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Microbial volatilome in food safety. Current status and perspectives in the biocontrol of mycotoxigenic fungi and their metabolites

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ABSTRACT

Fungal infection and mycotoxins contamination in food and feed products cause significant economic losses to the food and agricultural industry. Although the efficacy of synthetic fungicides is unquestionable, there are serious issues associated with their application in agriculture. Improper and/or prolonged application of these products may cause the emergence of resistant fungal populations, carry-over of chemicals in the human diet and adverse effects on non-target species. By contrast, ease in application and negligible effects on the environment makes microbial volatile organic compounds (VOCs) safe and sustainable substitutes to synthetic fungicides. A considerable research investment has highlighted the efficacy and suitability of VOCs emitted by bacteria, yeast and filamentous fungi for application in food crops and stored products. In this review, focus is made on the potential use of microbial VOCs as inhibitors of toxigenic food microbiota and their mycotoxins. The mode of action of microbial volatile compounds, possible application in different scenarios, limitations and perspectives are discussed.

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1. Introduction

Fungal infections of agricultural crops and their products trigger significant losses to the food and agricultural compartments (Alina, 2022; Shabeer et al., 2022; Xu et al., 2022). The old Food and Agriculture Organization (FAO) notion ‘25% of the food is annually lost due to fungal infection’ is in fact true and even slightly underestimates the actual damage (Almeida et al., 2019).

Apart from the mold-associated spoilage, infections of food products by mycotoxin-producing species results in the buildup of toxins (Al Attiya et al., 2021; Hassan et al.,

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2019; 2018; Ul Hassan et al., 2018; Xu et al., 2022). An ever-growing list of mycotoxins of human health significance includes mainly those produced by filamentous fungi. The toxic effects of mycotoxins could be as mild as short-duration gastrointestinal disorders to chronic (immunosuppression, growth retardation, reproductive disorders) and acute (hepatotoxicity, nephrotoxicity, neurological disorders and deaths) in the exposed animal and humans (Alshannaq & Yu, 2017; Cimbalo et al., 2020; Dey et al., 2022). These effects are generally severe in the vulnerable communities, including infants, elderly and immunocompromised patients (Omotayo et al., 2019).

Integrated control measures against fungi are proposed at all stages of agricultural production to minimise the damage. Best management practices at pre-harvest stages, including crop rotation, resistant crops, proper sowing and watering time, use of health propagative material and application of fungicides can help dropping the magnitude of the issue (Santiago et al., 2015; Shabeer et al., 2022; Tilocca et al., 2019). At post-harvest stages, there are several approaches (physical, chemical and biological) to preserve food from fungal attack and accumulation of mycotoxin (Ji et al., 2016; Sadiq et al., 2019). The inappropriate application of synthetic fungicides has led to serious concerns regarding the environment and public health (Tilocca et al., 2020). Moreover, the emergence of fungicide-resistant fungal strains is largely linked with the improper use of synthetic antifungal compounds in the field and at the postharvest stage (Fisher et al., 2022).

Physical methods, such as binding agents, UV exposure, sorting, cleaning, grading, washing, etc. are also adopted to reduce contamination with mycotoxins in susceptible agricultural commodities, albeit their effectiveness may vary according to the targeted toxin and of the food/feed material (Kolossova & Stroka, 2012; Sipos et al., 2021).

Several antagonistic bacteria, filamentous fungi and yeast strains have been registered and biocontrol commercial products are being marketed for the protection of food commodities subject to mycotoxin contamination (Freimoser et al., 2019; Moore, 2022; Moral et al., 2020; Tilocca et al., 2020). Antifungal formulations utilising non-aflatoxigenic *Aspergillus flavus* strains, e.g. Alfa-Guard (atoxigenic *A. flavus*), FUSAclean (non-pathogenic *Fusarium oxysporum*), AF36[®] (atoxigenic natural *A. flavus*) and Aflasafe[®] (four atoxigenic *A. flavus* strains) are currently being used with significant reductions in aflatoxins (AFs) in corn, peanuts, cotton seeds and other agricultural crops (Kagot et al., 2019). In addition to filamentous fungi, antagonistic yeast (*Cryptococcus albidus*, *Aureobasidium pullulans*, *Metschnikowia fructicola* and *Saccharomyces cerevisiae* and *Candida oleophila*,) and bacterial strains (*Streptomyces* spp., lactic acid bacteria (LAB), *Pseudomonas* spp., *Bacillus* spp.) are registered for their antifungal commercial use in agricultural and food industry (Freimoser et al., 2019; Salas et al., 2017).

Until recently it was known that most of the biocontrol strains employ competition for space and nutrients as a major mechanism of the antagonism. However, during the last two decades, the focus of attention has shifted from competition to volatile-mediated interaction between the target fungi and biocontrol agent. For instance, non-toxicogenic strains of *A. flavus* used in three commercial formulations (Afla-Guard[®], AF36[®], Aflasafe[®]) were thought to compete with the toxigenic *A. flavus* for the space and nutrients as a mechanism of their antagonism (Bandyopadhyay et al., 2019). However, Moore et al. (2021, 2022) have recently demonstrated that the volatiles released by non-aflatoxigenic *A. flavus* are also involved in this interaction.

Volatile organic compounds (VOCs) are characterised by their low solubility in water and high vapour pressure ≥ 10 Pa (Lammers et al., 2022; Tilocca et al., 2020) and play diverse physiological roles in the environment (Weisskopf et al., 2021). The use of volatiles for human benefits started with their application as perfumes, flavouring agents in food and developing specific aroma and taste of food products (Ebert et al., 2017; Verma et al., 2022). The volatile profile of microbes depends on several characteristics including the age of the microbes, physical parameters (temperature, pressure, humidity), presence of other organisms in their environment, aeration and the method of collection (Insam & Seewald, 2010). Biotechnological application of microbial volatiles was a neglected area of research, particularly due to lack of sophisticated collection and analytical methods (Weisskopf et al., 2021). However, during the past decade, application of VOCs in the food, agriculture, pharmaceutical and medicine industry has been largely explored (Lammers et al., 2022; Weisskopf et al., 2021).

In this review, we will summarise recent research achievements on the role of microbial (bacteria, yeast and filamentous fungi) volatiles in the control of mycotoxigenic fungi and their metabolites in food preservation, with emphasis on pre- and post-harvest damage. Furthermore, the potential utilisation of microbial volatiles in food preservation, their mode of action, limitations and perspective are discussed.

2. Biosynthesis of microbial volatiles

Like other living organisms, microbes also produce complex arrays of volatiles and secrete them during their routine metabolic processes. These molecules are regarded as products of their metabolism (Schmidt et al., 2015; Weisskopf et al., 2021) and are broadly classified as inorganic and organic compounds (Lammers et al., 2022; Schulz-Bohm et al., 2017). The major classes of organic volatiles of microbial origin include aromatic compounds, alkanes, alkenes, fatty acids, ester, alcohols, methyl ketones, aldehydes, ketones and short-chain fatty acids (Schmidt et al., 2015; Tilocca et al., 2020; Veselova et al., 2019; Weisskopf et al., 2021). The synthesis of these volatiles involves catabolic processes (Figure 1) such as glycolysis, lipolysis and proteolysis (Freimoser et al., 2019; Veselova et al., 2019).

In general, microbial volatiles molecules across Kingdom and within Kingdom are common in their nature (Mari et al., 2016; Salas et al., 2017; Tilocca et al., 2020). However, some molecules are peculiar to a microbial group or even a single strain, making them unique in their physicochemical role (Schmidt et al., 2015). Below, we provide a brief summary on overall biosynthesis of volatiles produced by bacteria, yeast and filamentous fungi.

During the aerobic cell environment, pyruvate is converted to acetyl-CoA and enters into fatty acid metabolism or tricarboxylic acid (TCA) cycle. Fatty acid metabolism generates alkanes, alkenes, ketones and aliphatic alcohols (Schmidt et al., 2015). Even numbered fatty acids are produced with the β -oxidation of acetyl-CoA. Fatty acids, aldehydes and ketones are the typical volatile end products of fatty acid pathways (Lammers et al., 2022). Aromatic compounds, such as 2-phenylethanol (2-PE) are produced mainly through the shikimate pathway and are particularly important in the antifungal activities. For example, several studies highlighted the production of 2-phenylethanol (2-PE) by bacteria (Weisskopf et al., 2021), yeast (Farbo et al., 2018), and filamentous fungi

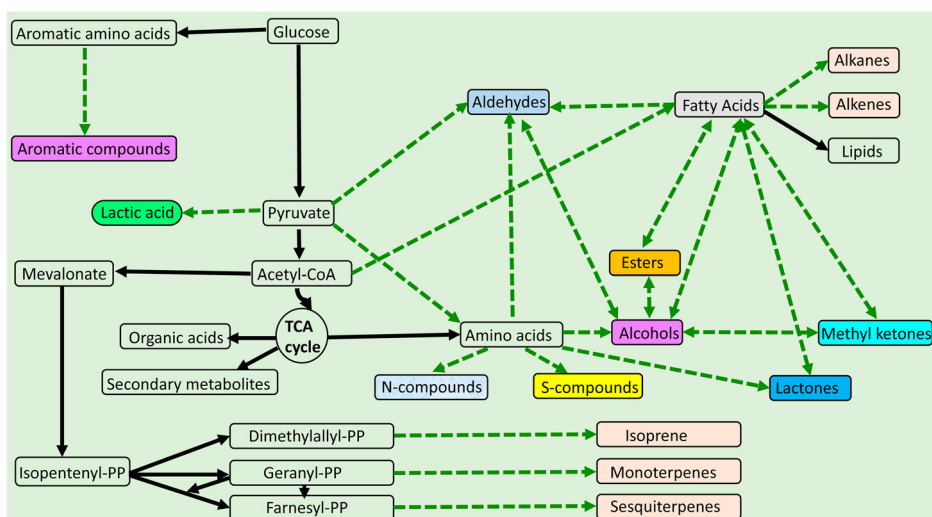


Figure 1. Pathways involved in the synthesis of microbial volatiles implicated in the antagonism of toxigenic fungi and mycotoxins. Dotted lines indicate the steps involved in the synthesis of known antifungal volatiles, while continuous line indicate non-volatiles intermediate or final products. This figure presents the modification of pathways previously illustrated by Schmidt et al. (2015) and Veselova et al. (2019).

(Medina-Romero et al., 2017), and its inhibitory role against toxigenic fungi and their mycotoxins. Sulphur compounds are important constituents of microbial volatilome and are synthesised from the methanethiol and hydrogen sulphide. Dimethyl disulphide is a dimer of methanethiol which is commonly detected in gas chromatography (GC) volatile profiles of many bacteria (Brock et al., 2014). Other sources of sulphur compounds are acids, such as methyl-butyrac acid. Terpene hydrocarbons are diverse groups of volatiles produced by fungi and bacteria and have been implicated in their antifungal mode of action (Corcuff et al., 2011; Medina-Romero et al., 2017; Tenorio-Salgado et al., 2013). Terpenes are synthesised by three pathways; (a) the mevalonate pathway, which was long being considered the only source of isopentenyl diphosphate and dimethylallyl diphosphate. This pathway starts with glycolysis leading to acetyl-CoA and isopentenyl diphosphate, which subsequently results in the production of terpenes (Freimoser et al., 2019). The other two pathways are leucine and the 2-methylerythritol-4-phosphate (Veselova et al., 2019) which also results in the synthesis of terpenes (isoprene, monoterpenes and sesquiterpenes). Along with organic compounds, microbes also produce inorganic molecules such as carbon monoxide, carbon dioxide, hydrogen cyanide, oxygen, hydrogen, hydrogen sulphide, ammonia, nitrogen dioxide, sulphur dioxide, etc. (Tilocca et al., 2020; Veselova et al., 2019).

