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INVITED REVIEW

Advances in the use of biocontrol applications in preharvest and postharvest environments: A food safety milestone

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Abstract

Increasing concerns toward food safety and public health have rendered the use of synthetic chemicals in agricultural environments unacceptable. A shift toward biologically safe approaches has been considered a preferred strategy within the food handling chain and has received increasing attention over the past years in managing undesirable microbial growth. Although several studies have looked at the mode of action of most antagonists, the manipulation of microbial communities in food safety has not been fully explored. Very little is known about the effect of microbial diversity and composition in developing a healthy environmental approach for pathogen management in the farm to fork continuum. In view of the progress made in recent years in metagenomic technologies, information generated should be used to develop a dynamic approach that will consider a comprehensive approach involving environmentally friendly strategies in dealing with food losses caused by microbes to ensure food safety. Thus, this review includes information on the latest biocontrol applications to suppress undesirable microbial growth and extend fresh produce shelf life along the farm to fork continuum. The role of recent trends related to the potential of microbiomes in food safety and quality is further discussed. The use of physical treatments against pathogen growth is also highlighted.

1 | INTRODUCTION

A global and internationalized food chain has allowed food producers from developing countries to access the international market. Gaining access to international markets meant the fresh produce sector had to address environmental and logistics challenges at every step along the farm to fork continuum to avert noncompliant produce and reduce/minimize food losses. Microbiological concerns account for many fresh produce losses and represent a topical issue facing the entire food industry and consumers alike. Hence, introducing synthetic chemicals as a measure to maintain quality and extend shelf life was imperative at some point.

The use of synthetic chemicals allowed for access to longer distance markets wherein prolonged cold storage is unavoidable. Indeed, a wide range of synthetic chemicals including prochloraz and bavistin (Shimshoni et al., 2020) have been used effectively to maintain the quality of fresh produce such as avocado and mushrooms, respectively. However, as the popularity of synthetic chemicals increased in

the early-to-middle 20th century, a number of adverse environmental (Fang, Peng, Muir, Lin, & Zhang, 2019) and public health effects (Gaston, Birnbaum, & Jackson, 2020) linked to their use came into the spot light. There is evidence indicating the negative effects of synthetic chemicals prevalent within the food chain, such as polycyclic aromatic hydrocarbons, and dioxins on human health. This signifies public health concerns due to toxicity, ability of synthetic chemical to accumulate in organisms (Jones & De Voogt, 1999), and degradation of environmental health.

Persistent exposure to these toxic chemicals has since been associated with several human health (producers, workers, and consumers) ailments including potential weakening of homeostatic processes, immune disruption (Liamin et al., 2017) and even onset of cancers (J. Shen et al., 2017). Recent evidence shows that exposure to fungicides has negative effects on gut microbiomes with potential to cause imbalances of microbial populations in humans (Lin et al., 2020). High risk populations to synthetic chemicals exposure in the fresh produce chain are farm workers,

farm owners, and communities living near agricultural farms. Occupational exposure of farmworkers to synthetic chemicals/pesticides resulting in a wide range of acute and chronic illnesses including headaches, seizures, vomiting, various cancers, neurologic disorders, respiratory symptoms, reproductive disorders, among others, are well documented (Amoatey, Al-Mayahi, Omidvarborna, Baawain, & Sulaiman, 2020; Fuhrmann et al., 2019). It is not surprising, therefore, that the risks posed to human health and increased food safety incidents necessitates a paradigm shift from chemicals to biological control and other nonchemical applications while assuring product quality and safety. Hence, in the 21st century, several scientific studies focused on the development of alternative and safe applications to ensure food safety and quality. Moreover, increased global chemophobia especially in developed countries has led to amendments of some food safety regulations, underpinning the prohibition or more stringent levels of synthetic chemicals used in the fresh produce chain.

Biocontrols and safe solutions include natural preservatives, plant extracts and essential oils (EOs; Bill, Korsten, Remize, Glowacz, & Sivakumar, 2017), probiotics, secondary microbial metabolites and enzymes. Alternative solutions maintain quality and safety by deterring the growth of undesirable plant and foodborne pathogens in food matrices at preharvest and postharvest settings, as well as processing stages. In the past, while only single microbial species were mainly considered for biocontrol products and regularly associated with erratic findings, the current focus is to use microbiome-based approaches. Science-based technologies are increasingly adopted in the fresh produce production and processing facilities that are based in areas far away from international markets. The adoption of novel biocontrol applications will help maintain access to premium markets that require compliance to stringent food quality and safety standards. Despite the development of several biological approaches in the past few decades, there are challenges of broad usage due to limited applicability in the current postharvest processes.

This review provides an overview of the latest biocontrol applications such as EOs and microorganism-based approaches used at different points along the fresh produce chain. We highlight the role of recent trends related to the potential of the host microbiome as a biocontrol strategy and nonchemical applications in food safety and quality. Furthermore, we highlight the advances brought by modern technology to utilize the microbiome to maintain the quality and safety of fresh produce. In particular, gene editing technology is discussed together with their application. To a lesser extent, we provide a brief discussion on the physical treatments against pathogen growth.

2 | ESSENTIAL OILS

2.1 | Activity against plant pathogens

EOs have received increasing interest as natural compounds capable of eliciting resistance against the growth of plant to extend shelf life and maintain food safety (Ambrosio et al., 2019; Glowacz & Rees, 2016). For instance, cinnamon oil, which primarily contains trans-cinnamaldehyde as an active ingredient, has proved to be a potential fungicide to prevent and control *Villosiclava virens*, an

important rice fungal pathogen worldwide (Zheng et al., 2019). The study also reported better inhibitory effect on conidium sporulation of *V. virens* under fumigation conditions compared to the conventional contact method. In addition, thyme oil vapors applied to avocado fruit led to increased expression of phenylalanine ammonia-lyase gene, a key factor in phenylpropanoid pathway and biosynthesis of epicatechin, a phenolic compound that enhances antioxidant capability (Bill et al., 2017). This key finding is significant for fruit susceptible to anthracnose as thyme oil vapors proved to be a safe alternative to prochloraz, a synthetic fungicide used commercially as a postharvest application against *Colletotrichum gloeosporioides*. Adoption of this alternative technology will ensure avocado and mango producers across the globe meet the amended food safety regulations (European Food Safety Authority, 2020) as stipulated by the European market, hence, maintaining market share.

