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REVIEW



## Biological control of postharvest fungal decays in citrus: a review

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### ABSTRACT

Citrus (*Citrus* spp.) species produce a variety of fruits that are popular worldwide. Citrus fruits, however, are susceptible to postharvest decays caused by various pathogenic fungi, including *Penicillium digitatum*, *Penicillium italicum*, *Geotrichum citri-aurantii*, *Aspergillus niger*, and *Aspergillus flavus*. Decays resulting from infections by these pathogens cause a significant reduction in citrus quality and marketable yield. Biological control of postharvest decay utilizing antagonistic bacteria and fungi has been explored as a promising alternative to synthetic fungicides. In the present article, the isolation of antagonists utilized to manage postharvest decays in citrus is reviewed, and the mechanism of action including recent molecular and genomic studies is discussed as well. Several recently-postulated mechanisms of action, such as biofilm formation and an oxidative burst of reactive oxygen species have been highlighted. Improvements in biocontrol efficacy of antagonists through the use of a combination of microbial antagonists and additives are also reviewed. Biological control utilizing bacterial and yeast antagonists is a critical component of an integrated management approach for the sustainable development of the citrus industry. Further research will be needed, however, to explore and utilize beneficial microbial consortia and novel approaches like CRISPR/Cas technology for management of postharvest decays.

### KEYWORDS

Antagonists; citrus fruits; fungal pathogens; genomics; mechanism of action; microbial community

### Introduction

Citrus (*Citrus* spp.) species (oranges, lemons, grapefruit, mandarin, etc.) are widely-consumed worldwide due to their refreshing flavor and nutritional value (Liu, Heying, and Tanumihardjo 2012). They contain relatively high levels of bioactive compounds that possess antioxidant properties, and are also major contributors to the dietary requirement for vitamin C in humans (Mditshwa et al. 2017). Citrus crops are globally cultivated in over 140 tropical and sub-tropical countries. Recent data from FAO indicated that the production of all citrus fruits, including orange, mandarin, grapefruit, lemon, and lime, was over 150 million tonnes in 2018, with oranges representing half of this production (<http://www.fao.org/faostat/en/?#data/QC>, Accessed June 15, 2020). Citrus fruits, however, are susceptible to a variety of phytopathogens, including fungi, bacteria, and viruses that cause diseases at different stages of citrus production (Aboutorabi 2018; Achachi, Barka, and Ibriz 2014; Chen et al. 2019; Cubero et al. 2016; Etebu and Nwauzoma 2014; Gottwald 2010).

In particular, infections by postharvest decay fungi, such as *Penicillium digitatum*, *Penicillium italicum*, *Geotrichum citri-aurantii*, *Aspergillus niger*, and *Aspergillus flavus*, with

*P. digitatum* being the most prevalent (Macarasin et al. 2007; Moraes Bazioli et al. 2019), result in significant reductions in quality and marketable yield. Postharvest losses, however, can be significantly reduced if appropriate and effective storage management practices are utilized. As public concerns over the impact of synthetic chemicals on food safety and environmental protection increase, eco-friendly management methods, such as biological control that utilize antagonistic bacteria and yeasts to control postharvest decays in fruits, including citrus, are being explored (Dukare et al. 2019; Liu et al. 2013; Palou, Smilanick, and Droby 2008). A representative sample of studies on the biocontrol of postharvest fungal decays of citrus utilizing antagonists is presented in Table 1.

The objective of the current review is to provide an overview on the use of antagonistic bacteria and yeasts used to control postharvest decays of citrus, and their corresponding mechanisms of action. Methods used to enhance the biocontrol efficacy of antagonists, such as combining microbial antagonists with other materials/methods are also reviewed. Novel approaches to control citrus postharvest decays, such as the use of beneficial microbial consortia and CRISPR/Cas technology are also presented and discussed.