3. Bacteria

3.1. Antifungal bacterial volatilome

Organic compounds of bacterial origin are characterised by acids, alcohols, terpenes, benzenoids, acids, ketones, pyrazines and alkenes (Veselova et al., 2019; Weisskopf

et al., 2021). These molecules alone or their consortia play significant antifungal activity against toxigenic fungi and mycotoxins during pre- and post-harvest stages of food systems (Chalivendra & Ham, 2019; Lammers et al., 2022; Veselova et al., 2019). Likewise, bacteria also produce inorganic volatiles such as carbon monoxide (CO), carbon dioxide (CO₂), hydrogen cyanide (HCN), oxygen (O₂), hydrogen (H₂), hydrogen sulphide (H₂S), ammonia (NH₃), nitrogen dioxide (NO₂), sulphur dioxide (SO₂), etc., play diverse roles including quorum sensing, electron donor or receptor and as defence molecules (Tilocca et al., 2020). Below is a detailed account of microbial profiles of different bacterial genera, with emphasis on their antagonistic activities against mycotoxigenic fungi.

3.1.1. *Bacillus* spp.

Bacillus spp. as a biocontrol agent have several advantages over the other microbial genera because of their convenience in application, environmental safety (with few exceptions), resilience to harsh conditions, genetic diversity, broad range of antifungal activity and minimal nutritional requirements (Chalivendra & Ham, 2019). These benefits associated with *Bacilli* place them on top of the list of commercialised biocontrol agents (Effmert et al., 2012). In the last few decades, there are many novel reports on the role of *Bacillus* spp. against toxigenic fungi and mycotoxin biosynthesis in food commodities (Table 1). The main species of *Bacillus* implicated in biocontrol of toxigenic yeast are *B. amyloliquefaciens* (Arrebola et al., 2010; Chaves-López et al., 2015; Shi et al., 2014; Yuan et al., 2012), *B. subtilis* (Arrebola et al., 2010; Chaves-López et al., 2015), *B. velezensis* G341 (Calvo et al., 2020; Lim et al., 2017), *B. cereus* (Chaves-López et al., 2015), *B. methylotrophicus* (He et al., 2020), *B. thuringiensis* (He et al., 2020), *B. licheniformis* (Ul Hassan et al., 2019), *B. megaterium* (Mannaa & Kim, 2018; Saleh et al., 2021), *B. simplex* (Al Attiya et al., 2021) and *B. pumilus* (Morita et al., 2019). The prominent antifungal volatile molecules synthesised by *Bacillus* spp., include (but not limited to) 2,3-butanediol, 3-hydroxy-2-butanone (Ryu et al., 2003), tetradecane, pentadecane (Yuan et al., 2012), 3-hydroxy-2-butanone, dimethylsulfoxide, 1-butanol, (Lim et al., 2017), 3-methyl-1-butanol (Ul Hassan et al., 2019), diacetyl, 2-undecanone, 2-nonanone, 1-butanol, 2-heptanone, benzaldehyde, acetoin (Calvo et al., 2020), quinoline, benzenemethanamine 1-octadecene (Al Attiya et al., 2021), tetracosane, palmitic acid (Saleh et al., 2021), 1-butanol, propanone, acetic acid, 2-methylpropanoic acid, ethyl acetate, carbon disulphide (Chaves-López et al., 2015), 3-hydroxy-2-butanone (acetoin) (Arrebola et al., 2010), ethanol, S-(-)-2-methylbutylamine, methyl isobutyl ketone (Morita et al., 2019), 2-butyl 1-octanol, 4-trifluoroacetyl hexadecane, 5-methyl-2-phenyl-1H-indole and dimethyl disulphide (Mannaa & Kim, 2018).

In a study by Shi et al. (2014), *B. amyloliquefaciens* isolated from the peanut shell inhibited *F. graminearum* by 41.4–54.5% in co-culture assay and by 92.7–100% in tip-culture assay. Additionally, upon *in-vivo* application on wheat kernels, this strain inhibited deoxynivalenol (DON) synthesis by 16.69–90.30%. Ul Hassan et al. (2019) demonstrated that volatiles (mainly 3-methyl-1-butanol) emitted by *B. licheniformis* inhibited all tested toxigenic *Aspergillus* and *Penicillium* species. *A. westerdijkiae* showed high sensitivity to *Bacillus licheniformis* strain 350-2 (BL350-2) volatiles with an inhibition ratio of 62%, while other representative strains including *A. carbonarius*, *A. ochraceus*, *A. niger*, *A. parasiticus*, *A. flavus* and *P. verrucosum* were all inhibited at

Table 1. Summary of antagonistic bacterial species/strains, their target toxigenic fungi, bioactive volatile molecule(s) and experimental application.

Antagonistic bacteria	Target fungi	Main biomolecules	Main effects	Experimental setup	Reference
<i>Lentilactobacillus (Lent.) buchneri</i> , <i>Lactococcus lactis</i> , <i>Lent. buchneri</i> , <i>Lactiplantibacillus plantarum</i> , <i>Levilactobacillus brevis</i> , <i>Lac.</i> <i>plantarum</i> , <i>Lacticaseibacillus</i> <i>rhamnosus</i>	<i>A. flavus</i>	Acetic acid; propionic acid; 1,2 propanediol	Degraded zearalenone (ZEN) and tenuazonic acid in silage.	<i>In situ</i> on maize silage	Gallo et al. (2022)
<i>Lactobacillus plantarum</i>	<i>A. niger</i> , <i>A. ochraceus</i> , <i>A. tubingensis</i> , <i>A. carbonarius</i> , <i>A. tubingensis</i> and <i>A. niger</i>	Acetic acid; phenyllactic acid; pyrazines	Inhibition of mycelium growth	<i>In vivo</i> on synthetic media and <i>in vitro</i> on detached red grapes	Dopazo et al. (2022)
<i>Lacticaseibacillus rhamnosus</i> , <i>Lac.</i> <i>plantarum</i>	<i>A. flavus</i>	1,2 propanediol	Reduction in AFB1 levels	<i>In situ</i> on corn silage	Gallo et al. (2021)
<i>Enterococcus faecium</i> , <i>Enterococcus</i> <i>casseliflavus</i>	<i>F. verticillioides</i>	Acetoin; diacetyl	Inhibition of mycelium growth and mycotoxin production	<i>In vitro</i> on synthetic media	Diaz et al. (2021)
<i>Bacillus megaterium</i>	<i>F. verticillioides</i> <i>A. flavus</i> , <i>P. verrucosum</i> ,	Palmitic acid; tetracosane	Suppression of fungal growth and mycotoxin synthesis; suppression of mycotoxin synthesis	<i>In vitro</i> on synthetic media and <i>in vivo</i> on maize ears	Saleh et al. (2021)
<i>B. simplex</i>	<i>A. flavus</i> , <i>A. carbonarius</i>	Quinoline; benzenemethanamine; 1- octadecene	Inhibition of mycelium growth and mycotoxin synthesis	<i>In vivo</i> application on stored coffee bean	Al Attiya et al. (2021)
<i>B. velezensis</i> , <i>B. atrophaeus</i> and <i>Psychrobacillus vulpis</i>	<i>Alternaria alternata</i> , <i>F. solani</i>	Isopentyl isobutanoate; 2,3-butanediol; acetoin; isopentanol; dimethyl; disulphide acetic acid	Mycelium growth inhibition	<i>In vitro</i> on synthetic media	Toral et al. (2021)
<i>B. velezensis</i>	<i>P. expansum</i>	Pyrazine; 2-heptanone; 1-butanol; acetoin; 2-undecanone; butyl for – mate; benzaldehyde; diacetyl; nonane; 2- nonanone,	Mycelium growth inhibition	<i>In vitro</i> on synthetic media and <i>in vivo</i> of grapes and apricot	Calvo et al. (2020)
<i>Streptomyces philanthi</i>	<i>A. flavus</i> and <i>A. parasiticus</i>	Geosmin; L-linalool; 2-mercaptoethanol; heneicosane	100% inhibition in mycelium growth and AFs synthesis	<i>In vivo</i> on soybean seeds and <i>in vitro</i> on synthetic media	Boukaew and Prasertsan (2020)
<i>S. kanamyceticus</i> , <i>S. misionensis</i> , <i>S. cangkringensis</i> , <i>S. kanamyceticus</i>	<i>A. alternata</i> , <i>F. solani</i>	<i>Trans</i> -2-hexenal	Inhibition of mycelium growth	<i>In vitro</i> synthetic media	Corral et al. (2020)

<i>Streptomyces yanglinensis</i>	<i>A. parasiticus</i> and <i>A. flavus</i>	2-methyl-2-bornene; 2-methylisoborneol	Inhibition of expression of AFs synthesis genes, conidial germination, mycelium growth, and sporulation	<i>In vitro</i> on synthetic media and <i>in vivo</i> on peanut kernels	Lyu et al. (2020)
<i>Burkholderia cenocepacia</i>	<i>F. solani</i> , <i>A. niger</i>	Nonanoic acid indole; methyl anthranilate; methyl benzoate; benzyl propionate; methyl salicylate; dimethyl trisulphide	Inhibition of mycelium growth	<i>In vitro</i> synthetic media	Chen et al. (2020)
<i>Pseudomonas aeruginosa</i>	<i>A. flavus</i> , <i>A. fumigatus</i>	2-heptanone; 2-undecanone; methyl thiobutyrate; 1-undecanol; 2-dodecanone	Inhibition of mycelium growth	<i>In vitro</i> on synthetic media	Nazik et al. (2020)
<i>B. methylotrophicus</i> , <i>B. thuringiensis</i>	<i>P. expansum</i>	Up to 30 compounds from the following groups. Pyrazines; phenols; ketones; aldehydes; acids; alcohols and other organic compounds	Mycelium growth inhibition	<i>In vitro</i> on synthetic media and <i>in vivo</i> on loquat fruit	He et al. (2020)
<i>Enterobacter asburiae</i>	<i>A. flavus</i>	Phenylethyl alcohol; 1 – pentanol	Complete growth inhibition <i>in vitro</i> ; inhibition of <i>A. flavus</i> infection on peanuts, downregulation of Afs synthesis genes, inhibition of AF synthesis, inhibition of conidial germination and conidial morphological alteration	<i>In vitro</i> on synthetic media and <i>in vivo</i> on stored peanuts	Gong et al. (2019)
<i>Streptomyces alboflavus</i>	<i>A. flavus</i>	Benzenamine; dimethyl trisulphide	Suppression of mycelium growth, sporulation, conidial germination and AFs pathway genes	<i>In vitro</i> on synthetic media	Yang et al. (2019)
<i>B. pumilus</i>	<i>A. niger</i>	S-()-2-methylbutylamine; 5-methyl-2-heptanone; ethanol; methyl isobutyl ketone	Enhancement of <i>A. niger</i> growth	<i>In vitro</i> on synthetic media	Morita et al. (2019)
<i>B. licheniformis</i>	<i>A. parasiticus</i> , <i>verrucosum</i> , <i>A. westerdijkiae</i> , <i>A. niger</i> , <i>A. ochraceus</i> , <i>A. flavus</i> , <i>carbonarius</i> ,	3-methyl-1-butanol	Inhibition of mycelium growth and mycotoxin production	<i>In vivo</i> on maize and <i>in vitro</i> on artificial media	Ul Hassan et al. (2019)
<i>Bacillus</i> sp.	<i>A. fumigatus</i> , <i>P. expansum</i>	Benzaldehyde; isovaleric acid; propanoic acid; 2-methylbutanoic acid; acetic acid	Fungal growth inhibition	<i>In vitro</i> on synthetic media	Osaki et al. (2019)
<i>Lactobacillus</i> sp.	<i>A. parasiticus</i>	6-octadecenoic acid methyl ester; 2-methyldecane; pentadecane; 7-hexadecenal; phenol; dotriacontane	Suppression of mycelium growth and mycotoxin synthesis	<i>In vitro</i> on synthetic media and <i>in vivo</i> on wheat grains	Shehata et al. (2019)

(Continued)

Table 1. Continued.