The inhibitory effects of black caraway, fennel and peppermint EOs against *Botrytis cinerea* have been reported (Aminifard & Mohammadi, 2012). The in vitro results showed inhibition to *B. cinerea* following the application of black caraway and fennel oils at concentrations of 400 and 600 μL^{-1} , respectively. The in vivo assays also showed that all EOs at various concentrations suppressed the growth of *B. cinerea*. Application of the EOs also at higher concentrations had positive effects in maintaining fruit quality and increasing storage life. Recent work has also shown the effect of phenological stage on effectiveness of EOs (Rguez et al., 2020). Extracts of *Tetraclinis articulata* at flowering were found most efficient in controlling *B. cinerea* in tomato, preharvest and postharvest.

Antifungal activity of EOs depends on characteristics of bioactive components including the functional group of molecules, shape, and their chemical structures (Kumar & Kudachikar, 2018). Bioactive compounds of EOs at low concentrations act on the functionality and the structure of the cell membrane (Viuda-Martos, Ruiz-Navajas, Fernández-López, & Pérez-Álvarez, 2008) thereby altering cell structure and shifting cell membrane permeability, while higher concentrations lead to severe membrane damage, homeostatic imbalance and cell death (Carson, Mee, & Riley, 2002). Furthermore, these compounds interact with enzymes associated with energy generation and biosynthetic processes of the cell, leading to inhibition of phytopathogens. Possible antifungal mechanisms of tea tree EO vapor or contact phase against *B. cinerea* showed mycelial morphology and ultrastructure alternation marked by flatted empty hyphae, thick cell walls, ruptured plasmalemma and cytoplasmic coagulation or leakage (Shao, Cheng, Wang, Yu, & Mungai, 2013). Transcriptomic profiles of *B. cinerea* versus tea tree EO and its active ingredients (terpinen-4-ol and 1,8-cineole) revealed that most differentially expressed genes of the pathogen participated in the biosynthesis of secondary metabolites, and the metabolism of amino acids, carbohydrates, and other essential compounds (Z. Li, Shao, et al., 2020). The researchers went on to state that there was evidence that terpinen-4-ol induced mitochondrial dysfunction, oxidative stress and transiently decreased activity of succinate dehydrogenase, α -ketoglutarate dehydrogenase, and isocitrate dehydrogenase. The presence of 1,8-cineole influenced differentially expressed genes associated with cell death. In Table 1, we provide a

TABLE 1 Overview of studies investigating inhibitory effect of essential oils on postharvest quality of fruits and vegetables

Fresh produce	Essential oil	Target organism	Aim of study	Summary of findings	Reference
Avocado	Thyme oil	<i>C. gloeosporioides</i>	Investigate the effect of thyme oil vapours on the expression of genes associated with plant defense (phenylalanine ammonialyase (PAL) and lipoxygenase (LOX)), and control of anthracnose during cold storage.	-Thyme oil exposure led to up-regulation and down-regulation of PAL and LOX genes, respectively. -Fruit with higher level of epicatechin had lower incidence of disease. -Thyme oil vapours triggers plant defense mechanisms against <i>C. gloeosporioides</i>	Bill et al. (2017)
Banana		<i>Colletotrichum musae</i>	- The inhibitory effect of thyme oil on <i>C. musae</i> .	-Thyme oil reduced disease severity on treated fruit. -Thyme oil prolonged shelf life of banana and did not alter physico-chemical and sensory quality of the fruit.	Vilaplana et al. (2018)
Jujube	Thyme, rosemary and cinnamon	<i>Alternaria alternata</i> and <i>Penicillium expansum</i>	-Effect of dual and triple EO combinations and synergistic inhibition of <i>A. alternata</i> and <i>P. expansum</i> on jujube fruit.	-Various combinations of EOs had antifungal synergistic effect against <i>A. alternata</i> and <i>P. expansum</i> , and maintained quality of jujube fruit.	Nikkhah & Hashemi (2020)
Mangosteen	Peppermint and lime oil	Moulds	- Investigating the optimal application ratio and mechanism of action of the combination of peppermint and lime EOs to inhibit mould and extend storability of mangosteen.	The combined EOs of peppermint and lime, applied at a ratio of 1:3, respectively, contributed to mycelial growth inhibition of moulds and maintained fruit quality for 9 days.	Owolabi et al. (2021)
Peach	EOs from tea tree, thyme, rosemary, and lemon.	<i>Monilinia fructicola</i>	-Antifungal effect and mechanism of action of four EOs against <i>M. fructicola</i> .	-Of the four EOs, tea tree oil showed the highest inhibitory effect on <i>M. fructicola</i> . -Tea tree oil alters the composition of <i>M. fructicola</i> cell membrane, mycelial morphology and membrane permeability.	Xu et al. (2021)
Potato	Oils of <i>Hyssopus officinalis</i> , <i>Satureja khuzistanica</i> and <i>Zataria multiflora</i> .	<i>Pectobacterium carotovorum</i> subsp. <i>carotovorum</i>	-Effect of three EOs from indigenous plants against <i>P. carotovorum</i> .	-The highest activity against control soft rot disease was shown by Eos of <i>S. khuzistanica</i> and <i>Z. multiflora</i> .	Hajian-Maleki et al. (2021)
Pomegranate	Cinnamon, lemon, and oregano	Species of <i>Botrytis</i> and <i>Penicillium</i> , and <i>Piidiella granati</i> .	-Effect of Eos combined with chitosan on the growth of selected fungal phytopathogens of pomegranate.	-Chitosan-EO mixture had higher bioactivity against fungal pathogens under direct coating than vapour treatments.	Munhuweyi et al. (2017)
Table grapes	<i>Rosmarinus officinalis</i> (rosemary); <i>Mentha piperita</i> (peppermint), and <i>Thymus vulgaris</i> (thyme)	<i>B. cinerea</i>	-Effect of several essential oils, applied individually or in combination, on <i>B. cinerea</i> .	-Rosemary and peppermint essential oils controlled gray mould but application is required at least 48 h prior to point of sale.	Servili et al. (2017)
Tomato	<i>T. articulata</i> oils	<i>T. articulata</i> essential oils on <i>B. cinerea</i> of tomato.	-Effect of <i>T. articulata</i> essential oils on <i>B. cinerea</i> of tomato.	-Pre-treatment of tomato with the essential oil, which are most active during flowering, significantly reduced <i>B. cinerea</i> infections and disease severity.	Rguez et al. (2020)

Abbreviations: LOX, lipoxygenase; PAL, phenylalanine ammonialyase.

summary of some reports focusing on the use of EOs to inhibit the growth of economically important postharvest pathogens of fresh produce.