**Table 1.** Representative literatures on biological control of postharvest fungal diseases in citrus.

Disease	Pathogen	Host	Antagonist	Source of isolate	Reference
Green mold	<i>Penicillium digitatum</i>	Orange ( <i>Citrus sinensis</i> cv. Newhall)	<i>Metschnikowia</i> sp., <i>Pichia kluyveri</i> , <i>Candida railenensis</i> , <i>Candida oleophila</i> , <i>Candida albicans</i> , <i>Candida fermentati</i> , <i>Pseudozyma antarctica</i> , <i>Pseudozyma hubeiensis</i> , <i>Hanseniaspora uvarum</i> , <i>Kazachstania bovina</i>	Leaf and fruit surfaces of orange	Liu et al. (2017)
Green mold	<i>P. digitatum</i>	Orange ( <i>C. sinensis</i> cv. Gongchuan)	<i>Rhodotorula mucilaginosa</i>	Fruit surface of peach	Ahima et al. (2019)
Green mold	<i>P. digitatum</i>	Orange ( <i>C. sinensis</i> cv. Jincheng 447#)	<i>Lactobacillus sucicola</i> , <i>Weissella paramesenteroides</i> , <i>Pediococcus acidilactici</i>	Orange fruit surface, leaves of orange and peanut, and soil in citrus orchard	Ma et al. (2019)
Green mold	<i>P. digitatum</i>	Kinnow ( <i>Citrus reticulata</i> )	<i>Saccharomyces</i> sp.	Fruit surfaces of mango, green chili, orange, grape, lemon and tomato	Habiba et al. (2019)
Green mold	<i>P. digitatum</i>	Lemon ( <i>Citrus limon</i> )	<i>Clavispora lusitaniae</i>	Citrus plant	Perez et al. (2019)
Green mold	<i>P. digitatum</i>	Orange ( <i>C. sinensis</i> cv. Newhall), Lemon ( <i>C. limon</i> ), Orange ( <i>C. sinensis</i> cvs. Tarocco & Jincheng 447#)	<i>Pichia galeiformis</i>	Citrus fruit, flower, leaf and soil	Chen et al. (2020)
Green mold	<i>P. digitatum</i>	Orange ( <i>C. sinensis</i> )	<i>Trichoderma harzianum</i>	Rhizosphere of citrus tree	Ferreira et al. (2020)
Green mold	<i>P. digitatum</i>	Orange ( <i>C. sinensis</i> )	<i>Bacillus</i> sp.	Soil of citrus orchard	Tian et al. (2020)
Green mold	<i>P. digitatum</i>	Lemon ( <i>C. limon</i> )	<i>Bacillus subtilis</i> , <i>Bacillus pumilus</i> , <i>Bacillus cereus</i> , <i>Bacillus megaterium</i> , <i>Agrobacterium radiobacter</i>	Rhizosphere and phyllosphere of plants	Mohammadi et al. (2017)
Blue mold	<i>Penicillium italicum</i>	Orange ( <i>C. sinensis</i> )	<i>Candida stellimalicola</i>	Citrus leaf	Da Cunha et al. (2018)
Blue mold	<i>P. italicum</i>	Mandarin ( <i>C. reticulata</i> cv. Oran)	<i>Cryptococcus laurentii</i>	Surface of apple fruit	Li, Shi, et al. (2019)
Blue mold	<i>P. italicum</i>	Orange ( <i>C. sinensis</i> cv. Jincheng 447#)	<i>Metschnikowia citriensis</i> , <i>Candida oleophila</i> , <i>Pseudozyma antarctica</i>	Surface of citrus leaf	Liu et al. (2019)
Blue mold	<i>P. italicum</i>	Mandarin ( <i>C. reticulata</i> cv. Clementine)	<i>Agrobacterium rubi</i>	Phyllosphere and rhizosphere of wild and traditionally cultivated plant	Tozlu et al. (2019)
Blue mold	<i>P. italicum</i>	Orange ( <i>C. sinensis</i> cv. Jincheng 447#)	<i>Pseudomonas fluorescens</i>	N/A	Wang, Mei, et al. (2020)
Aspergillus rot	<i>Aspergillus flavus</i>	Lemon ( <i>C. limon</i> cvs. Meyer & Interdonato)	<i>Pantoea agglomerans</i> , <i>Alcaligenes piechaudii</i> , <i>Bacillus subtilis</i> , <i>Burkholderia cepacia</i> , <i>Erwinia rhapontici</i> , <i>Erwinia chrysanthem</i>	Aerial part of pome fruit	Kotan, Dikbas, and Bostan (2009)
Soft rot	<i>Aspergillus niger</i>	Lemon ( <i>C. limon</i> )	<i>Bacillus subtilis</i>	Pigeon pea rhizosphere	Manjula, Kishore, and Podile (2004)
Sour rot	<i>Geotrichum citri-aurantii</i>	Mandarin ( <i>C. reticulata</i> )	<i>Cryptococcus laurentii</i> , <i>Rhodospiridium paludigenum</i>	N/A	Liu et al. (2010)
Sour rot	<i>G. citri-aurantii</i>	Mandarin ( <i>C. reticulata</i> cv. Wuzishatangju)	<i>Bacillus amyloliquefaciens</i>	Surface of mandarin fruit	Hong et al. (2014)
Sour rot	<i>G. citri-aurantii</i>	Orange ( <i>C. sinensis</i> )	<i>Rhodotorula minuta</i> , <i>Candida azyma</i> , <i>Aureobasidium pullulans</i>	Citrus plant	Ferraz et al. (2016)
Sour rot	<i>G. citri-aurantii</i>	Orange ( <i>C. sinensis</i> )	<i>Aureobasidium pullulans</i>	Citrus plant	Klein and Kupper (2018)
Sour rot	<i>G. citri-aurantii</i>	Orange ( <i>C. sinensis</i> cv. Jincheng 447#)	<i>Metschnikowia citriensis</i>	Citrus leaf surface	Wang, Ruan, et al. (2020)
Black rot	<i>Alternaria citri</i>	Orange ( <i>C. sinensis</i> cv. Valencia)	<i>B. amyloliquefaciens</i>	Orange fruit surface	Arrebola, Jacobs, and Korsten (2010)
Anthraco	<i>Colletotrichum gloeosporioides</i>	Orange ( <i>C. sinensis</i> cv. Valencia)	<i>B. amyloliquefaciens</i>	Orange fruit surface	Arrebola, Jacobs, and Korsten (2010)
Black spot	<i>Phyllosticta citricarpa</i>	Orange ( <i>C. sinensis</i> cv. Valencia)	<i>Saccharomyces cerevisiae</i>	Fermentation processes for fuel ethanol production	Toffano, Fialho, and Pascholati (2017)