Antagonistic bacteria	Target fungi	Main biomolecules	Main effects	Experimental setup	Reference
<i>B. megaterium</i> , <i>Pseudomonas protegens</i>	<i>P. fellutanum</i> , <i>A. fumigatus</i> , <i>P. islan – dicum</i> , <i>A. candidus</i>	4-trifluoroacetoxyhexadecane; heptanol; 5-methyl-2-phenyl-1H-indole; 2-butyl 1- octanol	Suppression of conidial germination, sporulation, fungal population, mycelial growth and germ-tube elongation	<i>In vitro</i> on synthetic media and <i>in vivo</i> on rice	Mannaa and Kim (2018)
<i>Pseudomonas donghuensis</i>	<i>F. culmorum</i>	1-undecan; methyl thiocyanate; S-methyl thioacetate; dimethyl trisulphide; dimethyl sulphide; HCN	Inhibition of myclium growth	<i>In vitro</i> on synthetic media	Ossowicki et al. (2017)
<i>B. megaterium</i> , <i>Pseudomonas protegens</i>	<i>A. flavus</i>	*VNA	Inhibition of sporulation, mycelial growth, conidial germination and reduction in AFs synthesis	<i>In vivo</i> on stored rice grains and <i>in vitro</i> on synthetic media	Mannaa et al. (2017)
<i>B. velezensis</i>	<i>F. oxysporum</i>	Dimethylsulfoxide; 1-butanol; 3-hydroxy- 2-butanone	Fungal growth inhibition	<i>In vitro</i> on synthetic media	Lim et al. (2017)
<i>Lactobacillus plantarum</i> , <i>Lactobacillus fermentum</i> , <i>Lactobacillus brevis</i> <i>Lactococcus</i> sp.	<i>A. niger</i> , <i>P. roqueforti</i> <i>P. chrysogenum</i> , <i>A. niger</i>	Polyporic acid Butyl phenol	Fungal growth inhibition Reduction of mycelium growth	<i>In vitro</i> on synthetic media <i>In vivo</i> on wheat grains and <i>in vitro</i> on synthetic media	Valerio et al. (2016) Varsha et al. (2015)
<i>Lactobacillus paracasei</i>	<i>Penicillium</i> spp.	Diacetyl	Suppression of mycelium growth	<i>In vitro</i> on synthetic media and <i>in vivo</i> in yogurt	Aunsbjerg et al. (2015)
<i>B. cereus</i> <i>B. amyloliquefaciens</i> , <i>B. subtilis</i>	<i>A. parasiticus</i> , <i>A. flavus</i> , <i>A. clavatus</i> , <i>A. niger</i> ,	Ethyl acetate; 1-butanol; acetic acid; carbon disulphide; 3-methylbutanoic acid; propanone	Mycelium growth inhibition	<i>In vitro</i> on synthetic media	Chaves-López et al. (2015)
<i>B. amyloliquefaciens</i>	<i>F. graminearum</i>	VNA	Inhibition of fungal mycelial mass mycotoxin synthesis	<i>In vitro</i> on synthetic media	Shi et al. (2014)
<i>Burkholderia ambifaria</i>	<i>Alternaria alternata</i>	Phenylpropanone; dimethyl Trisulphide; 4-octanone; 2-undecanone; methylmethanethiosulfonate; dimethyl disulphide	Mycelial growth inhibition	<i>In vitro</i> on synthetic media	Groenhagen et al. (2013)
<i>Burkholderia tropica</i>	<i>F. culmorum</i>	Limonene; alpha-pinene; ocimene	Mycelial growth inhibition	Plant root protection and dish plate growth assay	Tenorio- Salgado et al. (2013)

<i>Lactobacillus sanfranciscensis</i> , <i>Lactobacillus reuteri</i> , <i>Lactobacillus pontis</i> , <i>Lactobacillus hammesii</i> , <i>Lactobacillus plantarum</i>	<i>A. niger</i> , <i>P. roqueforti</i>	Monohydroxy octadecenoic acid; coriolic acid	Mycelial growth inhibition	<i>In vitro</i> on synthetic media	Black et al. (2013)
<i>B. amyloliquefaciens</i>	<i>F. oxysporum</i>	2,3,6-trimethyl-phenol; pentadecane; tetradecane	Mycelial growth inhibition	<i>In vitro</i> on synthetic media	Yuan et al. (2012)
<i>B. amyloliquefaciens</i> , <i>B. subtilis</i>	<i>P. crustosum</i> and <i>P. italicum</i>	3-hydroxy-2-butanone (acetoin)	Inhibition of germ tube elongation, fungal radial growth and spore germination	<i>In vitro</i> on synthetic media and <i>in vivo</i> in citrus (valencia)	Arrebola et al. (2010)
<i>Lactobacillus plantarum</i>	<i>A. flavus</i>	3,6-bis(2-methylpropyl)-2,5-piperazinedione	Complete inhibition of mycelial growth	<i>In vivo</i> on soybean	Yang and Chang (2010)
<i>Lactobacillus plantarum</i>	<i>A. fumigatus</i> , <i>P. roqueforti</i>	3-hydroxydecanoic acid; 3-phenyllactic acid	Mycelial growth inhibition	<i>In vitro</i> on synthetic media and <i>in vivo</i> on grass silage	Broberg et al. (2007)
<i>Lactobacillus plantarum</i>	<i>F. sporotrichioides</i> , <i>A. fumigatus</i>	3-phenyllactic acid	Inhibition of fungal mycelium	<i>In vitro</i> on synthetic media	Ström et al. (2002)

Note: This table is a summary of relevant findings on bacterial VOCs-mediated inhibition of mycotoxigenic fungi presented in descending chronological order. *VNA = Volatile Not Analysed.

44–60% compared to unexposed controls. In *in vivo* testing on maize ears, volatile of BL350-2 showed 88% inhibition of *A. flavus* and complete inhibition of AFs biosynthesis. In a study by Saleh et al. (2021), we found that a *B. megaterium* strain (BM344-1) producing tetracosane and palmitic acid significantly inhibited toxigenic *P. verrucosum*, *A. flavus*, and *F. verticillioides* by 67, 29% and 18%, respectively. Upon exposure to BM344-1 volatiles, there was 100% inhibition of AFs, ochratoxin A (OTA) and fumonisins (FUMs) synthesis by the three tested toxigenic fungi. *In vivo* tests performed on maize ears showed that the inhibition of *A. flavus* (51%) by BM344-1 was higher, whereas the effect on mycotoxin biosynthesis was lower compared to artificial media. These differences strongly suggest that antifungal activities of bacterial strains are associated with other factors, such as the effect of substrate and the experimental setup.

The volatiles of *B. simplex* BS350-3 showed 1-octadecene, benzenemethanamine and quinoline as the most bioactive molecules against toxigenic *A. carbonarius* and *A. flavus* on coffee beans (Al Attiya et al., 2021). The level of AFs contamination in artificially infected coffee beans was significantly lower ($26.65 \pm 3.33 \mu\text{g}/\text{kg}$) in the existence of BS350-3 volatiles, compared to the unexposed control coffee beans ($63.60 \pm 8.52 \mu\text{g}/\text{kg}$). Likewise, BS350-3 volatiles significantly inhibited OTA contamination at $1.88 \pm 0.33 \mu\text{g}/\text{kg}$ by *A. carbonarius* as compared to unexposed infected coffee beans, where the level was $4.13 \pm 0.81 \mu\text{g}/\text{kg}$ (Al Attiya et al., 2021).

3.1.2. Lactic acid bacteria (LAB)

LAB constitute acid-tolerant, heterogenous bacteria producing acid as an end product of carbohydrate fermentation (Salas et al., 2017), and are found in diverse ecological niches including soil, human body, animals and plants (Broberg et al., 2007; Crowley et al., 2013). LAB contribute significantly to agriculture industry in production and preservation of food, particularly in the control of toxigenic fungi (Chalivendra & Ham, 2019; Dopazo et al., 2022; Gallo et al., 2021, 2022; Sadiq et al., 2019). In accordance with their GRAS (Generally Considered as Safe) status, and some probiotic properties (Crowley et al., 2013), LAB are regarded as green preservatives (Nasrollahzadeh et al., 2022). The mode of action of LAB are diverse and involves the secretion of lytic enzymes, production of antifungal volatiles, competition for nutrients and space, degradation of produced mycotoxins, etc. (Nešić et al., 2021; Tilocca et al., 2020). LAB volatiles comprise a long list of antifungal molecules including 6-octadecenoic acid methyl ester, pentadecane, 7-hexadecenal, phenol, 2-methyldecane, hexadecanoic acid methyl ester, dotriacontane (Shehata et al., 2019), acetoin, diacetyl (Diaz et al., 2021), butyl phenol (Varsha et al., 2015), cyclo (L-Phe-*trans*-4-OH-L-Pro), 3-phenyllactic acid (Ström et al., 2002), polyporic acid (Valerio et al., 2016), 3,6-bis(2-methylpropyl)-2,5-piperazinedion (Yang & Chang, 2010), 3-phenyllactic acid, 3-hydroxydecanoic acid (Broberg et al., 2007), monohydroxy octadecenoic acid, coriolic acid (Black et al., 2013) and acetic acid, propionic acid, 1,2 propanediol (Gallo et al., 2021, 2022).

Antifungal volatiles of LAB (Table 1) were shown to inhibit toxigenic *Aspergillus* (Broberg et al., 2007; Gallo et al., 2022; Shehata et al., 2019), *Penicillium* (Aunsbjerg et al., 2015; Yang & Chang, 2010) and *Fusarium* (Diaz et al., 2021; Ström et al., 2002; Varsha et al., 2015), as well as their ability to produce mycotoxins. Acetoin and diacetyl were identified as bioactive volatile molecules of *Enterococcus faecium* and *Enterococcus casseliflavus* which resulted in 33% and 10% growth inhibition of *F. verticillioides*,

respectively. In this study, *Enterococcus* spp. also inhibited FB1 synthesis by 89% (Diaz et al., 2021). In another study, VOCs of *Lactobacillus* sp. RM1 showed antagonistic activities against toxigenic fungi and AFs and OTA synthesis *in vitro*. On wheat grains, *A. parasiticus* was completely inhibited by bacterial volatiles for at least 2 weeks of co-incubation. These antagonistic effects were mainly due to 6-octadecenoic acid methyl ester, 2-methyldecane, pentadecane, 7-hexadecenal, phenol, hexadecanoic acid methyl ester, dotriacontane (Shehata et al., 2019). *Lactobacillus paracasei* strain DGCC 2132 inhibited *P. solitum* and *Penicillium* sp. by producing a volatile (diacetyl) at pH 6.5 and 4.5, respectively (Aunsbjerg et al., 2015). A defined volume (200 µg/mL) of commercial diacetyl successfully inhibited both fungi for 14 and 20 days, respectively. A summarised account of antifungal activities of different LAB is presented in Table 1.