2.2 | Activity against human pathogens

Recent outbreaks of foodborne related diseases such as Listeriosis in South Africa (2017) which was responsible for at least 216 deaths out of a total of 1,060 reported cases, has heightened food safety related issues globally (Smith et al., 2019). Alternative growth deterring agents are necessary to provide a wide scope of more effective applications such as EOs and/or other natural products. Biocide activity of several EOs derived from citronella (*Cymbopogon nardus*) and lemongrass (*Cymbopogon citratus*) leaves have been tested against *Listeria monocytogenes* and associated biofilms. Complete elimination of *L. monocytogenes* was observed with citronella oils, compared to lemongrass oils (de Oliveira, Brugnera, das Graças Cardoso, Alves, & Piccoli, 2010).

Enterohemorrhagic *Escherichia coli* O157:H7 (EHEC) causing hemorrhagic colitis (Tarr, Gordon, & Chandler, 2005), has the capacity to form biofilms and produces Shiga-like toxins. Of note, no effective therapy exists because antimicrobial agents escalate the risk of EHEC induced hemolytic-uremic syndrome. Biofilms of EHEC are resistant to, among others, conventional antimicrobial agents, host defenses, and external stresses (Kim et al., 2016). Kim et al. (2016) screened several EOs for their ability to inhibit EHEC biofilm formation. Three EOs (bay, clove, and pimento berry oils) showed anti-biofilm activity against EHEC. The major and common active constituent among the three oils, eugenol, played a key role to inhibit biofilm formation and, in addition, reduced the virulence of EHEC. Accordingly, Kim et al. (2016) conclude that eugenol and clove oil provide realistic urgently required alternatives for the development of biofilm inhibitors and toxin producing inhibitors.

Citrus EOs resulted in a 1.4 log reduction of *E. coli* O157:H7 and *Salmonella* spp. (Pittman et al., 2011). The treatment also significantly reduced total aerobic bacteria and psychrotrophs counts. The authors recommended use of citrus EOs as a potential control measure against quality deteriorating microbes thereby protecting public health. It is important to note that other EOs may demonstrate a greater biological activity against gram-positive bacteria compared to gram-negative bacteria. However, cinnamon (*Cinnamomum zeylanicum*) bark EO demonstrated broad-spectrum activity against both gram-negative and gram-positive bacteria, including *Pseudomonas aeruginosa* and other known multidrug resistant species (Elcocks, Spencer-Phillips, & Adukwu, 2020).

Antimicrobial capability of EOs is encouraging amid the emergence of multidrug resistant bacteria and their effectiveness depends on a number of factors including mode of application with vaporized EOs proving to be more effective at low concentrations (Laird & Phillips, 2012). A previous study investigated the antibacterial potential of 11 commercial EOs against multidrug-resistant enterococci and aeromonads from food (Quendera, Barreto, &

Semedo-Lemsaddek, 2019). A majority of the EOs (8 out of 11) showed significant antimicrobial activity against aeromonads, with inhibition zones greater than 12 mm. *Mentha pulegium*, *Melaleuca alternifolia*, *Cymbopogon flexuosus*, and *Thymus vulgaris* EOs performed exceptionally well against aeromonads, exhibiting inhibitory zones of 21.7–42 mm. Moreover, *C. flexuosus* and *T. vulgaris* EOs exhibited antimicrobial activity against 24-hr *Aeromonas* biofilms. In a more recent study, EOs from the leaves of cerrado plants of Midwest Brazil showed moderate to good antibacterial activity against a panel of four standard and three clinical multidrug-resistant bacterial strains, including *Salmonella* serotype typhi and oxacillin-resistant *Staphylococcus* (de Jesus et al., 2020). These findings support the potential of EOs against foodborne bacteria particularly their putative applicability on multidrug-resistant strains. However, further toxicological studies are required to establish potential toxic effects and clinical relevance (Sharifi-Rad et al., 2018).

An application limitation of most EOs in food is potential interference with sensory properties of a product emanating from large volumes required to elicit bioactivity. More research is required to methodically concentrate EOs for application at small volumes yet with similar high antimicrobial activity against targeted pathogens. The development of technological solutions to improve the application of natural compounds in fresh produce has become important in recent years. Nanoemulsion technology provides promising results for microbial inactivation of foodborne pathogens (Prakash, Baskaran, Paramasivam, & Vadivel, 2018). A recent study by Garre, Espín, Huertas, Periago, and Palop (2020) combined nanoemulsified D-limonene with thermal treatments under isothermal conditions and showed remarkable antimicrobial properties against *L. monocytogenes*. Their study reports a reduction in the D-value by a factor of 25.

3 | MICROBIAL-BASED SOLUTIONS FOR PLANT PATHOGENS

Naturally, plants are associated with microbial populations, the majority of which represent natural epiphytes with only a small percentage being phytopathogens. The phylloplane and plant rhizosphere consist of both beneficial and detrimental microbes. An example of the former includes plant growth promoting rhizobacteria (PGPR) which, directly or otherwise, stimulate plant growth and elicit resistance that is often effective against several phytopathogens (Pieterse et al., 2014). Beneficial microbes are ideal candidates for development of potential biocontrol agents which heighten plant disease resistance mechanisms. These mechanisms may involve reprogramming of molecular components to differentially regulate genes related to activation of pathogen defense and phytohormone signals including jasmonic acid, and ethylene (Sharma, Chen, Navathe, Chand, & Pandey, 2019). As a result, rhizobacteria such as *Klebsiella* sp. are capable of demonstrating biocontrol activity against many fungal phytopathogens, and therefore, provide alternatives to synthetic chemicals (Sharma et al., 2019).

PGPRs produce antimicrobial volatile organic compounds (VOCs) that display inhibitory activity against fungi, bacteria and nematodes. Raza, Ling, Yang, Huang, and Shen (2016) showed that a consortium of VOCs produced by *Bacillus amyloliquefaciens* produced 70% growth inhibition and reduced virulence of *Ralstonia solanacearum*, the causal agent of tomato wilt. Their results show that proteins of *R. solanacearum* associated with antioxidant activity and virulence were downregulated, signifying the effectiveness of VOCs (e.g., 3-hydroxy-2-butanone) produced by a biocontrol strain (*B. amyloliquefaciens*) against tomato wilt pathogen.

