic fermentation, almost entirely carbon source was prioritized for energy production and cell growth, which entirely produced CO_2, leaving a small amount for the production of secondary metabolites including FVOCs. The level of acidity influences nutrient availability for fungi and their physiological condition, which can affect the production of FVOC (Stotzky et al. 1976). Similarly, the environmental temperature might be altered by FVOC production by modifying the fungal perception of environmental conditions (Almaliki et al. 2021). In the soil microenvironments, soil texture, soil moisture, as well as surrounding microbial activity play important roles to incite the production of FVOCs, thus determining their response to dynamic soil perturbations (McNeal and Herbert 2009).

FVOCs are synthesized in a very small quantity, making them strenuous to study and characterize. The information related to the biosynthesis pathway of FVOCs is relatively scarce compared to plant VOCs (Dudareva et al. 2013), although the efforts to integrate genomic, transcriptomic, and metabolomic approaches are at the start to tie in FVOC production with corresponding gene expression (Gianoulis et al. 2012). Obviously, by implementing gene modification on fungi with disrupted FVOC production, the biosynthesis mechanism in various fermentation and environmental conditions are possible to determine. Therefore, the connection between a certain gene to the production of volatile compounds and their biosynthesis pathways can be characterized. As a comparison, plants produce a complex mixture of FVOCs via four major metabolic pathways, namely in the lipoxygenase (LOX) to produce jasmonates and hydrocarbons, the mevalonic acid (MVA) to produce sesquiterpenes, the methylerythritol phosphate (MEP) to produce terpenes and ketones, and the shikimate pathway to produce benzenoids and phenylpropanoids (Razo-Belman and Ozuna 2023).

FVOCs in fungal interaction

FVOCs play important roles on mediated the intra- and inter-kingdom interaction of both below- and aboveground. Initially, the gasses emitted by fungi or other microbes have been considered as by-products of primary or secondary metabolism. However, recent findings showed that these volatile compounds possessed some significant biological activities (Karsli and Şahin 2021). The most important aspect of the biological function of FVOCs is related to their function in the interaction mechanism. Several recent investigations demonstrated that the production and emission of FVOCs can be suppressed or induced fungal physiology and morphology

Table 1 Chemical classes of some major fungal volatile organic compounds (FVOCs)

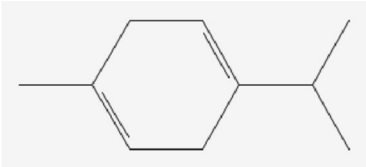
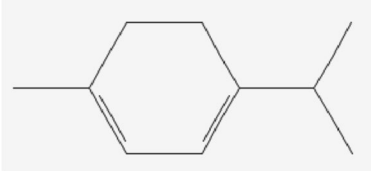
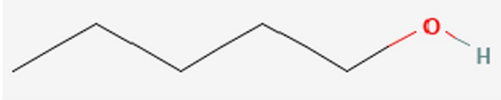
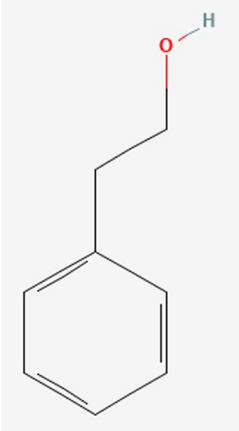
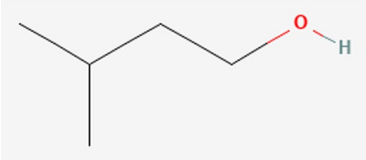
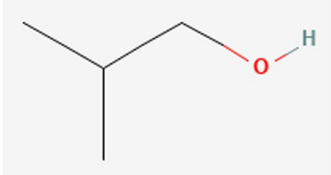
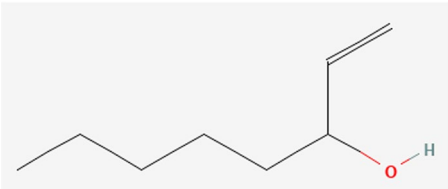
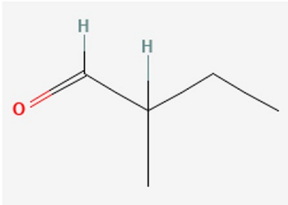
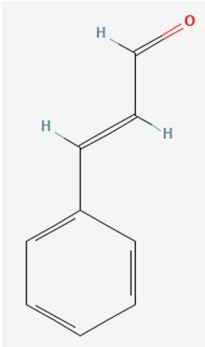
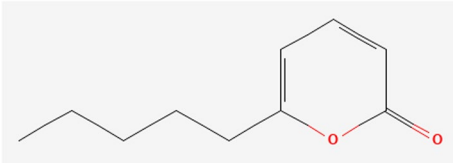
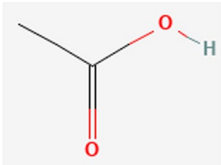
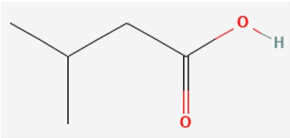
FVOC name	Chemical structure	Fungal source
Chemical group: hydrocarbons		
γ-terpinene		*Diaporthe apiculatum* (Song et al. 2019)
α-terpinene		*Fusarium culmorum* (Schmidt et al. 2016)
Alcohols		
Ethanol		*Aureobasidium pullulans* (Yalage Don et al. 2020)
1-pentanol		*Candida nivariensis* (Jaibangyang et al. 2020)
2-phenylethanol		*Monascus purpureus* (Zhang et al. 2021) *C. intermedia* (Tilocca et al. 2019) *Trichoderma asperellum* (Intana et al. 2021)
3-methyl-1-butanol		*Saccharomyces cerevisiae* (Dalilla et al. 2015)
Isobutanol		*Trichoderma viride* (Hung et al. 2013)