3.1.3. *Pseudomonas* spp.

There are several studies on the inhibitory role of volatiles synthesised and released by *Pseudomonas* spp., against toxigenic fungi (Cordero et al., 2014; Lal et al., 2022; Mannaa et al., 2017; Mannaa & Kim, 2018; Nazik et al., 2020; Ossowicki et al., 2017; Wang et al., 2021). The VOCs mix of some hydrocarbons emitted by *Pseudomonas fluorescens* MGR12 significantly inhibited *F. proliferatum* both on rich and minimal media (Cordero et al., 2014). Nazik et al. (2020) performed series of experiments to explore the role of *Pseudomonas aeruginosa* volatiles against different representative strains of *A. flavus* and *A. fumigatus*. Only in the volatile mix collected from the antagonistic strains a number of bioactive molecules were identified, including methyl thiobutyrate, 2-undecanone, methyl thiocyanate, methyl thio isovalerate, heptane, 2-heptanone, decanone, mercaptoacetone, 2-undecanol, 1-undecanol, 2-tridecanone and 2-dodecanone. Among these, methyl thiobutyrate, 2-undecanone and 2-heptanone, when tested alone, showed strong antifungal activity against the tested *Aspergilli*. In contrast to the reported results of Scott et al. (2019), Nazik et al. (2020) concluded that VOCs released by *P. aeruginosa* never promote *A. fumigatus* growth (Table 1).

In another investigation, Ossowicki et al. (2017) reported the emission of volatiles active against *F. culmorum* by a soil isolate of *Pseudomonas donghuensis* P482. The list of molecules showing *in vitro* inhibitory effects includes S-methyl thioacetate, dimethyl sulphide, dimethyl trisulphide, 1-undecan, methyl thiocyanate and HCN.

3.1.4. *Streptomyces* spp.

Streptomyces was believed to be the largest antimicrobial producing genus in the twentieth century (Watve et al., 2001), and hence there exist several registered commercial products based on *Streptomyces* strains (Bubici, 2018). Biocontrol activities of *Streptomyces* spp., volatiles against toxigenic *Aspergillus*, *Penicillium*, *Fusarium* and *Alternaria* are documented in several studies (Cho et al., 2017; Corral et al., 2020; Li et al., 2010; Lyu et al., 2020; Wang et al., 2013). In an *in vitro* assay, the volatiles emitted by *Streptomyces alboflavus* significantly inhibited *A. flavus*, *F. moniliforme*, *A. niger*, *P. citrinum* and *A. ochraceus*. A major component of *S. alboflavus* TD-1 volatilome was identified as 2-methylisoborneol by GCMS (Wang et al., 2013). Similarly, Corral et al. (2020) tested the volatiles of four maize and apple isolates of *Streptomyces* (*S. kanamyceticus*, *S. misionensis*, *S. cangkringensis* and *S. kanamyceticus*) on *Alternaria alternata* and *F. solani*. Bacterial volatiles (*trans*-2-hexenal as a major molecule) inhibited the fungal

growth up to 96.7%. Lyu et al. (2020) exposed toxigenic *A. parasiticus* and *A. flavus* to the VOCs emitted by *Streptomyces yanglinensis* strain 3–10, both *in vitro* and on peanut kernels. Bacterial volatiles repressed the expression of AFs biosynthesis genes along with fungal sporulation, vegetative growth and conidial germination. Likewise, on peanut kernels, bacterial volatiles showed significant inhibition of both fungal infection and AFs biosynthesis. GCMS-based analysis showed high concentrations of 2-methyl-2-bornene and 2-methylisoborneol in bacterial volatiles among 19 other compounds. Commercial methyl 2-methylbutyrate showed the highest *in vitro* activity, suggesting it as a major responsible for inhibition. *S. alboflavus* TD-1, an isolate from wheat bran produced two antifungal volatiles (dimethyl trisulphide and benzenamine), which strongly inhibited *A. flavus* by suppressing growth of fungi and its AFs biosynthetic potential, as evidenced by downregulation of key AFs synthesis genes (Yang et al., 2019).

3.1.5. *Burkholderia* spp.

The volatiles of a few species in the genus *Burkholderia* including, *Burkholderia ambifaria* (Groenhagen et al., 2013), *Burkholderia tropica* (Tenorio-Salgado et al., 2013), *Burkholderia gladioli* (Elshafie et al., 2012) and *Burkholderia cenocepacia* (Chen et al., 2020) have shown to produce inhibitory effects on toxigenic fungi and their mycotoxin synthesis (Table 1). Elshafie et al. (2012) reported the production of 1-methyl-4-(1-methylethenyl)-cyclohexene, an antifungal volatile by *B. gladioli* active against a range of toxigenic fungi such as *A. flavus*, *A. niger*, and *P. expansum*. Likewise, Chen et al. (2020) reported the antagonistic activity of *B. cenocepacia* against *F. solani* and *A. niger* by producing volatile inhibitory molecules including indole, dimethyl trisulphide, methyl salicylate, methyl benzoate, methyl anthranilate, benzyl acetate, allyl benzyl ether and nonanoic acid. Like other bacteria, the volatiles of *Burkholderia* showed inhibitory activities against toxigenic *Aspergillus*, *Fusarium*, *Alternaria* and *Penicillium* species (Chen et al., 2020; Elshafie et al., 2012; Groenhagen et al., 2013; Tenorio-Salgado et al., 2013).

3.2. Antagonistic mechanism of bacterial volatiles

The precise mechanism of interaction of bacterial volatiles with toxigenic fungi resulting in the suppression of fungal growth and mycotoxin biosynthesis is not well outlined. However, diverse effects are reported on the fungal strains as well as the host commodity/crop to produce biological effects (Schmidt et al., 2016, 2015; Tilocca et al., 2020). In laboratory settings, inhibition of fungal growth and/or mycotoxin production are primary criteria to declare/screen the biological agents (Al Attiya et al., 2021; Saleh et al., 2021; Ul Hassan et al., 2019). In reality, the composition of volatiles produced by any antagonistic strain is regulated by several physicochemical parameters including the nature of microbial strains, substrate composition, existence of other microbes, environmental conditions (temperature, vapour pressure, water activity) and the age of bacterial cells (Corcuff et al., 2011; Effmert et al., 2012; Ezra & Strobel, 2003; Lammers et al., 2022). To achieve optimal antifungal activity, it's critical to validate specific physicochemical conditions and environmental attributes. For instance, at 0.98 aw, 20 out of 59 *Bacillus* isolates inhibited both *A. flavus* and *A. parasiticus*. However, on lower 0.95 aw, only 3 isolates showed their effectiveness (Bluma & Etcheverry,

2006). Similarly, on maize kernel extract agar, *Bacillus* isolates from maize field displayed a higher inhibition of *F. verticillioides* and *A. flavus* compared to the same strains being cultured on PDA, suggesting specific nutritional requirements for optimal metabolite biosynthesis (Palumbo et al., 2007). The lack of inhibitory activity by candidate/known biocontrol agents on popular growth media are likely due to unavailability of desired nutrients (Chalivendra et al., 2018), leading to poor growth and toxic metabolite synthesis. Under such stress situations, antagonistic bacterial strains may also produce growth-promoting substances and increase disease severity as well as mycotoxin production (Cray et al., 2016). Additionally, microbes needing nutrient-rich media for the production of inhibitory molecules might not be an economically viable choice for field application (Chalivendra & Ham, 2019).

The reduction of mycelium growth may not necessarily be associated with the inhibition of mycotoxin biosynthesis. There are several reports on enhanced mycotoxicity by *Fusarium* and *Aspergillus* when mycelial growth was inhibited (Santiago et al., 2015). Chalivendra et al. (2018) tested 29 *Bacillus* isolates for their antifungal and anti-aflatoxigenic potential on *A. flavus*. In total, 3 isolates inhibited *A. flavus* growth, while 26 were able to suppress AFs synthesis. These findings suggest that screening for biocontrol activity should include both the effect on fungal growth as well as on mycotoxin biosynthesis, to reduce the chances of losing effective strains. A mycotoxin biocontrol cocktail could include microbial strains with different inhibitory potential over a range of species. Another possibility is to include microbial strains with strong mycotoxin inhibiting (but no antifungal) activity with fungicides for a robust toxin control measure (Ons et al., 2020).

HCN, a common inorganic volatile, leads to production of cyanide ions, which are known inhibitors of metallic enzymes such as cytochrome c oxidases. The inhibition of key fungal enzymes consequently leads to a cascade of events passing over the impaired function and finally death (Effmert et al., 2012). Antifungal effects include the suspension of hyphal growth inducing cell injury, thereby affecting mycotoxins synthesis and stability (Chalivendra & Ham, 2019). In many fungi-bacteria interactions, it has been reported that exposed fungi recover once removed from the bacterial volatiles environment, suggesting a clear fungistatic effect, while in others the effects of bacterial compounds are irreversible (Chalivendra & Ham, 2019; DeFilippi et al., 2018).

Bacterial volatiles interact with cell wall of target fungi by releasing enzymes as reported by Tamreihao et al. (2016). In a study, on exposure to caryolan-1-ol (a major volatile) of *Streptomyces* spp, Cho et al. (2017) reported inhibition of endomembrane systems of target fungi.

4. Yeast

4.1. Antifungal yeast volatilome

Application of yeast volatile molecules in the protection of food crops and their products have several advantages over synthetic fungicides (Freimoser et al., 2019; Tilocca et al., 2020). Yeasts in general are easy to cultivate in cheaper growth media without costly equipment, are safer to handle in BSL1 facilities and are Generally Regarded As Safe (GRAS) organisms (Breuer & Harms, 2006; Ebert et al., 2017; Papp et al., 2021;

Table 2. Summary of antagonistic yeast species/strains, their target toxigenic fungi, bioactive volatile molecule(s) and experimental application.