Despite the ability of biocontrol agents to inhibit phytopathogens, unilateral application has not been favored compared to an integrated management strategy that has been developed to achieve commercial levels of safety and postharvest decay control (Romanazzi, Smilanick, Feliziani, & Droby, 2016). For example, a combination of *Pseudomonas* spp. and *Trichoderma* spp. showed to be a promising approach for the control of green mold of citrus, based on the combined mechanisms of action (Panebianco, Vitale, Polizzi, Scala, & Cirvilleri, 2015). Eco-friendly management approaches, such as physical treatments (e.g., hot water) could improve the efficacy of biocontrol agents (Zhou, Deng, & Zeng, 2014). Biocontrol products currently being used in the fresh produce sector include (a) Shemer, based on the yeast *Metschnikowia fructicola* (Droby, Wisniewski, Macarasin, & Wilson, 2009) and used

for both preharvest and postharvest application on several crops and (b) Biosave, a *Pseudomonas syringae*-based product that effectively controls various fungal pathogens such as *Penicillium* and *Botrytis* (Moraes Bazioli et al., 2019). Other commercial biocontrol products are summarized in Table 2.

4 | MICROBIAL-BASED BIOCONTROL SOLUTIONS FOR FOODBORNE PATHOGENS

Microbial-based applications that inhibit the growth of foodborne pathogens such as *L. monocytogenes*, *Campylobacter jejuni* and *E. coli* O157:H7 (Mirkovic et al., 2020; Thung et al., 2020) have been recently explored. Mirkovic et al. (2020) revealed biocontrol potential of *Lactococcus lactis* subsp. *lactis* against organisms such as *L. monocytogenes* during cold storage of cheese. In addition to *L. monocytogenes*, there was successful inhibition of *Staphylococcus aureus*, yeasts and molds, and more importantly, *L. lactis* did not alter the product's chemical composition and pH. The implication and potential application of these results signify an encouraging prospect given the previously reported presence of *L. monocytogenes* in food production systems (Jongman & Korsten, 2017) and, thereafter, the Listeriosis outbreak in South Africa that was linked to contaminated meat products (Smith et al., 2019).

TABLE 2 Summary of selected commercial biocontrol products, target pathogens, and mode of action

Biological agent	Product name	Application	Target pathogen / disease	Mode of action	Reference
<i>Trichoderma harzianum</i> T-39	Trichodex	Pre-harvest	<i>B. cinerea</i>	Competition for nutrients, interference with production of pathogenicity enzymes by the infecting pathogen, and induced resistance.	Shafir, Dag, Bilu, Abu-Toamy, & Elad (2006)
<i>Candida oleophila</i>	Aspire	Post-harvest	<i>Penicillium</i> spp; <i>Botrytis</i> spp	-Competition for nutrients and space. Induce pathogenesis-related genes in host tissues. Production of extracellular lytic enzymes.	Gao, Zhang, & Xiong (2021); Y. Liu et al. (2017)
<i>Agrobacterium radiobacter</i> strain 84	Galtrol	Pre-harvest	<i>Agrobacterium tumefaciens</i>	Produces agrocin, an antibiotic that targets DNA synthesis in the pathogen by inhibiting aminoacylation.	Stockwell et al. (1996)
<i>Agrobacterium radiobacter</i> strain 1026	Nagol	Pre-harvest	<i>Agrobacterium tumefaciens</i> ; <i>Penicillium digitatum</i>		Parisa, Elif, Recep, & Şenol (2017); Vicedo, Peñalver, Asins, & López (1993)
<i>Bacillus subtilis</i> strain GB03	Kodiak, companion	Pre-harvest	<i>Aspergillus</i>	-Synthesis of hormones, enzymes, and antioxidants against pathogens. Induce acquired systemic resistance in hosts.	Shafi, Tian, & Ji (2017)
<i>Pseudomonas fluorescens</i> A506	Frostban, Blightban A506	Pre-harvest	Bunch rot	Produce secondary metabolites: pyrrolnitrin and pseudomononic acids, which inhibits the synthesis of protein, RNA and cell wall of pathogens.	Wilson (1997)
Essential oil of mint (<i>Mentha piperita</i>)	Fungastop™	Pre-harvest	Broad spectrum of fungal species	-Hydrophobicity enables the essential oils to break the lipids of the pathogen's cell membrane and damage its inorganic ion equilibrium	Ojaghian et al. (2020)

5 | BACTERIOPHAGES AND PHAGE LYSIN

Bacteriophages are commonly applied not only for medical purposes but also in agricultural settings (Sillankorva, Oliveira, & Azeredo, 2012); however, there is no report of commercial application for fresh produce safety. Here, we provide the current and future outlook on the use of these viral entities.

Several studies have provided evidence of phage-based applications to inhibit proliferation of plant and human pathogens of fresh produce origin. López-Cuevas, Castro-del Campo, Ramirez, and Chaidez (2016) reported inhibitory activity of phage P22 against *Salmonella typhimurium* on artificially contaminated tomato. A phage cocktail, used alone and in combination with other natural compounds, led to inhibition of *E. coli* O157:H7 strains artificially applied on leafy green vegetables (Viazis, Akhtar, Feirtag, & Diez-Gonzalez, 2011). A new lytic phage (vB_EcoM-ECP26) decreased *E. coli* O157:H7 growth and remained viable on romaine lettuce for 5 days (Park, Lim, Lee, & Park, 2020). For *L. monocytogenes*, efficacy of phage Listex™ P100 was explored on several fresh produce items, for example, melon and apples and recommended its use at high pH while an integrated approach is necessary for low pH food items (Oliveira et al., 2014). A recent study showed the effectiveness of a lytic phage against *Xanthomonas campestris* pv. *campestris* (cause of black rot of crucifers) and also revealed the associated host metabolic response (Papaianni et al., 2020). The results highlighted the potential of phage-based approaches to thwart phytopathogen proliferation and modify host defense mechanism.

Bacteriophages selected for biocontrol purposes on fresh produce should have characteristics that include lytic capabilities, devoid of virulence genes, and the ability to proliferate in a strain of bacteria (nonpathogen) (Parmar, Dafale, Tikariha, & Purohit, 2018). It is more desirable for the selected phages to withstand environmental conditions prevailing where their use is intended (Bao et al., 2015). Despite possible development of bacterial resistance due to constant exposure, phages are constantly in a race to evolve and overcome the molecular modification of their hosts.

The increasing interest in the application of phage-based biocontrol agents necessitates for improved novel application approaches for example, spraying and encapsulation. Due to the stability of phage particles in many neutral solution, the application of phage-biocontrol agents allow for the preservation of flavor and texture in food. A novel encapsulation strategy using phage UFV-AREG1 achieved significant reduction of bacterial contaminants at levels comparable to antimicrobial chemicals (Boggione et al., 2017).

It is important to mention that contradictory results have limited the application of phage-based biocontrol formulations in fresh produce, largely due to lack of in-depth knowledge of phage biology. Hence, the acceptable strategy involves a detailed characterization of phages which is necessary to select candidate phage biocontrols (Parmar et al., 2018). The use of modern genome sequencing assays will continue to provide more information on specific bacteriophages intended for biocontrol application (P. Li, Zhang, et al., 2020).