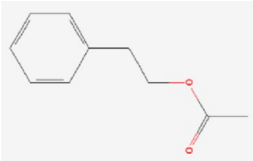
Table 1 (continued)

FVOC name	Chemical structure	Fungal source
1-octen-3-ol		*Tricholoma matsutake* (Ohta 1983)
Chemical group: aldehydes		
2-methyl-butanal		*Cladosporium halotolerans* (Jiang et al. 2021)
Trans-cinnamaldehyde		*Hanseniaspora uvarum* (Guo et al. 2019)
Chemical group: ketones		
6-pentyl-2H-pyran-2-one		*Trichoderma atroviride* (Garnica-Vergara et al. 2015)
Chemical group: organic acid		
Acetic acid		*Saccharomyces cerevisiae* (Giannattasio et al. 2013) *Trichoderma asperelloides* (Phoka et al. 2020)
3-methyl butanoic acid		*Kwoniella heveanensis* (Jaibangyang et al. 2021)

through intra- as well as inter-kingdom interactions (Freitas et al. 2022).

FVOCs have been considered as long-distance modes of cellular communications, while soluble metabolites including enzymes are associated with short-distance communications accompanying physical interaction. From the ecological perspective, FVOC function as environmental signaling compounds (semiochemicals) to

Table 1 (continued)

FVOC name	Chemical structure	Fungal source
Chemical group: esters		
2-phenyl ethyl acetate		*Pichia* spp. (Masoud et al. 2005)

deliver chemical signals or environmental cues to mediate, either beneficial or antagonistic, interactions (Cale et al. 2016). In the soil microenvironment, FVOCs are able to diffuse through the soil matrix to reach other organisms, including bacteria, other fungi, plant roots, or worms (Werner et al. 2016). In the aboveground environment, fungi are able to emit FVOCs that are able to influence insects (Lozano-Soria et al. 2020). Moreover, FVOCs were used by mass-aggregating ambrosia beetle *Xylosandrus germanus* as the signal compounds for fungal selection (Gugliuzzo et al. 2023).

In the bacterial-fungal interaction, fungi play important roles in long-distance communication that can lead to various phenotypical changes. Some bacterial growth can be suppressed after being exposed to FVOCs. For example, FVOCs emitted by *Pleurotus ostreatus* inhibited the growth of *Bacillus* spp. (Pauliuc and Botau 2013). On the other hand, FVOCs are able to affect bacterial secondary metabolite production and change the physiological behavior of bacterial cells. *F. culmorum* produced FVOCs that stimulate the production of sodorifen, a terpene, in *Serratia plymuthica* and influence various physiological of the bacterium including signal transduction, motility, cell envelope biogenesis, and energy metabolism (Schmidt et al. 2017).

In intra-kingdom communication, FVOCs play important roles in stimulating or suppressing other fungal counterparts. A common and well-known FVOC, 1-octen-3-ol, modulated the secondary metabolism and growth between *Aspergillus flavus* and *A. oryzae* during interspecies interaction (Singh et al. 2020). Meanwhile, various *Trichoderma* species have been reported to inhibit the mycelial growth of phytopathogenic fungi through the emission of FVOCs (Ruangwong et al. 2021). Besides their function as semiochemicals, a recent study showed that FVOCs can be utilized as carbon sources in interspecific interactions of fungal symbionts of mountain pine beetle (Cale et al. 2016).