Antagonistic yeast	Target fungi	Main biomolecules	Main effects	Experimental setup	Reference
<i>Hanseniaspora uvarum</i> , <i>H. opuntiae</i>	<i>A. flavus</i> , <i>A. niger</i>	Octanoic acid; 2-phenethyl acetate; furfuryl acetate	Inhibition of fungal mycelial mass, spore germination, repression of aflR, pks genes, non-sporulation of hyphae	<i>In vivo</i> on figs and <i>in vitro</i> on synthetic media	Galván et al. (2022)
<i>Candida pyralidae</i> , <i>Pichia kluyveri</i>	<i>P. expansum</i>	*VNA	Inhibition of mycelial growth	<i>In vivo</i> on apple	Gomomo et al. (2022)
<i>Cyberlindnera jadinii</i>	<i>A. parasiticus</i> , <i>A. niger</i> , <i>P. verrucosum</i> .	VNA	Fungal growth inhibition	<i>In vitro</i> on synthetic media	Alkuwari et al. (2022)
<i>Saccharomyces cerevisiae</i> , <i>Candida intermedia</i> , <i>Lachancea thermotolerans</i>	<i>A. flavus</i>	VNA	Fungal growth and AFs synthesis inhibition	<i>In vitro</i> on synthetic media	Ul Hassan et al. (2021)
<i>Kluyveromyces marxianus</i>	<i>P. verrucosum</i> , <i>P. italicum</i> , <i>P. expansum</i> , <i>P. digitatum</i> , <i>P. camemberti</i> , <i>F. verticillioides</i> , <i>F. oxysporum</i> , <i>F. solani</i> , <i>F. graminearum</i> , <i>F. subglutinans</i> , <i>F. proliferatum</i> , <i>F. culmorum</i> , <i>A. westerdijkiae</i> , <i>A. carbonarius</i> , <i>A. ochraceus</i> , <i>A. parasiticus</i> , <i>A. carbonarius</i> , <i>A. niger</i>	Tetracosane; hexatriacontane; docosane; heptacosane; eicosane; nonadecane	Mycelial growth inhibition, extension in shelf life of tomatoes and grapes	<i>In vitro</i> on synthetic media and <i>in vivo</i> protection of tomatoes pathogenic <i>F. oxysporum</i>	Alasmar et al. (2021)
<i>Debaryomyces hansenii</i>	<i>F. avenaceum</i> , <i>P. roqueforti</i>	2-pentanone; acetic acid; acetone; 2-phenylethanol; 3-methylbutanoic acid	Inhibition of fungal mycelium and spore germination	<i>In vitro</i> on synthetic media	Huang et al. (2021)
<i>Hanseniaspora uvarum</i>	<i>A. parasiticus</i> , <i>A. westerdijkiae</i> , <i>A. steynii</i> , <i>A. carbonarius</i> , <i>A. flavus</i>	VNA	Inhibition of fungal growth and detoxification of AFs and OTA	<i>In vitro</i> on synthetic media	Gómez-Albarrán et al. (2021)
<i>H. uvarum</i> , <i>H. opuntiae</i>	<i>A. flavus</i>	2-methylbutanoic acid; acetic acid; isobutyric acid	Fungal growth and AFs synthesis inhibition, suppression of aflR gene expression	<i>In vitro</i> on synthetic media	Tejero et al. (2021)
<i>Aureobasidium pullulans</i> , <i>Meyerozyma guilliermondii</i>	<i>P. expansum</i> , <i>P. digitatum</i>	VNA	Inhibition of fungal mycelial growth and spores germination	<i>In vitro</i> on synthetic media	Agirman and Erten (2020)
<i>Meyerozyma guilliermondii</i> / <i>Meyerozyma caribbica</i> , <i>Pichia occidentalis</i> , <i>Pichia kudriavzevii</i>	<i>P. chrysogenum</i> , <i>P. expansum</i> , <i>A. flavus</i> , <i>F. poae</i>	Ethyl esters; phenylethyl alcohol; acetate ester	Reduction in mycelial growth	<i>In vitro</i> on synthetic media	Choińska et al. (2020)

(Continued)

Table 2. Continued.

Antagonistic yeast	Target fungi	Main biomolecules	Main effects	Experimental setup	Reference
<i>Candida nivariensis</i>	<i>A. flavus</i>	1-pentanol	Inhibition of fungal growth and spores germination, reduction in AFs synthesis	<i>In vitro</i> on synthetic media	Jaibangyang et al. (2020)
<i>Candida intermedia</i>	<i>A. carbonarius</i>	2-phenylethanol	Inhibition of fungal growth and mycotoxins synthesis, reduction in protein synthesis, mitochondrial metabolism, detoxification mechanism	<i>In vitro</i> on synthetic media	Tilocca et al. (2019)
<i>Streptomyces alboflavus</i>	<i>A. ochraceus</i>	Dimethyl trisulphide; denzenamine	Inhibition of spore germination and mycelial growth, fungal morphological alteration, membrane disruption, reduced sporulation, inhibition	<i>In vitro</i> on synthetic media	Yang et al. (2018)
<i>Cyberlindnera jadinii</i>	<i>A. carbonarius</i> , <i>A. ochraceus</i>	2-phenylethanol	Inhibition of mycelial growth and mycotoxins synthesis, downregulation of pks synthase, peptide synthase, <i>laeA</i> and <i>veA</i> genes	<i>In vivo</i> on grapes berries and <i>in vitro</i> on synthetic media	Farbo et al. (2018)
<i>Saccharomyces cerevisiae</i> , <i>Metschnikowia pulcherrima</i> , <i>Wickerhamomyces anomalus</i>	<i>A. carbonarius</i> , <i>P. digitatum</i>	Ethyl acetate	Inhibition of fungal growth	<i>In vitro</i> on synthetic media and <i>in vivo</i> on strawberries	Oro et al. (2018)
<i>Lachancea thermotolerans</i>	<i>A. parasiticus</i> , <i>P. verrucosum</i> , <i>F. graminearum</i>	VNA	Inhibition of fungal mycelium, sporulation and mycotoxins synthesis	<i>In vitro</i> on synthetic media and <i>in vivo</i> on cherry tomatoes	Zeidan et al. (2018)
<i>Candida sake</i>	<i>P. expansum</i> , <i>Alternaria alternata</i> ,	VNA	Mycelial growth inhibition	<i>In vitro</i> on synthetic media and <i>in vivo</i> on apple	Arrarte et al. (2017)
<i>H. opuntiae</i> , <i>Metschnikowia pulcherrima</i>	<i>P. expansum</i>	VNA	Delayed fungal growth	<i>In vivo</i> on cherries	de Paiva et al. (2017)
<i>Debaryomyces hansenii</i>	<i>Aspergillus sp.</i> , <i>Fusarium spp.</i>	VNA	Reduction in fungal growth 97.2-98.3%, delayed fungal growth, reduction in FUM synthesis by 58.9%	<i>In vivo</i> on maize grains and <i>in vitro</i> on synthetic media	Medina-Córdova et al. (2016)

(Continued)

Table 2. Continued.

Antagonistic yeast	Target fungi	Main biomolecules	Main effects	Experimental setup	Reference
<i>Saccharomyces</i> and non- <i>Saccharomyces</i>	<i>A. caelatus</i> , <i>A. versicolor</i> , <i>A. terreus</i> , <i>A. carbonarius</i>	VNA	Inhibition in mycelial growth, germ tube elongation and spore germination	<i>In vitro</i> on synthetic media	Nally et al. (2015)
<i>Pichia anomala</i>	<i>A. flavus</i>	2-phenylethanol	Fungal growth inhibition and suppression of AFs synthesis genes	<i>In vitro</i> on synthetic media	Chang et al. (2015)
<i>Debaryomyces hansenii</i>	<i>P. verrucosum</i>	2-methyl-1-propanol 2-methyl – 1-butanol	Growth reduction of fungi	<i>In vivo</i> exposure on fermented sausages	Núñez et al. (2015)
<i>Aureobasidium pullulans</i>	<i>P. expansum</i> , <i>P. digitatum</i>	2-phenylethanol	Inhibition of spore germination, spread and mycotoxins synthesis	<i>In vitro</i> on synthetic media and <i>in vivo</i> on apples and oranges	Di Francesco et al. (2015)
<i>Pichia anomala</i>	<i>A. flavus</i>	2-phenylethanol	Inhibition of spore germination and expression of AFs synthesis genes	<i>In vitro</i> on synthetic media	Hua et al. (2014)
<i>Lachancea thermotolerans</i> , <i>Candida friedrichii</i> , <i>Cyberlindnera jadinii</i> , <i>Candida intermedia</i>	<i>A. carbonarius</i>	VNA	Inhibition of fungal vegetative growth on synthetic media and grapes berries	<i>In vitro</i> on synthetic media and <i>in vivo</i> on grape berries	Fiori et al. (2014)
<i>Pichia pastoris</i>	<i>P. italicum</i>	2-phenylethanol	Inhibition of conidial germination and growth of fungi, mitochondrial membrane abnormalities	<i>In vitro</i> on synthetic media	Liu et al. (2014)
<i>Cryptococcus victoriae</i> , <i>P. membranifaciens</i>	<i>P. expansum</i>	VNA	Inhibition of mycelial spread and spore germination	<i>In vitro</i> on synthetic media and <i>in situ</i> on pear	Lutz et al. (2013)
<i>Aureobasidium pullulans</i>	<i>P. expansum</i>	VNA	Mycelial growth inhibition	<i>In vitro</i> on synthetic media and <i>in vivo</i> on infected apples	Mari et al. (2012)
<i>Candida albicans</i>	<i>A. brasiliensis</i> (formerly <i>A. niger</i>)	Phenethyl alcohol; isoamyl alcohol; isoamyl acetate	Inhibition of spore germination	<i>In vitro</i> on synthetic media	Ando et al. (2012)
<i>Hanseniaspora uvarum</i>	<i>A. carbonarius</i>	2-phenylethyl acetate	Inhibition of mycelial growth and mycotoxins synthesis	<i>In vitro</i> on synthetic media	Masoud and Kalsoft (2006)
<i>Hanseniaspora uvarum</i> , <i>P. anomala</i> , <i>P. kluyveri</i>	<i>A. ochraceus</i>	2-phenyl ethyl acetate; isoamyl alcohol; isobutyl acetate; ethyl propionate; ethyl acetate	Suppression of mycelial growth and OTA production	<i>In vitro</i> on synthetic media	Masoud et al. (2005)

This table is a summary of relevant findings on yeast VOCs-mediated inhibition of mycotoxigenic fungi presented in descending chronological order. *VNA = Volatile Not Analysed.

Spadaro & Droby, 2016). Table 2 summarises recent studies (after the year 2000) on the yeast volatiles, their spectrum of antifungal activities, and mode of action to minimise the impact of toxigenic fungi and mycotoxins in food.

4.1.1. *Hanseniaspora* spp.

Two species of genus *Hanseniaspora*, namely *H. uvarum* and *H. opuntiae* are known for postharvest protection of food by releasing VOCs effective against toxigenic *Aspergillus* (Apaliya et al., 2018; Galván et al., 2022; Gómez-Albarrán et al., 2021; Masoud & Kaltoft, 2006; Masoud et al., 2005; Tejero et al., 2021), *Penicillium* (de Paiva et al., 2017) and *Fusarium* (Hameed et al., 2019). The antagonistic volatiles of *Hanseniaspora* spp., are mainly acids including acetic acid, isobutyric acid, 2-methylbutanoic acid, octanoic acid (Galván et al., 2022; Tejero et al., 2021) or 2-phenethyl acetate, furfuryl acetate (Galván et al., 2022; Masoud et al., 2005), isoamyl alcohol, ethyl propionate, isobutyl acetate and ethyl acetate (Masoud & Kaltoft, 2006).

4.1.2. *Debaryomyces* spp.