The future of phage-based approaches relies on natural hydrolytic enzymes called phage encoded lysins which provide the final step during disintegration of the bacterial cell wall. Rather than using whole phages, direct application of these highly specific enzymes signify the recent advances in biocontrol strategies (Xu, 2021). The use of endolysins is not associated with development of resistance by the host bacterium because the enzymes target conserved bonds of the peptidoglycan layer, representing a significant advantage compared to whole phages.

Several endolysin studies have focused on, among others, identification, efficacy and application in various food systems such as milk (Van Tassell, Ibarra-Sánchez, Hoepker, & Miller, 2017) and other products. Genetically modified endolysins, PlyP100 (Van Tassell et al., 2017) and CBO1751 (Z. Zhang, Lahti, Douillard, Korkeala, & Lindström, 2020) inhibited *L. monocytogenes* and *Clostridium botulinum*, respectively. Endolysins also showed improved inhibitory activity when used simultaneously with other biocontrol agents (García, Martínez, Rodríguez, & Rodríguez, 2010). Despite potential of endolysins for application in fruits and vegetables, we are not aware of any recent findings in this regard. Recent information on phage lysins provides a new viewpoint of food safety strategies that are applicable along the farm to fork continuum. More in-depth knowledge on phage-based products is needed for effective application fresh produce.

6 | MICROBIOMES FOR IMPROVED POSTHARVEST QUALITY AND FOOD SAFETY

Studies of the phyllosphere using traditional culture-based approaches have focused on the detection of selected members of the microbial consortia (e.g., known plant pathogens or human pathogens). In contrast, the advent of culture independent molecular-based technologies in microbial ecology has utilized a holistic approach that provides a more thorough understanding of the diversity and dynamics of surface associated microbial populations. Currently, one of the technologies includes the amplification of specific gene regions (e.g., 16S and 18S rRNA gene fragments, ITS region, etc.) using metabarcoding sequencing, or focusing on the entire community DNA/RNA, metagenome, or metatranscriptomic analysis to determine microbial community associations. The high throughput molecular approaches highlight the significance of microbiomes during the lifecycle of fresh produce and reveal unknown sequences prevailing within the farm to fork value chain; and such studies have received increasing attention. A more comprehensive understanding of the relationship between the resident microbiota and the host plant provides prospects for developing new approaches of biocontrol (Kusstatscher et al., 2020). Metagenomic sequencing of surface microbiomes of apple provided insights about the presence of biocontrol agents and the potential for identification of many as yet nonsequenced microorganisms absent in databases (Angeli, Sare, Jijakli, Pertot, & Massart, 2019). Hence, the composition of the microbiome associated with the carpoplane and/or phylloplane of fresh produce is significant for postharvest quality

(Abdelfattah, Wisniewski, Droby, & Schena, 2016; Angeli et al., 2019) and safety (Gomba, Chidamba, & Korsten, 2017). Despite several reports on the importance of postharvest microbiome (Droby & Wisniewski, 2018; Wisniewski & Droby, 2019), very few have used the knowledge of high throughput sequences to develop biocontrol formulations. However, the high potential and applicability of this technology to increase postharvest quality has been established.

Plant-associated microbiomes do not only influence plant health during preharvest stages but also contribute to postharvest quality (Droby & Wisniewski, 2018). Few studies have focused on the complex interactions between the resident microbiome and antagonistic microorganisms during postharvest stages and these interactions contribute to biocontrol efficiency pre and postharvest (Massart, Martinez-Medina, & Jijakli, 2015; Schreiter, Babin, Smalla, & Grosch, 2018). So far, our current understanding of microbial dynamics shows distinct disparities between the microbiota of healthy and diseased hosts. For instance, previous findings showed significant changes in metagenomic sequences of healthy and diseased onions and kiwi fruit, including evidence of loss in diversity (Wu et al., 2019; Yurgel, Abbey, Loomer, Gillis-Madden, & Mammoliti, 2018). Onset of infections lead to altered diversity and composition of the microbial community when compared to healthy fruit. The composition of fungal populations on the surface of apples were determined from the point of harvest throughout postharvest storage and revealed a significantly higher diversity of fungal species during storage than at harvest (Y. Shen et al., 2018). Of the identified fungal pathogens, the increased proliferation of postharvest pathogens belonging to the genus *Penicillium*, *Aspergillus*, and *Botrytis* during cold storage of apple indicate higher risks of quality deterioration during storage. Of concern, some of the detected fungal species are not only associated with fruit decay but also associated with aflatoxin contamination.

The assessment of bacterial biomes of different vegetables throughout the supply chain revealed unique populations for each plant and also indicated the influence of postharvest processes on the microbiome at each stage (Jarvis et al., 2018). Gomba et al. (2017) investigated the effect of postharvest drenching on microbiomes of orange fruit and reported significant decrease on fungal communities, but not on bacterial populations. Of note, the postharvest drenching was carried out with several fungicides, which are increasingly facing restrictions by the society and regulatory agencies, and the higher loss of fungal diversity compared to bacteria is not surprising. Part of their findings included genomic sequences of some well represented bacterial genus such as *Sphingomonas*, which were also reported on apples and leaves of grapes (Leveau & Tech, 2010). Despite reports of high prevalence on several fresh produce of economic importance, the role played by this genus on the carpoplane/phylosphere remains to be described. For cucumbers that grow on the ground, soil microbiomes are highly likely to impact the microbial composition of the vegetable and its postharvest quality (Abdelfattah et al., 2016). The detection of *Acinetobacter* as part of microbiomes associated with cucumber provided an indication of decay because the bacteria is linked with food spoilage (Jarvis et al., 2018). The significance of high throughput sequencing techniques extend to determination of the degree of

spoilage. Increased proportions of *Leuconostoc* and *Lactococcus* species indicated that fresh sprouts were in advanced stages of spoilage (Jarvis et al., 2018).

All these reviewed findings substantiate the ability of holistic approaches of the high-throughput sequencing tools to reveal deeper insights of microbiome interactions and microbial community shifts during postharvest processing and storage of fresh produce. Therefore, there is a great potential for the use of microbial consortia to positively influence postharvest quality and also help develop improved postharvest applications of fresh produce.