FVOCs have biological activity as plant growth promotion metabolites. Besides their ability to promote plant growth via the production of soluble secondary metabolites, fungi are also able to produce gasses that act as chemical signaling to intrigue plant physiology. Two FVOCs produced by *C. halotolerans*, 2-methyl-butanal and 3-methyl-butanal, significantly modulated plant growth and modified the development of the root system (Jiang et al. 2021). *Trichoderma* species, besides their well-known ability to promote plant growth via the production of soluble metabolites, have been known to emit volatile metabolites with act as signaling compounds to affect some plant physiology processes (Lee et al. 2016). Furthermore, FVOCs produced by endophytic fungi have a remarkable potential as biofumigant. *Diaporthe* sp., an endophytic fungus isolated from leaves of *Chloranthus elatior* Sw. have been reported to emitted FVOCs that possess antifungal activity against some postharvest fungal pathogens (Santra and Banerjee 2023).

Bioprospecting of FVOCs

Underestimated previously, the study of FVOCs started to flourish in the last decades due to the recent findings of their biological activities, particularly in the agricultural, food, and energy field (Fig. 1). FVOCs were formerly recognized as side metabolic products with very few physiological functions. However, the recent breakthroughs in microbial interaction studies found that the FVOCs play important roles in intra- or inter-kingdom interactions, and act as small signaling molecules that regulate many important biological processes. These findings lead to emerge the bioprospecting of the FVOCs regarding their interactions, either antagonistic or mutualistic.

The chemical composition of FVOCs of some filamentous fungi showed an abundance of alkanes, cyclohexenes, cyclopentane, terpenes, benzenes, and polyaromatic hydrocarbons. Many of these compounds are found similar to a group of molecules in diesel or fuel-related hydrocarbons (Strobel 2014). An endophytic fungus, *Nodulisporium* sp. produced biofuel volatile compounds when grown in agricultural waste substrates under microaerophilic conditions (Schoen et al. 2017). Another report showed that several oleaginous endophytic fungi associated with biodiesel plants such as *Jatropha curcas* and *Ricinus communis* have great potential to be explored as biofuel sources (Paul