A *Debaryomyces hansenii* isolate from marine environment showed several biotechnological benefits (Breuer & Harms, 2006; Medina-Córdova et al., 2018), including the reduction of toxigenic fungal growth and mycotoxins in different food matrices (Huang et al., 2021; Medina-Córdova et al., 2016; Núñez et al., 2015; Gil-Serna et al., 2011; Gil-Serna et al., 2009). This yeast is considered as safe (BIOHAZ, 2012) by European Food Safety Authority (EFSA) and interacts with the toxigenic fungi using different mechanisms of action including downregulation of the expression of mycotoxin synthesis genes (Gil-Serna et al., 2011) and synthesis of antifungal volatiles (Núñez et al., 2015). In a study by Medina-Córdova et al. (2016), volatiles of *D. hansenii* antagonise the growth of *Aspergillus* sp., *F. subglutinans* and *F. proliferatum* at 97–98%. In *in vivo* testing, the volatiles of this yeast were able to entirely suppress growth on maize grains, showing a partial inhibition of these fungi and disease appearance. Additionally, there was 60% reduction in FUMs synthesis by *F. subglutinans* upon exposure to yeast VOCs. In another study, *D. hansenii* volatiles suppressed toxigenic *Penicillium* spp. at >60% in co-culture experiments (Núñez et al., 2015). The main antifungal volatile molecules released by *D. hansenii* include 2-methyl-butanol, 2-methyl-propanol, 3-methyl-butanol, (Núñez et al., 2015), 2-pentanone, acetic acid, acetone, 2-phenylethanol and 3-methylbutanoic acid, (Huang et al., 2021). In the Table 2, antifungal activities of *Debaryomyces* spp., are summarised.

4.1.3. *Saccharomyces* spp.

Saccharomyces spp. play an important role in food safety particularly in controlling fungi and mycotoxins in food products (Papp et al., 2021). *Saccharomyces cerevisiae* volatiles exert inhibitory effects on growth and on mycotoxin biosynthesis (Nally et al., 2015; Oro et al., 2018; Ul Hassan et al., 2021). The VOCs-mediated antagonistic activity of *Saccharomyces cerevisiae* is mainly due to ethyl acetate (Oro et al., 2018), as reported against *A. flavus* (Ul Hassan et al., 2021), *A. caelatus*, *A. versicolor*, *A. terreus*, *A. carbonarius* (Nally et al., 2015) and *Penicillium* spp. (Oro et al., 2018).

4.1.4. *Candida* spp.

Candida spp. demonstrated significant inhibition of fungi including *A. flavus* (Jaibangyang et al., 2020; Ul Hassan et al., 2021), *A. carbonarius* (Farbo et al., 2018; Tilocca et al., 2019; Tilocca et al., 2020), *A. ochraceus* (Farbo et al., 2018), *A. niger* (Ando et al., 2012), *Penicillium* (Arrarte et al., 2017; Gomomo et al., 2022) and *Alternaria* spp., (Arrarte et al., 2017) as well as their mycotoxin synthesis. The volatiles of *Candida pyralidae* (Gomomo et al., 2022), *Candida intermedia* (Tilocca et al., 2019; Ul Hassan et al., 2021), *Candida nivariensis* (Jaibangyang et al., 2020), *Candida sake* (Arrarte et al., 2017), *Candida friedrichii* (Farbo et al., 2018; Fiori et al., 2014) and *Candida maltosa* (Ando et al., 2012) inhibited toxigenic fungi. The bioactive volatile molecules produced by different *Candida* species include isoamyl alcohol, phenethyl alcohol, isoamyl acetate (Ando et al., 2012), 2-phenylethanol (Farbo et al., 2018) and 1-pentanol (Jaibangyang et al., 2020). *Candida* volatiles inhibit fungal sporulation, mycelial growth and mycotoxin synthesis (Farbo et al., 2018; Jaibangyang et al., 2020; Ul Hassan et al., 2021) by direct cytolytic effects (Fiori et al., 2014), downregulating the expression of relevant pathway genes (Farbo et al., 2018) or mitochondrial metabolic activity (Tilocca et al., 2019).

4.1.5. *Pichia/Wickerhamomyces* spp.

The biocontrol efficacy of *Pichia* spp. by releasing inhibitory volatiles play an important role against pre- and post-harvest spoilage fungi (Gomomo et al., 2022; Masoud et al., 2005). In this regard, *Pichia kluyveri* (Gomomo et al., 2022; Masoud et al., 2005), *Pichia kudriavzevii*, *Pichia occidentalis* (Choińska et al., 2020), *Pichia pastoris* (Liu et al., 2014), *P. membranifaciens* (Lutz et al., 2013), *P. anomala* (Chang et al., 2015; Contarino et al., 2019; Hua et al., 2014; Masoud et al., 2005; Oro et al., 2018) are well known for their inhibitory role. In a study on *P. anomala* strain WRL-076, Hua et al. (2014) reported production of antifungal volatile 2-phenylethanol which resulted in depressed spore germination, suppression of vegetative growth and of AFs synthesis in *A. flavus*. The inhibition of AFs synthesis was associated with the 10,000-fold downregulation of AFs biosynthetic genes, as well as altered chromatin modifying genes.

4.1.6. *Lachancea* and *Cyberlindnera* spp.

There are a couple of studies describing the role of volatiles emitted by *Lachancea* and *Cyberlindnera* spp., in the biocontrol of *Aspergillus*, *Penicillium* and a few *Fusarium* fungi. The first ever work was performed by Fiori et al. (2014) on *Lachancea thermotolerans* 751 and *Cyberlindnera jadinii* 273 against OTA-producer strains of *A. carbonarius*. The yeast volatiles significantly inhibited growth on detached grape berries and on synthetic media. Later on, toxigenic species of *Aspergillus* (Alkuwari et al., 2022; Farbo et al., 2018; Tilocca et al., 2019; Ul Hassan et al., 2021; Zeidan et al., 2018), *Penicillium* and *Fusarium* (Alkuwari et al., 2022; Zeidan et al., 2018) were exposed to the same yeast volatiles to investigate the mechanism of antagonism (Table 2). Zeidan et al. (2018) exposed mycotoxin-producing strains of *F. graminearum*, *P. verrucosum* and *A. parasiticus* to the volatiles emitted by *L. thermotolerans* and observed up to 48% reduced mycelium growth and much higher (96%) depression in their mycotoxin biosynthesis. In another study, Farbo et al. (2018) reported the precise nature of bioactive compound in the volatile blend of *L. thermotolerans* and *C. jadinii* as 2-phenylethanol (2-PE); this compound is

involved in the inhibition of vegetative growth, sporulation and downregulation of the key genes (*pks*, *laeA*, *veA* and others) involved in growth and mycotoxin synthesis. Taking forward the findings of Farbo et al. (2018), a step ahead proteomic investigation was carried out by Tilocca et al. (2019) to explore the metabolic profile of *A. carbonarius* exposed to 2-PE. An array of metabolic alterations was observed in the VOCs – exposed *A. carbonarius*, including the reduction in protein synthesis, inhibition of fungal growth and defence system. Among the biocontrol benefits, more recently it was demonstrated that fermentation processes involving *L. thermotolerans* improve the sensory profiles of wines (Hranilovic et al., 2022; 2021).

4.1.7. *Metschnikowia* spp.

There is plenty of information about the antifungal efficacy of *Metschnikowia* spp., cell-free extracts against phytopathogenic and mycotoxin-producing fungi (Settier-Ramírez et al., 2021), however only one species, i.e. *Metschnikowia pulcherrima* is known for its antifungal volatiles (de Paiva et al., 2017; Oro et al., 2018). In *in vitro* assays, VOCs released by *M. pulcherrima*, the major component being ethyl acetate, were able to suppress the growth of *A. alternata* and *A. carbonarius*. Likewise, ethyl acetate fumigation completely protected apple fruit from spoilage and fungal infection. In another study, *M. pulcherrima* L672 volatiles significantly delayed the infection by *P. expansum* (a patulin producer) on sweet cherries (de Paiva et al., 2017).

4.1.8. *Cryptococcus* spp.

Cryptococcus victoriae and *Cryptococcus albidus* are two important species of the genus *Cryptococcus* known for their antifungal volatiles. Apart from fungal spore germination inhibition, Lutz et al. (2013) demonstrated 100 and 62% inhibition of *P. expansum* growth upon exposure to *C. albidus* and *C. victoriae* volatiles, respectively. The precise nature of antifungal volatiles was not studied.

Among yeast species being registered or commercialised as plant protecting agents against different pathogens, *S. cerevisiae*, *M. fructicola*, *A. pullulans*, *C. albidus* and *C. oleophila* are preminent in the list of approved yeasts (Freimoser et al., 2019). However, biocontrol products based solely on the antifungal volatiles and their contactless application for the preservation of food is still awaited.

4.2. Antagonistic mechanism of yeast volatiles

Pre-harvest application of yeast's VOC for the control of toxigenic fungi in agricultural settings has received marginal attention. This is because of low molecular weight of VOCs, leading to less chances to concentrate enough in the open environment to interact with fungal communities (Freimoser et al., 2019; Papp et al., 2021; Tilocca et al., 2020). However, their use in post-harvest storage is applicable, where there are enough chances particularly in a closed environment to interact with their target fungal strains and inhibit their growth and/or mycotoxin synthesis (Tilocca et al., 2020). There are several mechanisms by which yeast VOCs antagonise the growth and mycotoxins accumulation activities of toxigenic fungi. Among these, down regulation of mycotoxins pathways genes in VOCs exposed fungi is widely accepted (Farbo et al., 2018). However, this is not a general mechanism of antagonism involved in all type of fungal communities in

any situation. Farbo et al. (2018), in their same study noted no effect in gene expression of *A. ochraceus*, whereas *A. carbonarius* was strongly inhibited. Exposure of *A. flavus* to 2-phenylethanol (a major bioactive molecule in yeast volatiles) resulted in suppressed AFs synthesis by inhibition of expression of all pathway genes (Chang et al., 2015), while at high 2-phenylethanol exposure levels fungal protein and amino acid synthesis was strongly altered (Liu et al., 2014). A proteomic investigation on a toxigenic *A. carbonarius* by Tilocca et al. (2019) revealed that yeast VOCs significantly target protein synthesis, detoxification of toxic metabolites, mitochondrial metabolism and their proliferative activity.

Another direct interaction of the yeast VOCs is the permeability changes in the target fungi membranes, thereby leading to abnormal diffusion of molecules and ions and eventually the death of the affected cells (Ando et al., 2012; Di Francesco et al., 2015; Simoncini et al., 2015). This further suggested that less volatile molecules, staying for a longer time on the membrane of fungi, might have stronger inhibitory potential on fungal cells. Pennerman et al. (2019) studied the effect of a volatile compound (1-octen-3-ol) on two non-toxic strains of *P. expansum* and found that exposed fungi were able to synthesise more patulin as compared to unexposed ones. He correlated this increased production with the upregulation of glucose oxidase.

5. Filamentous fungi

5.1. Role of fungal volatiles in the biocontrol of mycotoxin-producing fungi

The role of filamentous fungal volatiles in the biocontrol of mycotoxin-producing fungi has least been studied and largely limited to the post-harvest decay prevention of fruits and vegetables (Mari et al., 2016). VOCs of a few filamentous species from genus *Aspergillus*, *Penicillium*, *Ceratocystis*, *Muscodor*, *Galactomyces*, *Trichoderma* have been tested to be potentially inhibitory towards toxigenic fungi. However, *Muscodor albus* and non-aflatoxigenic *A. flavus* have been best characterised so far for their biocontrol volatiles (Mari et al., 2016; Moore, 2022). Below is a brief account of both of these genera and details are reported in Table 3.