## Major postharvest fungal decays

### Green mold

Green mold caused by *P. digitatum* is the most prevalent and serious postharvest decay of citrus fruit. It causes significant losses worldwide and can account for up to 90% of the total postharvest losses in the citrus industry (Cheng et al. 2020; Macarasin et al. 2007; Marcet-Houben et al. 2012). *P. digitatum* is a necrotrophic phytopathogen that infects citrus fruit through wounds resulting from insect and mechanical damage, as well as environmental factors, such as adverse temperatures, wind, rain, and hail (Perez et al. 2017). *P. digitatum* conidia germinate under suitable conditions and produce germ tubes that penetrate into pericarp cells, extend into mesocarp cells, and gradually invade the surrounding tissues. The initial infection often appears as a water-soaked lesion and eventually, in the case of green mold, white mycelia and newly-generated grayish/green conidia, appear at the infected sites. As the infection progresses and the fruit rots, pericarp and mesocarp cells are plasmolyzed, and their inclusions and organelles become degraded as cellular constituents leak from the cells (Cheng et al. 2020; Ladaniya 2008; Lin et al. 2019). Previous studies showed that terpene down-regulation in transgenic orange triggered defense responses against *P. digitatum* (Rodríguez et al. 2011, 2014). Moreover, Tao et al. (2019) reported that terpene limonene induced the green mold of citrus fruit through regulation of reactive oxygen species (ROS) homeostasis in *P. digitatum* spores, while Che et al. (2020) conducted metabolomics analysis to reveal that myrcene stimulates the spore germination of *P. digitatum* via the upregulation of central carbon and energy metabolism. In addition to direct economic losses due to green mold, *P. digitatum* also produces mycotoxins that pose a potential human health risk. Alkaloids, including tryptoquialanines A, B, and C, produced by *P. digitatum* in citrus fruit have been detected and identified (Araujo et al. 2019; Ariza et al. 2002; Costa et al. 2019).