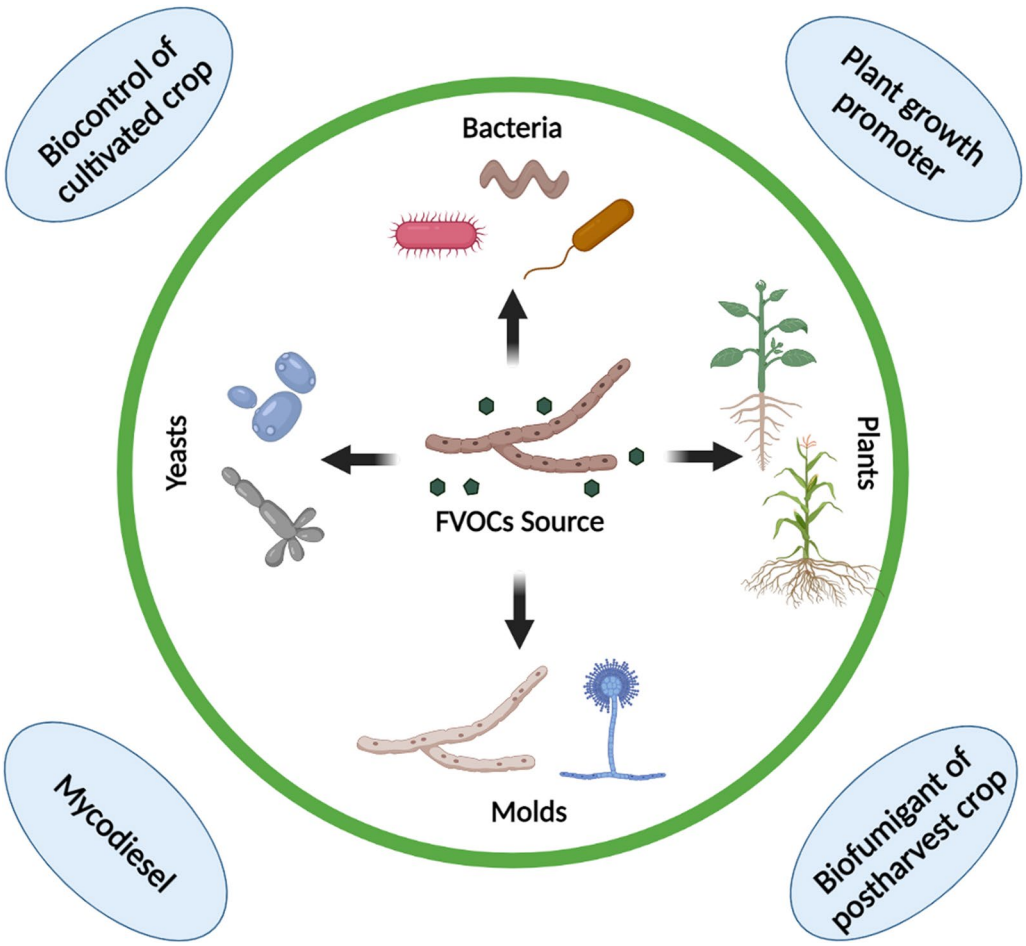


Fig. 1 Fungal volatile organic compounds (FVOCs) have roles as an indirect mode of intra- and inter-kingdom communication, either mutualistic or antagonistic (Freitas et al. 2022). Based on this biological function, FVOCs can be utilized for various purposes, particularly in the food industry and agriculture (Veronico et al. 2023). Recently, FVOCs have prospects as a novel renewable energy sources (Strobel 2014)

et al. 2020). This source of carbon is very potential as a green renewable energy source as an alternative to fossil fuels. Moreover, these filamentous fungi utilized cellulolytic polymer and its derivative that are abundantly found in plant-based waste as substrate, making it a novel and very promising candidate as renewable biofuels in the future.

In agricultural practices, the FVOCs have been implemented for biological control of plant pathogens, ranging from microbes to nematodes, even insects and their ability as plant growth-promoting agents has potency to be developed further. Various previous studies showed the activity of FVOCs as inhibitors of bacterial growth (Schmidt et al. 2016). Furthermore, FVOCs were also found as an antagonistic agent in intra-kingdom communications, thus proliferating their roles to control the growth of the fungal counterpart particularly the phytopathogenic (Ruangwong et al. 2021). Recent findings also showed that FVOCs have the ability to inhibit the growth of nematodes causing deteriorating plant roots and growth (Veronico et al. 2023).

The antagonistic effects of certain FVOCs bring a useful application of these compounds on the industrial scale, emphasizing on the application of biocontrol activity of several plant pathogens causing the postharvest disease. The loss caused by the diseases toward postharvest fruits and vegetables is remarkable annually with a tendency to increase every year. This effect brings devastation from an economic perspective globally. The effort to bio controlling the effect of the disease is not only beneficial in the economic aspect but also in the improvement of human health and quality of life. It has been reported that several bacterial as well as fungal phytopathogens causing postharvest disease in fruits and vegetables produced mycotoxins that are harmful to human health in short or long time exposure (Abdallah et al. 2022). In a confrontation with these microbial phytopathogens, several fungi emitted FVOCs that significantly decreased the

growth as well as disturbed the physiological functions of the counterpart microbes, thus lowering the fruit and vegetable rot incidences. The identification and characterization of FVOCs of various fungal strains through volatolomics analysis often showed the abundance of common and less toxic antifungal compounds. Therefore, these notions supported FVOC as a good candidate for biofumigant application in the food industry. For example, *Candida* spp. was reported to produce isoamyl alcohol, a common C5 alcohol that is commonly found as a side product in food and beverage fermentation (Ando et al. 2012). This compound possessed a remarkable and promising antimicrobial property. Another example is octan-3-one, an important bio flavor from edible mushrooms, which was reported to have antifungal activity against cabbage spot disease caused by *Alternaria brassicicola* (Muto et al. 2023). Moreover, an epiphytic yeast *Metschnikowia* sp. emitted FVOCs that were able to reduce production of aflatoxin B_1, a mycotoxin produced by *A. flavus* (Dikmetas et al 2023).

Antagonistic mechanism of FVOCs

The mechanisms of antimicrobial property of FVOCs toward fruit and vegetable postharvest disease are currently still limited, and the study to reveal the exact mode of action is still in progress. However, some mechanisms underlying the antagonistic effect of FVOCs emitted by fungi toward their cells counterpart are proposed (Fig. 2).