From a food safety perspective, the presence of human pathogens alongside phyllospheric microbial consortia of fresh produce may be a concern given that these are not likely to be removed prior to consumption if the produce is consumed raw or with minimal processing. For food safety reasons, it is worthy to mention the importance of determining viability of foodborne pathogens to inform risk analysis and the quantification thereof. We know that the presence of genomic amplicons does not necessarily imply that the target pathogen is viable. To circumvent this shortcoming, metatranscriptomic analysis, which involves sequencing complementary DNA generated from community RNA (mRNA), can be used (Kovac, den Bakker, Carroll, & Wiedmann, 2017). The technology enables the identification of genes that are being transcribed and probably translated, and some researchers consider this approach to separate live and dead cells in a sample. However, since the majority of mRNA degrades immediately after microbial cell-death, and some RNAs remain stable for some time following the death of a microbe which can impact this proposed purpose of metatranscriptomics (Kovac et al., 2017). An integrated approach by using both metagenomics and metatranscriptomic sequencing may benefit the description of baseline microbiomes along the farm to fork supply chain and detect safety hazards (Edlund et al., 2016).

It is important to consider the naturally occurring microbial assemblages on fresh produce because they may be more persistent, and even interact more with potential pathogens. Current knowledge of microbiome profiling have revealed that the natural microbial communities of several fresh produce can influence the detectability of foodborne pathogens because their incursion occur at a very low abundance relative to indigenous microbiomes (Jarvis et al., 2015; Ottesen et al., 2016). For example, detection of pathogenic *E. coli* was disadvantaged by nonpathogenic *E. coli* on spinach and this was similar for *Salmonella* and closely related species (Grim et al., 2017).

The microbiome and associated species richness led to reduced concentration of *Salmonella enterica* (Klerks, Franz, van Gent-Pelzer, Zijlstra, & Van Bruggen, 2007). Despite being poorly understood, the mechanism for the reduction of *S. enterica* at high microbial diversity strongly suggests antagonism to the pathogen. In addition, composition of phyllospheric bacterial consortia on a leafy green differed on the basis of viability of *E. coli* O157: H7 or the lack thereof (Williams, Moyne, Harris, & Marco, 2013). There are reports of natural plant microbiomes that outcompete potential human pathogens (e.g., *Salmonella* and *E. coli* O157:H7) (Cooley, Chao, & Mandrell, 2006) in the absence of antagonistic interactions. The presence of genomic sequences belonging to

Paenibacillus on cucumber provided encouraging prospects from a food safety perspective since species belonging to this genera have been reported to inhibit the growth of *Salmonella* (Sprando et al., 2017). Thus, deliberate inclusion of competitive natural microbiomes could be a potential strategy to reduce contamination of fresh produce by human pathogens.

6.1 | Manipulating microbiomes and gene edition

Given the uniqueness of microbiomes on specific fresh produce, the composition and functional dynamics of the microbial consortia in the field is crucial. Our knowledge of natural microbiomes and interactions with the host can be used to deliberately manipulate the microbial composition in an effort to affect postharvest quality and safety of fresh produce (Padmaperuma, Butler, Shuhaili, Almalki, & Vaidyanathan, 2020). It is noteworthy to point out that the presence of microbes in food might be undesirable but not always a public health concern. However, from a food safety standpoint, pathogenic microorganisms that grow and survive in fresh produce may cause health problems. Despite the recent focus on the COVID-19 pandemic, foodborne pathogens linked to fresh produce continue to threaten global food safety every year. In 2020, there were several confirmed foodborne disease outbreaks caused by *E. coli* O157:H7, *L. monocytogenes*, *Salmonella*, and *Cyclospora* associated with fresh produce (Batz et al., 2021).

The recently introduced clustered regularly interspaced short palindromic repeats (CRISPR) technology (Monsur et al., 2020) can be exploited along the farm to fork food supply chain to advance food safety by selectively inactivating pathogens and reducing foodborne illnesses (Barrangou & Notabaart, 2019). The technology, which has transformed molecular biology applications through genome editing, is a sophisticated adaptive immune mechanism used by bacteria as a defense system against viruses and other invading genetic material (Marraffini & Sontheimer, 2010). The revolutionary CRISPR system employs a family of protein called Cas endonucleases to cleave foreign nucleic acids or the genome of invading pathogens (Sapranaukas et al., 2011). Mechanism of target recognition and substrate preferences are different for homologues of Cas endonuclease, but the enzyme cleaves sequences if (a) a protospacer adjacent motif is close to the target area and (b) there is complementarity between the nucleic acid sequence adjacent to the protospacer adjacent motif and the RNA that is bound to the Cas protein.

The CRISPR-mediated manipulation of microbiomes can be used at various stages of the fresh produce continuum, from primary production to processing. The increasing interest in microbiome research is helping to provide more information on the benefits of microbiomes in relation to yield increase, drought tolerance and other aspects associated with plant growth and health (Corte et al., 2019; T. Wang, Zhang, Zhang, & Zhu, 2021; T. Wang, Zhang, & Zhu, 2019). The accurate detection and successful inhibition/elimination of human pathogens of public health concern is a key priority for fresh produce and ready to eat products. The ability to use specific CRISPR techniques to suppress the growth of *L. monocytogenes* is a positive development

given the proliferation of the pathogen at cold temperatures. The CRISPR-based approach can also be used to target pathogens, which are known to persist in irrigation water systems (Van der Merwe, Duvenage, & Korsten, 2013) and surfaces of packhouses. An integrated approach that combines the CRISPR-based technology and phage therapy currently being used in processing facilities (Gutiérrez, Rodríguez-Rubio, Martínez, Rodríguez, & García, 2016) could be implemented as a spray, shower or bath, depending on the produce.

These novel approaches have applications that also include extending shelf life and the potential to be widely adopted in the fresh produce sector. For instance, white button mushrooms (*Agaricus bisporus*) were genetically edited to resist browning by targeting a group of genes that encodes polyphenol oxidase. By deleting bases along the mushroom's genome, one of the six genes coding for polyphenol oxidase was knocked out and significantly reduced the enzyme's activity (Waltz, 2016). The United States of America decided against regulating the CRISPR-edited mushroom but, currently, any gene-edited plants in Europe will be subjected to similar stringent regulations of traditional GM crops (Kupferschmidt, 2018).