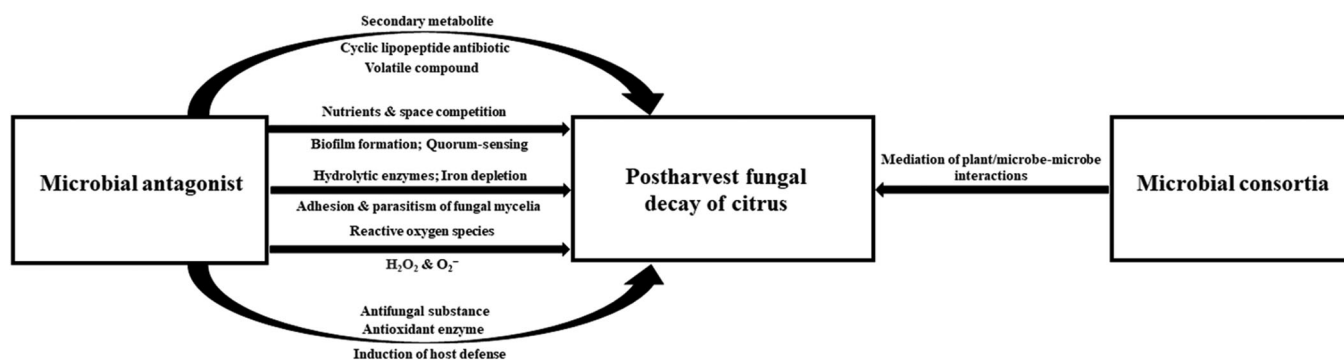
Increasing amounts of genetic and pathogenicity data on *P. digitatum* have become available due to advances in high-throughput sequencing technologies and bioinformatic tools. Notably, analysis of the genome sequence of *P. digitatum* (Marcet-Houben et al. 2012) has revealed absence of the genes required for patulin biosynthesis, a major mycotoxin produced by *Penicillium expansum*, another postharvest fungal pathogen that mainly infects pome fruit and is closely-related to *P. digitatum*. Furthermore, Julca et al. (2015) reported the genomic variation that exists between *P. digitatum* and *P. expansum*, and reflected underlying differences of population dynamics related to host specificity and agricultural practice. Sun, Li, and Yu (2011) published the mitochondrial genome sequence of *P. digitatum* and described its close relationship to the mitochondrial genomes of closely-related species in *Penicillium* and *Aspergillus*. Wang and Li (2008) first demonstrated that *Agrobacterium tumefaciens*-mediated transformation (ATMT) of *P. digitatum* could be used for insertional mutagenesis in *P. digitatum* to study functional genomics. López-Pérez, Ballester, and

González-Candelas (2015) utilized ATMT to generate knock-out mutants for two genes, *pectin lyase* (*Pnl1*) and *naphthalene dioxygenase* (*Ndo1*), in *P. digitatum*, and found that the  $\Delta$ *pnl1* mutant was less virulent, compared to the parental strain or an ectopic transformant. No decrease in virulence was observed, however, in  $\Delta$ *ndo1* mutants. Yang et al. (2019), in a transcriptomic study of *P. digitatum* infection of citrus fruit, reported that the genes related to pathogenicity factors, antioxidant activity and iron transport were involved in the infection process. Collectively, these recent molecular and genetic studies are providing a more comprehensive understanding of the molecular mechanisms underlying pathogenicity and virulence of *P. digitatum* in citrus.