FVOCs targeting cell wall and organelle membrane

Cell walls and membranes maintained microbial cell shape through increasing mechanical resistance. The integrity of microbial cell membranes that are composed of phospholipids, sugars, and proteins is essential to the survival of microbes. Moreover, the cell wall compositions of major molecules (chitin, β-glucan, peptidoglycan) are vital to sustain cell morphology and protect the microbes from mechanical damage. However, FVOCs are able to damage membranes and cell walls, changing the morphology of microbes.

FVOCs are able to change the permeability of cells by peroxidation of the lipid layer. FVOCs released by a yeast-like fungus, *A. pullulans*, showed antifungal activity against *Botrytis cinerea* and *A. alternata* by enhancing peroxidation of lipids, production of reactive oxygen species (ROS), and loss of electrolytes (Don et al. 2021). Moreover, 3-methyl-1-butanol and 2-methyl-1-butanol, two FVOCS produced by *S. cerevisiae*, increased membrane lipid peroxidation level in *C. gloeosporioides* and *C. acutatum*, the fungal phytopathogens that responsible for anthracnose in postharvest guava (*Psidium guajava*) (Dalilla et al. 2015). The increasing level of ROS production changes the composition of the lipid layer and stimulates peroxidation of lipids by polarized unsaturated lipids, thus changing the membrane permeability, resulting disintegration of the membrane, stimulation of free radical reaction, and cell apoptosis (Vázquez et al. 2019).

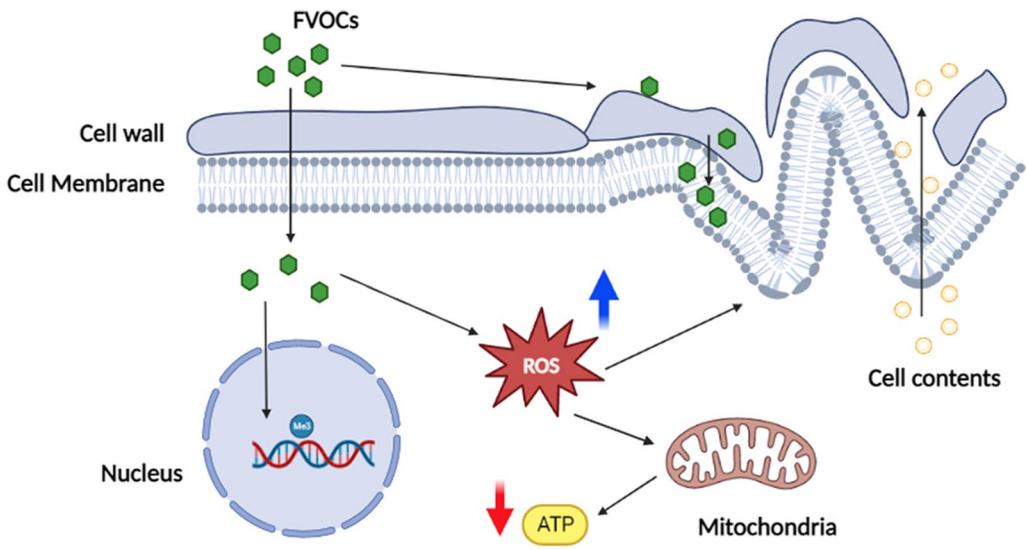


Fig. 2 Proposed mechanisms of antagonistic effect of fungal volatile organic compounds (FVOCs) toward cell target. FVOCs alter the morphology of cell walls and cell membranes (Yang et al. 2021), resulting damaging of cells and the leaking of cell contents (Vázquez et al. 2019; Gao et al. 2022). FVOCs also influence intracellular redox balance and elevate ROS levels, thus proceeding with peroxidation of the lipid membrane, disrupting mitochondrial function, and decreasing ATP production (Tilocca et al. 2019). Furthermore, the FVOCs are also possibly damaging DNA targets (Hutchings et al. 2017)

Volatile compounds were also able to directly target microbial cell membranes by increasing their permeability, hence leading to cellular leakage. Low molecular fatty acids, for example, are able to elevate the fluidity of the cell membrane, resulting in alteration of its conformity, and leading to leakage of protoplasm. Capric acid, a decanoic saturated fatty acid, is able to disrupt the cell membrane of *C. albicans*, leading to intracellular content leakage, subsequently effective to kill this fungal pathogen (Bergsson et al. 2001).