Due to the current knowledge concerning the impact of several biotic and abiotic factors on fresh produce microbiome, CRISPR-Cas9 technology has been used to develop plants that are resistant to diseases and chilling injury, among others (Arora & Narula, 2017; R. Li et al., 2018). In tomato, the CRISPR-Cas9 technology showed that mitogen-activated protein kinase 3 plays a positive role by conferring resistance to *B. cinerea* (S. Zhang et al., 2018). The knockout of *SIMAPK3* led to increased susceptibility to *B. cinerea* in *Slimapk3* mutants and reduced the activity of defense enzymes when compared to wild type species. The functions of genes that confer resistance against *B. cinerea* in grape berries were validated using CRISPR-Cas9 as mutants showed increased immunity (X. Wang et al., 2018). A summary of other recent findings focusing on CRISPR-edited crops to confer resistance to diseases is provided in Table 3. As for abiotic parameters, R. Li et al. (2018) used CRISPR-Cas9 to demonstrate that C-repeat binding factors are highly conserved and help protect against chilling injury because *cbf1* mutants, showed severe chilling-injury symptoms than wild type tomato crop. The CRISPR technology does not only involve deletion of genes but also entails their addition. The technology was used to introduce three orthologs into ground cherry to improve flowering and fruit size of the crop (Lemmon et al., 2018). This serves as the basis for the introduction of any desired characteristics which could include improved post-harvest quality and longer storability.

Strategic manipulations of the microbiome and gene edition in fresh produce can improve biocontrol approaches. Treatment with microbiome oriented biocontrol agents could lead to healthier crops while gene edition could generate disease-resistant and environment-adaptive fresh produce. Ultimately, application of these strategies could lead to improvement of fresh produce quality and prolong their storability. A multifaceted intervention involving the use of microbiome and gene edition technologies can be used in place of synthetic chemicals against postharvest diseases. However, CRISPR-edited plants and biocontrol products face registration challenges and have to navigate public acceptance as well.

6.2 | Antimicrobial peptides

Antimicrobial peptides (AMPs) have increased in popularity because of inhibitory properties and, in addition, thermostability and water solubility. These natural preservatives are viable alternative strategies that have little effect on organoleptic properties of food items when compared to other antimicrobial agents such as EOs (Leon Madrazo & Segura Campos, 2020).

Globally, nisin is one of the most widely used AMP in many preserved food products including canned vegetables (Santos et al., 2018). Other important AMPs such as polylysine and pediocin show good inhibitory ability against foodborne pathogens that is, *E. coli* and *L. monocytogenes*; however, we are not aware of their commercial application on fresh produce (Santos et al., 2018). Enterocin AS-48 has been applied alone and in combination with other antimicrobial agents to inactivate *E. coli*, *L. monocytogenes*, and *Bacillus cereus* in sprouts, strawberries, pear and other fruits (Leon Madrazo & Segura Campos, 2020). These findings highlight the importance of AMPs and motivate for their wide application to assure food safety along the fresh produce chain.

The specificity of AMPs toward resident microbial populations of fresh produce is key to the spectrum of activity. Hence, we recognize the intricate interactions between candidate AMPs and microbiomes of the product of interest as a useful step during the selection of the natural compounds. Several reports have highlighted the specificity of AMPs against gram-negative and gram-positive bacteria (Schmitt, Rosa, & Destoumieux-Garzón, 2016). More recently, proliferation of *Staphylococcus epidermis* led to increased production of AMPs, and this new finding can be leveraged to reveal key AMPs-microbiomes interactions (Q. Liu et al., 2020).

Notwithstanding the several studies on AMPs, technology uptake and wide application of authorized products in the fresh produce industry is limited. Comprehensive research is still needed to determine conducive conditions suitable for AMPs in fresh produce chains. Including response of AMPs and effect of both biotic and abiotic parameters. Efforts to develop suitable AMPs should be reciprocated by adaptations and subsequent inclusion in the farm to fork chain.

TABLE 3 Summary of recent studies on CRISPR-edited crops for disease resistance

Fruit/vegetable	Target region	Resistance traits	Key findings	References
Banana	ORF region of virus	Banana streak virus	75% of the gene-edited crops were asymptomatic when compared to the non-edited which confirmed inactivation of eBSV into infectious viral particles.	Tripathi, Ntui, Tripathi, & Kumar (2020)
Citrus	CsLOB1 promoter	Citrus canker/ <i>Xanthomonas citri</i> subsp. <i>citri</i>	Mutants, in which CsLOB1 promoter was disrupted, showed increased resistance against citrus canker compared to the wild type.	Peng et al. (2017)
Grapevine	VvPR4b	Downy mildew/ <i>Plasmopara viticola</i>	-Gene deletion occurred without off-target. -The VvPR4b knockout mutants were more susceptibility to <i>P. viticola</i> compared to wild type crops, confirming the role played by the gene in the defense of grapevine against downy mildew.	M. Y. Li et al. (2021)
Papaya	alEPIC8	<i>Phytophthora palmivora</i>	-Mutant strains with cystatin-like cysteine protease inhibitors showed reduced pathogenicity of <i>P. palmivora</i> on papaya fruit compared with wild type strains. -The finding confirmed the active role of cystatin-like cysteine protease inhibitors in <i>P. palmivora</i> virulence.	Gumtow, Wu, Uchida, & Tian (2018)
Potato	DMR6	Late blight/ <i>Phytophthora infestans</i>	-Knockout of StDMR6-1 led to increased resistance against late blight but this was not observed in StDMR6-2 knockout mutants. -StDMR6-1 and StDMR6-2 have different functional roles during infection of potato by <i>P. infestans</i> .	Kieu et al. (2021)
Table grapes	WRKY52	Gray mould disease/ <i>B. cinerea</i>	Knockout of VvWRKY52 enhanced resistance to <i>B. cinerea</i> .	Wang et al. (2018)
Tomato	JAZ2	Bacterial speck disease/ <i>Pseudomonas syringae</i>	Gene edited mutants had JAZ2 repressors, lacked the C-terminal Jas domain, and prevented stomatal reopening which is significant for <i>P. syringae</i> .	Ortigosa, Gimenez-Ibanez, Leonhardt, & Solano (2019)

Abbreviation: CRISPR, clustered regularly interspaced short palindromic repeats.

7 | APPLICATION OF PHYSICAL TREATMENTS

The use of physical treatments against microbial growth on fresh produce has received increased attention over the past decades (Munhuweyi, Mpai, & Sivakumar, 2020). The primary mode of action for such applications is through surface disinfection and induced resistance. Commonly used applications include, heat treatment, ultraviolet (UV)-C light, low temperature storage, and CO₂ treatment.