5.1.1. *Muscodor spp.*

Muscodor albus was discovered in late 1990s as an excellent bio-preservation candidate for the post-harvest fumigation of fruits and vegetables. The bioactive molecules in the volatiles of *M. albus* were identified by Ezra and Strobel (2003) as propanoic acid and 2-methyl-ester. These volatiles showed strong antifungal activity against toxigenic and phytopathogenic *F. solani*, *A. ochraceus*, and *P. expansum*. In the following year, Mercier and Jiménez (2004) reported isobutyric acid and 2-methyl-1-butanol as volatiles of *M. albus* being effective against *P. expansum*. The exploration of bio-preservative potential of *M. albus* continued on, and Corcuff et al. (2011) reported that fumigation of potatoes with *M. albus* volatiles can protect tubers from important pathogens including *F. sambucinum*. In a more extensive work, Braun et al. (2012) found a strong antifungal activity of *M. albus* volatiles on a range of toxigenic fungi including *A. flavus*, *A. carbonarius*, *A. ochraceus*, *A. niger*, *F. graminearum* and *P. verrucosum* (Table 3). In their study, 2-methyl-butanol and isobutyric acid were reported as major antifungal

biomolecules. Meanwhile, other *M. albus* strains were isolated, but their activity against fungal pathogens was not comparable, nor the nature of their produced volatile molecules showed any similarity with good biocontrol strains. However, in spite of its huge biofumigation potential, *M. albus* was not able to obtain registration as a commercial bio-preservative product by the US Environment Protection Agency, because of toxicity of one of its metabolites (Mari et al., 2016).

5.1.2. *Aspergillus spp.*

Among all mycotoxins, control of AFs and their producing fungi remained a major focus of the scientific communities for decades (Ji et al., 2016; Shabeer et al., 2022). This is mainly because of the range of their toxic effects, and established regulation by the food regulatory authorities in most of the developed nations as well as in several developing countries (van Egmond et al., 2007). Thus, in many of the published reports, the biocontrol efforts are directed mainly towards *A. parasiticus* and *A. flavus*, the two major producers of AFs in food (Moore, 2022). In these efforts, the use of non-aflatoxigenic fungal strains (*A. flavus*) for the control of aflatoxigenic strains showed the most prominent role (Moore et al., 2021; Moore, 2022). It is advisable to employ the non-toxicogenic intra-specific strains against the toxigenic strains to achieve the optimal benefits because these strains normally share the same ecological niche. Non-aflatoxigenic strains are presumably more aggressive colonisers than the toxigenic ones, as it's generally assumed that mycotoxins synthesis in fungi is inversely associated with mycelial growth (Ehrlich et al., 2011), and for a good biocontrol agent good colonising property is a prerequisite, so that it can out-compete toxigenic strains (Moore, 2022). According to Horn and Dorner (2009) non-toxicogenic fungal strains retain the ability to degrade the products of toxigenic strains or convert and then potentially utilise them for their metabolic processes (Maxwell et al., 2021). Application of high dose and annual recommended use of non-aflatoxigenic fungal strains not only protect the subjected crops in pre-harvest, but their biocontrol effects diffuse to the neighbouring agricultural plots (Weaver & Abbas, 2019) as well as to the post-harvest storage of grains (Alberts et al., 2017; Dorner & Cole, 2002).

There is overwhelming evidence on the application of intraspecies fungal volatile in the control of counterpart toxigenic species (Ehrlich, 2014; Singh & Lee, 2018) that can display a significant activity in the inhibition of toxigenic fungi (Table 3). Application of fungal volatiles in biocontrol of mycotoxins and toxigenic fungi has been most successful among all other microbial volatiles.

The story of potentially safe biocontrol of *A. flavus* and AFs started with in discovery of a non-aflatoxigenic strain of *A. flavus* (AF36) back in 1980s, which was later on (Ehrlich & Cotty, 2004) found to be having a mutation in a key cluster gene *pksA* (*aflC*). Meantime, another aggressive coloniser, the non-aflatoxigenic *A. flavus* NRRL21882, was discovered and used in a biocontrol formulation (Alfa-Guard®) for application on the peanuts field (Dorner & Lamb, 2006). The successful field trials of AF36 and NRRL21882 led to their US environmental protection agency (EPA)-approval for pre-harvest use only. Nowadays, two commercial formulations AF36, namely Prevail® (used in western part of USA) and Alfa-Gurad® (licenced by Syngenta) are being used Eastern US and other countries like Turkey (Lavkor et al., 2019) and Brazil (Reis et al., 2020) for the effective control of *A. flavus* and AFs. Interestingly, Alfa-Guard® apart

Table 3. Biocontrol activities of filamentous fungal species/strains against mycotoxigenic fungi, major bioactive volatile molecule(s) and experimental application.

Antagonistic filamentous fungi	Target toxigenic fungi	Main biomolecules	Main effects	Experimental setup	Reference
<i>Trichoderma koningiopsis</i>	<i>F. oxysporum</i>	Twenty-four compounds were detected, dominated by alkenes; alkanes and ester	Inhibition of <i>F. oxysporum</i> mycelium by 43.68%, delayed conidial germination and germ tube elongations	<i>In vitro</i> on synthetic media	You et al. (2022)
<i>A. flavus volatiles</i>	Three <i>A. flavus</i> strains were non-aflatoxigenic and non-CPA – producing, a toxigenic, and toxigenic producing AFs and CPA, respectively. LA4 (SRRC 594) produces B + G AFs and CPA species	Decane; 3-octanone; 2,3-dihydrofuran	Individual volatile molecules showed minimal effect on mycelial growth. Combination of all three molecules inhibited fungal growth and AFs and CPA synthesis	<i>In vitro</i> on synthetic media	Moore et al. (2022)
<i>Trichoderma atroviride</i>	<i>F. oxysporum</i>	6-pentyl-2H-pyran-2-one	Inhibition of fungal mycelium	<i>In vitro</i> on synthetic media and <i>in vivo</i> on tomato seedling	Rao et al. (2022)
<i>A. flavus</i>	Two <i>A. flavus</i> LA2 and LA3, one <i>A. parasiticus</i> LA4	Trans-2-methyl-2-butenal; 3-octanone; 2,3 dihydrofuran and decane	Inhibition of AFs and CPA synthesis	<i>In vitro</i> on synthetic media	Moore et al. (2021)
Non-aflatoxigenic <i>A. flavus</i> NAFFHB396 and 707	<i>A. flavus</i>	*VNA	Inhibition of AFs synthesis up to 99.33%	<i>In vivo</i> on peanuts	Yan et al. (2021)
<i>Galactomyces geotrichum</i> , <i>G. candidum</i> , <i>G. candidum</i>	<i>F. proliferatum</i> <i>Fusarium</i> sp.	VNA	Suppression of mycelial growth and conidial germination	<i>In vitro</i> on synthetic media and <i>in vivo</i> on tomatoes	Cai et al. (2021)
<i>Sarocladium brachiariae</i>	<i>F. oxysporum</i>	2-methoxy-4-vinylphenol; 3,4-dimethoxystyrol; caryophyllene	Induction of plasma membrane aging process, expression of chitin synthases genes leading to cell wall damage and accumulation of ROS	<i>In vitro</i> on synthetic media	Yang et al. (2021)
<i>Hypoxyton anthochroum</i>	<i>F. oxysporum</i>	Terpinolene; monoterpenes eucalyptol; 2-methyl-1-butanol; ocimene; phenylethyl alcohol	Inhibition of fungal growth, alteration in hyphal morphology, cell membrane permeability, and inhibition of hyphal cell respiration	<i>In vivo</i> on cherry tomato fruit and <i>in vitro</i> on synthetic media	Medina-Romero et al. (2017)
<i>Ceratocystis fimbriata</i>	<i>F. verticillioides</i> , <i>F. oxysporum</i> , <i>P. italicum</i>	VNA	Inhibition of conidial production, mycelial growth, and germ tube elongation	<i>In vitro</i> on synthetic media	Li et al. (2015)

(Continued)

Table 3. Continued.

Antagonistic filamentous fungi	Target toxigenic fungi	Main biomolecules	Main effects	Experimental setup	Reference
<i>P. expansum</i> strain	Six <i>P. expansum</i> strains	Phenethyl alcohol and geosmin	Inhibition of fungal growth	<i>In vitro</i> on synthetic media	Rouissi et al. (2013)
<i>Nodulisporium</i> spp.	<i>P. digitatum</i> , <i>P. expansum</i> , <i>F. oxysporum</i>	Eucalyptol	Inhibition of mycelial growth	<i>In vitro</i> on synthetic media	Suwannarach et al. (2013)
<i>Muscodora albus</i>	<i>A. ochraceus</i> , <i>A. flavus</i> , <i>A. carbonarius</i> , <i>A. niger</i> , <i>F. graminearum</i> , <i>F. culmorum</i> , <i>P. verrucosum</i> ,	2-methyl-1-butanol; isobutyric acid	Suppression and/or killing of conidial germination	<i>In vitro</i> on synthetic media under controlled environment	Braun et al. (2012)
<i>Muscodora albus</i>	<i>F. sambucinum</i>	Ethanol; 2 and 3-methyl-1-butanol; isobutyric acid	Inhibition of fungal infections	<i>In vivo</i> on potatoes	Corcuff et al. (2011)
<i>P. decumbens</i>	<i>A. sydowii</i>	(+)-Thujopsene	Fungal growth inhibition	<i>In vitro</i> on synthetic media	Polizzi et al. (2011)
<i>Oxyporus latemarginatus</i>	<i>Alternaria alternata</i> , <i>F. oxysporum</i>	5-pentyl-2-furaldehyde	Inhibition of fungal growth	<i>In vitro</i> on synthetic media	Lee et al. (2009)
<i>Muscodora albus</i>	<i>P. expansum</i>	2-methyl-1-butanol; isobutyric acid	Inhibition of fungal mycelia and bio-preservation of apples	<i>In vivo</i> study on infected apples	Mercier and Jiménez (2004)
<i>Muscodora albus</i>	<i>F. solani</i> , <i>A. ochraceus</i>	Propanoic acid; 2-methyl-ester	Inhibition of mycelial growth	<i>In vitro</i> on synthetic media	Ezra and Strobel (2003)

Note: This table is a summary of findings on filamentous fungal volatiles mediated inhibition of toxigenic fungi and mycotoxins presented in the order of most recent to older. *VNA = Volatile Not Analysed.

from AFs control also protects maize crops from *F. verticillioides* and fumonisin contamination (Reis et al., 2020). The success story of biocontrol strains kept on going with the discovery of K49 (Abbas et al., 2006) in U.S.A. and A2085 (active ingredient of AF-X1™ in Italy), MyToolBox Af01 used in maize crops in Serbia. All these strains were either having single gene mutation (K49, AF36), absence of complete AFs genes cluster (A2089, NRRL21882) or missing couple of cluster genes (MyToolBox Af01). The technology of *A. flavus* biocontrol with the use of non-aflatoxigenic strains is still evolving and a composite formulation of four non-aflatoxigenic strains in each Afla-Safe® (being used in Africa) (Bandyopadhyay et al., 2016), and FourSure™ in U.S.A. (Moral et al., 2020) are being practiced with high success. However, the mechanism of action of these non-aflatoxigenic *A. flavus* strains is still not completely understood. Competitive exclusion and competition for nutrients and space are certainly major mechanisms, but these are not sufficient to fully explain the efficacy of biocontrol strains. In recent years, the role of antagonistic volatiles is being explored in their biocontrol mechanism (Moore et al., 2021, 2022). Based on the volatile profiles of non-aflatoxigenic *A. flavus* (Lucca et al., 2010) in an *in vitro* environment, Moore et al. (2021) applied 3-octanone, trans-2-methyl-2-butenal, 2,3-dihydrofuran and decane against toxigenic *A. flavus* strains. All the volatile molecules significantly inhibited AFs and later two molecules (2,3-dihydrofuran and decane) along with AFs synthesis inhibition, also suppress cyclopiazonic acid CPA production (Moore et al., 2021). In another study, the same team reported significant reduction in AFs and CPA synthesis in toxigenic *A. flavus* when exposed to three VOCs of non-toxigenic *A. flavus* (i.e. 2,3-dihydrofuran, 3-octanone and decane), while there was a minimal effect on fungal growth of toxigenic *A. flavus* strain. To further investigate the antagonistic mechanism of action of non-aflatoxigenic strains, Moore et al. (2019) hypothesised the possible role of extrolites produced by non-aflatoxigenic *A. flavus* on the inhibition and AFs synthesis of toxigenic *A. flavus*. The precise chemical nature of extrolites and their mode of action remain unexplored.