Exposure of microbial toward FVOCs can cause morphological changes in cell walls or cell membranes. For example, 3,4-dimethoxy styrol, a major FVOC produced by an endophytic fungus *Sarocladium brachiate*, altered the morphological structure of the *F. oxysporum* f.sp. *cubense* cell wall by disrupting the expression of chitin synthetase (Yang et al. 2021). Moreover, the microscopical observation of postharvest pathogen fungi after contact with FVOCs emitted by *Ceratocystis fimbriata*, an ascomycete, showed some severe damages, including deformation of mycelia and conidia, curling appearance, and cell collapse (Gao et al. 2022).

FVOCs causing oxidative stress on microbial target

During the interaction, volatile compounds produced by fungi are able to induce the accumulation of ROS and oxidative stress on microbial cells' counterparts. Consequently, the ROS accumulation will lead to some physiological disturbances, including disturbing redox balance and undesired reactions with important macromolecules such as proteins and lipids. These disturbances will eventuate dysfunction in cell homeostasis that further leads to cell death.

ROS are mostly formed in the course of aerobic respiration in the mitochondrial respiratory chain, catalyzed by complex I enzyme (Don et al. 2021). During ethanolic fermentation by *S. cerevisiae*, decanoic acid is a byproduct and is considered an inhibitor through its ability to accumulate in the endocellular and contribute to yeast toxicity mainly through lowering intracellular pH and cellular ATP exhaustion (Borrull et al. 2015). Moreover, Fialho et al. (2014) showed that FVOCs produced by *S. cerevisiae* disrupted the cellular redox state in *Guignardia citricarpa*, a phytopathogenic fungus that causes citrus black spot, by elevating activities of superoxide dismutase and catalase, resulting cellular stress oxidative.

FVOCs affect cellular metabolism and DNA on microbial target

Fungi through their FVOCs might influence the regulation of some metabolites of other microbes. This alteration can affect their physiological homeostasis which leads to inhibition of growth or even cell death. The exposure of 2-phenyl ethanol, a yeast-derived volatile organic compound, targeted some metabolic pathways in *A. carbonarius* such as decreasing proliferative ability, metabolism activity in mitochondria, biosynthesis of some proteins, and especially toxic substance detoxification (Tilocca et al. 2019). Similarly, a study conducted by Farbo et al. (2018) showed that 2-phenyl ethanol suppressed the production of ochratoxin A, the harmful mycotoxin for animal and human health, that is produced by *A. carbonarius* and *A. ochraceus*, along with the inhibition of the mycelial growth of these filamentous fungal pathogens. In another example, FVOCs produced by *F. culmorum* altered the expression of genes and proteins of *S. plymuthica* that related to the energy metabolism, cell signaling, biogenesis of cell envelope, motility, and production of secondary metabolites (Schmidt et al. 2017). More specifically, the exposure to the fungus volatiles triggered the bacterium to biosynthesize sodorifen, an uncommon terpene, as a response mechanism to the inter-kingdom interaction.

Another possible antagonistic mechanism is the effect of FVOCs on the DNA damage of the microbial counterpart. *Muscodor albus* produced N-methyl-N-nitrosoisobutyramide, a potent volatile mycotoxin, that affect primarily as a non-specific DNA methylating agent for various organisms (Hutchings et al. 2017). Moreover, a study showed that several pure FVOCs, including 1-octen-3-ol the common mushroom volatile, caused DNA damage under cytotoxic conditions without mutagenic and clastogenic effect (Kreja and Seidel 2002).

Prospects and strategies of FVOC application as biocontrol for management of postharvest fruit

Much information and publications have been reported regarding the antifungal potency of FVOCs of yeasts as well as filamentous fungi to control postharvest crop diseases, thus limiting the mycotoxin level in the food (Xing et al. 2023). Plentiful examples of these fungal species are demonstrated under in vitro as well as in vivo approaches to examine the antagonistic ability in controlling toxigenic and virulence activities of phytopathogens (Moore 2022). Furthermore, some studies were extended to examine the affectivity and efficacy of these FVOCs *in planta* or *in fructo* (Bandyopadhyay et al. 2019). Consequently, these studies pave the way to integrated pest management (IPM) perspective in order to gain awareness for green and environmentally friendly agricultural practices.

FVOCs are easily dispersed in food commodities, thus providing maximum protection by reaching even small and empty spaces, particularly during distribution and storage (Passone and Etcheverry 2014). Moreover, in a small and closed container, FVOC as a biofumigant gave

satisfaction protection and extended shelf life of postharvest produce, even by applying a small dose of the biofumigant (Herrera et al. 2015). These desirable outcomes of product application with a small dose of natural fungal volatile molecules are very beneficial in economic, environmental, and health perspectives in comparison with their synthetic volatile molecule counterpart.