7.1 | Heat treatment

Heat treatment prestorage is a potential postharvest method in reducing microbial inoculum on fresh produce which can be applied in the form of vapor heat, hot water dips, and hot dry air. Postharvest heat treatment reduced development of *B. cinerea* (Marquenie et al., 2002) and *Penicillium expansum* (Conway et al., 2004) in berries and apples, respectively. Heat treatment at 52.5°C applied after inoculation of berries with *B. cinerea* showed a significantly reduced infection level by 72–95% after 9 days compared to control (Lydakakis & Aked, 2003). The treatment was also effective against natural inoculum of *B. cinerea* on berries stored at 0.5°C. The effect of hot water treatment on gene expression revealed key genes associated with mango resistance to pathogens, peel color improvement, and other important phenotypic responses (Luria et al., 2014). The authors conclude that heat stress led to upregulation of stress-response mechanism and subsequently improved fruit quality. Other heat treatment studies have shown reduction in food borne pathogens, such as *E. coli* and *Salmonella*. A reduction by more than 5-log CFU/g in contaminated mung bean, radish and alfalfa sprouts was reported (Weiss & Hammes, 2005); however, efficiency of the heat treatment on the food borne pathogens could not be conclusive due to possibilities of heat resistance (H. Li & Gänzle, 2016). The application of some heat treatment strategies such as water-based methods help reduce water loss in produce, preserves fruit firmness, and improves resistance to mycopathogens, to mention but a few. Future studies on heat treatment approaches should reveal key information on the pathophysiology, biochemistry, and metatranscriptomic profiles of produce following specific methods used. This will provide baseline knowledge for the development of improved heat treatment methods. Moreover, heat treatment strategies can also be applied in combination with other methods to yield better and cost effective outcomes.

7.2 | UV light treatment

UV lighting is one potential nonchemical method applied in reducing/eradicating pathogen inoculum on fresh produce. Low doses at short wavelengths between 190 and 280 nm of UV-C light were found to control a wide range of postharvest rots in fruit and vegetables

(Abdipour, Hosseinifarahi, & Naseri, 2019; Mercier, Baka, Reddy, Corcuff, & Arul, 2001). Such has been attributed to the activation of phenolic pathways (W. Zhang & Jiang, 2019) which induce antifungal activity. Although use of UV light is effective in disinfecting pathogenic and spoilage microbes on food surfaces, it may have negative effects on the quality of the product. A previous study reported a reduction in the tomato carotenoid profile after UV treatment (Charles & Arul, 2007). The lycopene content was lower in UV tomato treated fruit compared to non-treated. These findings were in agreement with (L. H. Liu, Zabarar, Bennett, Aguas, & Woonton, 2009), but this was subject to doses of irradiation. Such negative effect may be a setback since lycopene is a highly valuable phytochemical in human health. Other effects observed in other food products such as chicken fillet included changes in odor and sunburn after UV light exposure (McLeod et al., 2018); however, this did not affect the organoleptic properties of the product.

7.3 | CO₂ treatment

CO₂ treatment is generally used in combination with low temperature storage at postharvest to enhance shelf life of fresh produce. CO₂ treatments have been reported effective in reducing postharvest decay caused by postharvest pathogens in fresh produce such as table grapes. Fungal decay of table grapes was reduced after short-term application of CO₂, which induced defense protein modulation and organic osmolyte (Vazquez-Hernandez, Navarro, Sanchez-Ballesta, Merodio, & Escibano, 2018). However, its use must be applied with caution, since high concentrations may induce softening and “off-flavor” (Cantín et al., 2012), particularly in soft fruit.

7.4 | High pressure processing

High pressure processing (HPP) is a nonthermal and globally accepted food processing technology used for microbial safety and improved storability. Basically, HHP utilizes a sealed nonrigid container which is placed in a pressure vessel for a determined period (Varalakshmi, 2021). The mechanism of HPP involves bursting a large array of pathogen cells at high pressure while preserving color and low molecular weight compounds, which helped accelerate adoption of the technology (Huang, Hsu, & Wang, 2020). Postharvest HHP application can help achieve pathogen reduction on fresh produce and can be used for high acid products (Varalakshmi, 2021). Nevertheless, tissue injury can be a drawback.

Current knowledge of HHP treatment showed 3.7-log CFU/g reduction in *Listeria innocua* (Inanoglu et al., 2021) and elimination of *Salmonella* (Agregán et al., 2021) despite the ability of the food matrix in protecting microorganisms to pressure. From a shelf life perspective, downstream products of HHP-treated fruits were more resistant to spoilage microbes and preserved nutritive quality. However, HHP is more effective against vegetative microbes compared to bacterial spores, which forms part of the technology's disadvantage.

8 | CONCLUSION AND FUTURE PROSPECTS

As the world population and the demand for safe fresh produce continues to grow, there is an increasing need to develop eco-friendly and effective methods to reduce postharvest losses and ensure food safety. Needless to say, the twilight of synthetic chemicals along the farm to fork nexus is imminent. Biological control remains a key strategic component of an integrated plant and foodborne pathogen management approach in the face of stringent measures and calls to phase out synthetic chemicals along the farm to fork nexus. This includes increased focus on the use and cost effective application of plant extracts and microbial-based formulations. More importantly, formulation of biocontrol agents has to remain at par with evolutionary processes of pathogens. For this reason, the manipulation and utilization of beneficial microbial consortia is required at a molecular level to enable widespread adoption of genetic manipulation of antagonists and improve biocontrol activity. Understandably, more insights into microbiomes of plant surfaces and unearthing unknown microbial associations within their natural ecological niches will contribute significantly to improved biocontrol performance or development of novel approaches, and a shift from synthetic chemicals. Research also needs to focus on microbiomes not as containing harmful microorganisms but also as a way of harnessing beneficial species that can be of use. The diversity of microbiomes is linked to plant health and the ability to resist attack by phytopathogens. In addition, the use of genetic sequences belonging to pathogenic taxa can be useful to develop disease predictive models and help determine duration of storage. Added to this, the use of CRISPR/Cas technology is an area also deserving more attention as the technology can be used to transiently improve efficacy of biocontrol agents. However, methodological improvements are still required to optimize specificity and efficiency, and capitalize on the potentiality of this novel technology. A multifaceted approach is therefore needed to simultaneously tackle foodborne disease outbreaks and minimize crop losses while signifying the dawn of sustainable practices along the food chain using biocontrol solutions. In fact, combining microbial-based products with physical biocontrol approaches have potential to yield better results. This will indeed indicate a significant food safety milestone.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Mosimanegape Jongman and **Annancietar Gomba**: Conception and design, and drafting the manuscript. **Mosimanegape Jongman**, **Annancietar Gomba**, **Patricia Carmichael**, and **Daniel Loeto**: Revising the manuscript. **Mosimanegape Jongman**, **Annancietar Gomba**, **Patricia Carmichael**, and **Daniel Loeto**: Final approval of the version to be published, and agreed to be accountable for all aspects of the work.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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