It has been more than a decade (Bandyopadhyay et al., 2019) on the successful commercial application of non-aflatoxigenic fungi for the control of toxigenic *A. flavus* and mycotoxins. However, Moore (2022) presents certain important considerations that must be met to supplement continuous application as well as expand the knowledge to the other toxigenic fungi and their toxins. These considerations are digging information about the: (a) persistence of atoxigenic fungi under climatic stresses and particularly their vulnerability to climate change (if any); (b) genetic stability of non-aflatoxigenic strains, as fungi are existing and evolving since thousands of years, sexual interaction might result in production of other mycotoxins; (c) efforts/managerial practices to supplement the effectivity of atoxigenic fungi; and (d) outlining the precise mode of action of atoxigenic strains.

Apart from the application of non-aflatoxigenic *A. flavus*, atoxigenic strains of other fungi can be tested for their bio-preservation potential. For instance, Wani et al. (2010) found the production of a volatile 2-PE by a strain of *A. niger*: this molecule is similar to the one produced by yeasts for the inhibition of toxigenic *A. flavus*, *A. carbonarius*, *A. ochraceus* (Chang et al., 2015; Farbo et al., 2018; Tilocca et al., 2019) and can potentially be used as biocontrol means. The exploration of non-toxigenic fungal strains from genus *Aspergillus*, *Penicillium* and *Fusarium* is continuing, with focus on their potential for commercial application such as aggressiveness, genetic stability, environmental

impact and ease and suitability in application. Below is a tabulated summary of such efforts made in the years after 2000.

5.2. Volatilome of filamentous fungi: mode of action against toxigenic fungi

The precise mechanism of action of filamentous fungal volatiles in the control of toxigenic fungi and mycotoxins has not been fully elucidated. However, based on the nature of biocontrol strains and their reported *in vitro* and *in vivo* activities, some hypotheses can be inferred. The volatiles of biocontrol strains have shown genetic effects such as altered expression levels in the key genes involved in the mycotoxins synthesis (Moore et al., 2021) and those involved in cell membrane aging process and expression of chitin synthase (Yang et al., 2021). There are different patterns of genes alteration in the biocontrol strains, spanning from point mutation in a single gene (Ehrlich & Cotty, 2004), missing some pathway genes (Yin et al., 2008), or complete deletion of mycotoxin pathway gene cluster (Chang et al., 2005). Yet, there might be other possibilities, probably at post-transcriptional level, as several non-aflatoxigenic *A. flavus* strains are known to have intact gene clusters (Criseo et al., 2008; Scherm et al., 2005). Moreover, aggressive colonisation of the substrate by non-toxigenic strains suggests that competitive exclusion in terms of ‘fight for space and nutrients’ is also operative in these fungi-fungi interactions (Mauro et al., 2018; Yan et al., 2021).

Filamentous fungi may share with yeast the same antagonistic mechanisms of action because the nature of their biomolecules is not different (Moore et al., 2021; Moore et al., 2022; Rao et al., 2022; Yang et al., 2021). Wani et al. (2010) reported the production of 2-PE (2-phenylethanol) by *A. niger*; whereby 2-PE-producing yeasts are known to affect the cellular metabolic processes and the expression of key mycotoxin synthesis pathway genes in the exposed fungi (Farbo et al., 2018; Tilocca et al., 2019). Another possible mechanism of action involves DNA-methylation as a result of the exposure to the volatile N-methyl-N-nitroso isobutyramide (MNIBA) released by *M. albus* (Alpha et al., 2015; Hutchings et al., 2017; Jimenez et al., 2012). The decomposition of MNIBA results in the production of methyl diazohydroxide and isobutyric acid: the first one is converted to methyl diazonium ion, which interacts with the nucleophilic site on DNA and leads to DNA-methylation. Consistently with this pathway, isobutyric acid (a derivative of MNIBA), has been found in the fungal volatiles of previous studies (Braun et al., 2012; Corcuff et al., 2011; Mercier & Jiménez, 2004). This mechanistic pathway is particularly relevant to the *M. albus* biocontrol activity, as isobutyric acid is not reported in the volatiles of non-aflatoxigenic *A. flavus* strains (Lucca et al., 2010; Moore et al., 2021).

Suppression of fungal spore production and germination (Li et al., 2015), alteration in plasma membrane permeability and hyphal cell respiration (Medina-Romero et al., 2017), accumulation of reactive oxygen species (Yang et al., 2021) are other mechanisms of action of fungal volatiles on toxigenic fungi. It is not unreasonable to hypothesise that non-toxigenic biocontrol strains are working in multidimensional ways to limit the growth and mycotoxins synthesis potential of the toxigenic strains. These approaches might include release of antifungal molecules (volatiles and diffusible), competition for the space and nutrients, lytic enzymes, etc.

6. Application of microbial volatiles in different scenarios for the protection of horticultural crops

There are promising evidences of bacterial, yeast and filamentous fungal strains possessing strong antifungal potentialities to limit the mycotoxins in food (Dopazo et al., 2022; Gallo et al., 2022; Medina-Romero et al., 2017; Moore et al., 2022, 2021; Saleh et al., 2021; Wang et al., 2021; Yang et al., 2021). A handful number of these strains are proven under *in vitro* and *in vivo* environment to retain antagonistic activities in limiting key toxigenic fungal species (Alasmar et al., 2021; Farbo et al., 2018; Galván et al., 2022; Gomomo et al., 2022; Moore, 2022). Fewer of these, however, were successfully tested *in fructo/in planta* (Bandyopadhyay et al., 2019; Gallo et al., 2022; Moore, 2022). Microbial volatile molecules can easily diffuse in the stored food commodities making it possible to ensure maximum protection by reaching every empty space and surface, at least during post-harvest storage and transportation (Lammers et al., 2022; Passone & Etcheverry, 2014). In most of the post-harvest closed environment studies, even smaller volumes were able to produce long-standing protection with an increasing shelf life of the biofumigated commodities (Aunsbjerg et al., 2015). The results obtained with low volumes of volatile molecules also present an economical and environmental advantage compared to their chemical fungicide counterpart.

Another approach could be incorporating VOCs in edible films, which are being used as smart food packaging material (Okcu et al., 2018; Sultan et al., 2021). These films can be used as a routine coating material for hard-textured fruits like avocado, mango and orange. These films may retain the molecules on the fruit for extended duration of time, ensuring protection against microbial spoilage during long-distance transportation and storage. However, this approach wouldn't be viable for highly perishable fruits like strawberry, table grape, peach, as these are much prone to handling damages. In such cases, these fruits can be preserved by treating sterile gauze with antimicrobial VOCs and distributing them within the fruit packages this approach has been proven very effective for 56 days at 1°C (Valero et al., 2006; Valverde et al., 2005). Incorporating VOCs on specialised slow release material such as polyethylene terephthalate (PET), and packing in sachets or pouches to be inserted in the food storage boxes can effectively reduce the food spoilage during the transport and storage chain (Almenar et al., 2007).

The first successful biocontrol effort emerged with the commercialisation of Aflaguard® to limit the spread of toxigenic *A. flavus* and AFs in the peanut fields in U.S.A. (Dorner & Lamb, 2006; Moore et al., 2021). Alfagurad®, a formulation of non-toxigenic *A. flavus* coated on roasted sorghum seeds, is applied during the sowing of crops (Moore, 2022; Moore et al., 2022). Atoxigenic *A. flavus* mainly produce *trans*-2-methyl-2-butenal, 2,3-dihydrofuran and decane to control the growth of toxigenic *A. flavus* and/or AFs synthesis (Moore et al., 2021). An observation based on 10-years application of this product showed 70–90% reduction in AFB1 in the treated commodities (Bandyopadhyay et al., 2019; Moore, 2022; Moore et al., 2019). Despite this milestone success, antifungal products based on yeast and bacterial volatilome have not been achieved yet. In any case, before adopting such approaches it is absolutely necessary to correlate laboratory findings with commercial context in terms of physicochemical appearance, sensorial evaluation and quality standards of the product.

7. Concerns and limitations associated with the application of VOC

Application of microbial volatiles for the control of mycotoxigenic fungi and mycotoxins in food shows a significant potential to replace the synthetic fungicides, thereby avoiding associated environmental and health effects. Additionally, it adds significant economic benefits to the food and agriculture industry by controlling pre- and post-harvest losses at low cost. However, with increasing efforts in developing and application of VOC in commercial settings, some concerns and limitations were outlined by the scientific community as well as by consumers, namely: (a) chances of interaction of VOCs with food molecules, leading to the production of toxic products that might raise the regulatory issue; (b) VOCs might behave differentially in different food material, possibly inhibiting their diffusion and effectivity; (c) range, effectiveness, spectrum and safety of the VOC, as there is a common concern about microbial volatiles being not as effective as synthetic fungicides, particularly in the open environment and against a diversified range of spoilage microbes. In these scenarios, it is imperative to assess the effect of microbial volatiles in a real food protection system: the appropriate concentration of VOCs for optimal protection needs to be explored for each different food commodity under variable environmental conditions; (d) safety associated with fumigation of microbial volatile is another important consideration that can be enhanced with the application of proper concentration of the fumigant; (e) the registration process, as with any new products, registration process for the commercial application is not easy nor fast, (f) genetic stability of non-toxic microbes: this concern is particularly relevant to the use to non-toxic fungal strains for the control of toxigenic ones. There are chances that genetic makeup of the biocontrol strains (atoxigenic) will change with time, leading to emergence of super-toxigenic strains.

8. Conclusions and perspectives

The antifungal spectrum of microbial volatiles is generally wider because of rapid conversion to gaseous state in water and air diffusion (Lammers et al., 2022; Passone & Etcheverry, 2014), and needs no physical contact with the treated commodity, hence organoleptic qualities of the food matrices are preserved (Valero et al., 2006; Valverde et al., 2005). Other restrictions posed by the chemical and physical methods of fungal control such as high cost of production, heavy equipment, denaturation of nutrition value and energy consumptions are overcome by microbial methods (Smaoui et al., 2022). All in all, it is not unreasonable to foresee a big scope and future of microbial VOC in the food and agriculture industry for the biological control of mycotoxins.

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