FVOCs with their small molecular weight are advantage-able to be used as a biocontrol agent. Besides the antagonistic ability of FVOCs toward pathogens of postharvest produces, the compound toxicity level toward human and environmental health is also important to be considered. A collection of previous reports showed that some FVOCs may act as mycotoxins to mammals (Josselin et al. 2021), thus limiting their wide range of application as a biocontrol agent for foods. The presence of FVOCs in foods can also be utilized as bioindicators of spoilage and the production of mycotoxins by fungi (Schnürer et al. 1999). Moreover, some common and well-known FVOCs that have antimicrobial activity such as 1-octen-3-ol, 2-methyl-1-propanol, isoamyl alcohol, ethyl acetate, and geosmin can be used to indicate the formation of mycotoxin produced by *Penicillium*, *Aspergillus*, and *Fusarium*. However, the study and information about toxicity and level of safety of these FVOCs in postharvest biocontrol products are still lacking. For example, 1-octen-3-ol, an FVOC that responsible for common distinctive mold odor, is effectively reduced disease incidence in postharvest peaches caused by *Monilinia fructicola* at a concentration of 55.80 μg mL^{-1} (Wang et al. 2022). However, an experimental study of a group of human subjects after exposure to 10mg/m^3 of this FVOC for 2 h showed a sign of acute effects such as light mucosal and eye irritation, followed by symptoms of nausea and headache (Wålinder et al. 2008).

Along with their antimicrobial ability to combat fruit decay caused by microbial pathogens, volatile compounds are also able to influence the physiological and biochemical ripening processes of postharvest fruit, thus extending their shelf life (Fig. 3). FVOCs produced by *H. uvarum*, an endophytic yeast of strawberry fruit, were able to suppress the growth of a fungal postharvest pathogen, *B. cinerea*, thus preventing microbial decay of strawberries (Cai et al. 2015). Furthermore, the FVOCs of this yeast were also able to improve fruit flavor and increase the strawberry defense capability during cold stress, possibly by interfering enzymatic activities of related key enzymes in postharvest strawberries (Wang et al. 2019). The application of volatile compounds also affected volatilomics profile of the postharvest fruit. The application of hexanal vapor affected the volatile composition of Rubygem strawberry during a storage period, in which the increasing alcohol concentration at the end

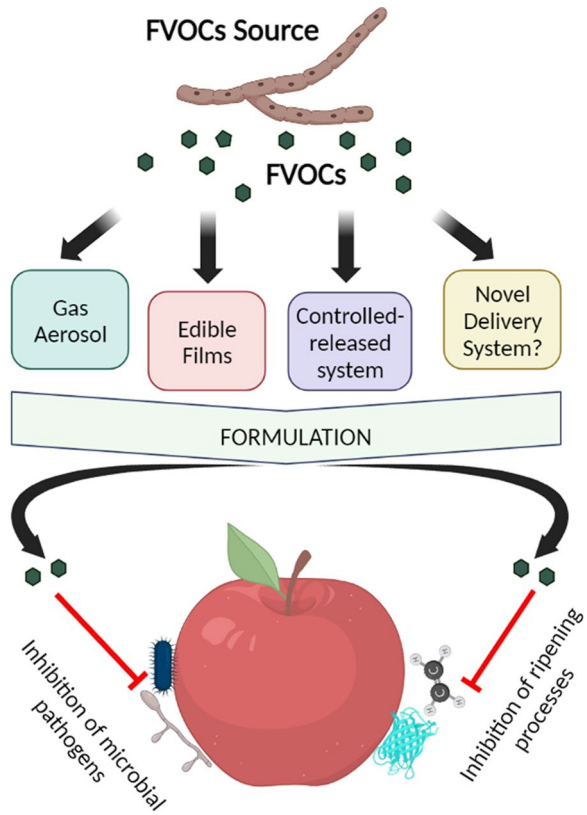


Fig. 3 The aim of bioprospecting of fungal volatile organic compounds (FVOCs) is not only to inhibit microbial pathogens of postharvest decay (Xing et al. 2023) but also to delay ripening processes, hence extending storage time (Wang et al. 2019). In order to achieve these purposes, the suitable formulation of FVOC-loaded biofumigant is very crucial to make sure the FVOC as the active compound acts effectively and efficiently

of the shelf life (Öz and Kafkas 2022). Regarding ripening processes, ethylene, a gaseous plant hormone, plays an important role in this process along with other hormones (Iqbal et al. 2017). Therefore, this compound and its biosynthesis are potential targets in order to innovate a promising technology for expanding the shelf life of postharvest fruit. On the other hand, some cyclopropanes have been evaluated to have anti-ethylene properties, thus extending fruit ripening time (Grichko 2006). Furthermore, some previous reports showed that FVOCs of some fungi consist of cyclopropanes as one of the major compounds (Yang et al. 2021). Therefore, it is possible that emitted compounds by these fungi play roles as ethylene antagonists and can be utilized to lengthen the expiry time of fruits.

In a product development, good formulation of FVOC-loaded biofumigant is crucial to ensure the efficacy and effectiveness of the active compounds. Moreover, it is necessary to develop a product in a formulation that can be used with minimum toxic effects on humans or

other organisms, to avoid its harmful effects. Some factors must be considered carefully to obtain a desirable biofumigant product according to good IPM practices. In complement to the toxicity consideration of FVOC(s) as an active compound, the excipients of the formula should be biologically safe for human consumption as well. Moreover, the chemical and physical compatibility of each component in the formula should also be carefully considered, to make sure there is no chemical reaction between active components and excipients as well as among excipients. Lastly, the economic aspect is an evitable factor, particularly for commercial products. Among the economic considerations are the price of each component, the availability of each raw material, and the cost of process production.

Various formulas of volatile organic compound-based biofumigant have been developed, but very few of these product candidates or prototypes were successfully released as commercial products (Fig. 3). One of the most important considerations in developing a suitable formula is the physical and chemical properties of the FVOC candidate, particularly their small molecular weight and lipophilic property. The easiest and most affordable formulation form for FVOC-based biofumigant is an aerosol spray. The FVOCs as active compounds can be dispersed in other volatile organic solvents such as ethanol or in fixed oil as micro/nanoemulsion (Ziedan et al. 2022). However, most of the current formulas are based on plant essential oils. Therefore, there is a possibility of nanoemulsion formulation of microbial volatile compound-based products in the future. Another approach is combining FVOCs with edible films that are usually used for coating hard-texture fruits such as oranges, apples, avocados, and mango, but this method is not suitable for soft-texture and easily perishable fruits such as grapes and strawberries (Zuhal et al. 2018). One of the prominent benefits of this approach is the ability to increase retain time of FVOC molecules, ensuring the prevention of microbial spoilage. This is particularly important for long-term storage and long-chain distribution. Another possible breakthrough is the development of controlled-released biofumigant. The volatile active compound is formulated in the suitable matrix to regulate in such a way that the active compound is controlled and released so that it remains at an effective concentration as an effective biocontrol agent. Although such an idea is probably still in the infancy of developing biofumigant formulation, this delivery system has been advanced in the pharmaceutical field (Opoku-Damoah et al. 2022). Similar to pharmaceutical gasses, direct delivery of FVOCs for biofumigant purposes might face some problems, particularly the uncontrollable and toxicity consideration of these gasses. Therefore, it is important to develop a more targeted and controlled delivery formula. Finally, the development of novel delivery formulas to improve the quality and effectiveness of biofumigant products is inevitable as a future prospect.

Conclusion

As semiochemicals, FVOCs play an important and unique role in indirect inter- and intra-kingdom communication between fungi and other organisms, either mutualistic or antagonistic. In the antagonistic effect, the proposed mechanism of FVOCs includes alteration of the morphology of cell wall and cell membrane, influencing intracellular redox balance, elevating ROS level, and also possibly damaging DNA target. Based on this antagonistic property, some beneficial FVOCs can be utilized as a biological control agent and biofumigant to combat microbial pathogens in postharvest fruit. The antimicrobial spectrum of FVOCs is generally broader because of their expeditious conversion to gasses phase, dispersed easily in fruit commodities without direct physical contact, thus persevering organoleptic properties of the fruit. For the development of an FVOC-based biocontrol product, the formulation should consider the compatibility of the formula with fruits, the toxicity effect to humans, and cost production to ensure the effectiveness of the formula.

Abbreviations

FVOCs	Fungal volatile organic compounds
IPM	Integrated pest management
PHL	Postharvest losses
ROS	Reactive oxygen species
VOCs	Volatile organic compounds

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Author contributions

TPN collected the data for writing the review under various headings and did the preliminary preparation of the manuscript. TPN wrote this review.

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Availability of data and materials

Data sharing is not applicable to this article as no data sets were generated or analyzed during the current study.

Declarations

Ethical approval and consent to participate

Not applicable.

Consent for publication

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Competing interests
The authors declare that they have no competing interests.

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