### Other decay fungi

In addition to green mold, other fungal decays of citrus are also economically-important (Table 1). *Penicillium italicum* causes blue mold on citrus, and is characterized by white mycelia that cover infected fruit producing bluish spores. This is in contrast to green mold which produces white mycelia and grayish/green spores (Cheng et al. 2020; Ladaniya 2008). Blue mold can represent a bigger problem than green mold due to nesting, a process by which the infection rapidly spreads to intact, healthy fruit present in the same packing box or crate as the infected fruit, regardless of injury (Latifa et al. 2011). *P. italicum* could produce hydrolytic enzymes which soften adjacent fruit peel, thus providing an infection court. Green mold, however, does not spread by nesting and so adjacent, non-injured fruit in the same packing container do not become infected. Conidial spores, however, will surround fruit, so that the fruit needs to be repacked (Ladaniya 2008). Li, Shi, et al. (2019) recently reported that cell wall degradation/modification of fruit host was one of the mechanism of action for *P. italicum* in its infection of “Shatangju” mandarin.

Sour rot caused by *G. citri-aurantii* is another important disease that spreads in all citrus producing countries and influences various citrus varieties (Ferraz et al. 2016; Hong et al. 2014; Klein and Kupper 2018; Wang, Ruan, et al. 2020). Mandarin varieties, in general, develop sour rot more readily, compared to grapefruit and orange varieties (Ferraz et al. 2016). *Aspergillus* spp. are phytopathogenic fungi that most commonly produce a variety of different aflatoxins (Jaibangyang, Nasanit, and Limtong 2020). *Aspergillus flavus* not only causes postharvest decay of citrus fruit, but certain toxigenic isolates also produce aflatoxin B1, a very potent carcinogen. When produced in fruit, the aflatoxin may contaminate the fruit and downstream processed products, such as orange juice (Bamba and Sumbali 2005; Kotan, Dikbas, and Bostan 2009; Samuel, Ifeanyi, and Ugochukwu 2015). *A. niger* also causes soft rot in harvested citrus fruit (Manjula, Kishore, and Podile 2004; Samuel, Ifeanyi, and Ugochukwu 2015; Sibi et al. 2012). In addition, other phytopathogenic fungi, such as *Alternaria citri* and *Colletotrichum gloeosporioides* also cause postharvest decays of citrus fruits (Arrebola, Jacobs, and Korsten 2010; Jing et al. 2020; Shehata et al. 2018).



**Figure 1.** Diagram of postharvest fungal decay control by the microbial antagonist and the microbial consortia.

The group of postharvest decays discussed in this review not only cause marked economic losses in citrus, but also have a direct impact on food safety in some cases. Fortunately, a number of eco-friendly management practices, including biological control, have been identified that can be used to reduce the economic losses resulting from these fungal diseases and address the health concerns surrounding the use of synthetic chemical fungicides.

### Mechanisms of biocontrol of postharvest fungal decays

A comprehensive understanding of the mechanism of action of biocontrol agents (BCAs) is vital for their effective use in disease management (Köhl, Kolnaar, and Ravensberg 2019). Competition for nutrients and space, antibiosis, mycoparasitism, secondary metabolite production, and induction of disease resistance in the host are major mechanisms displayed by BCAs against postharvest fungal decays (Dukare et al 2019; Francesco, Martini, and Mari 2016). The role of biofilm formation, quorum sensing, oxidative bursts, and antifungal volatile compound (VOC) production in suppressing postharvest fungal pathogens have also been elucidated. More recently, Wisniewski and Droby (2019) proposed that understanding the functional role and impact of the endophytic/epiphytic microbiome of fruit would provide essential information to develop effective and biofunctional biocontrol systems. They further proposed that natural and synthetic microbial consortia could be used to prolong shelf life of harvested horticultural produce by controlling pathogens and regulating physiological disorders. The main mechanisms of action underlying the control of postharvest decays of citrus fruit by BCAs are shown in Figure 1 and discussed below.

#### Competition for nutrients and space

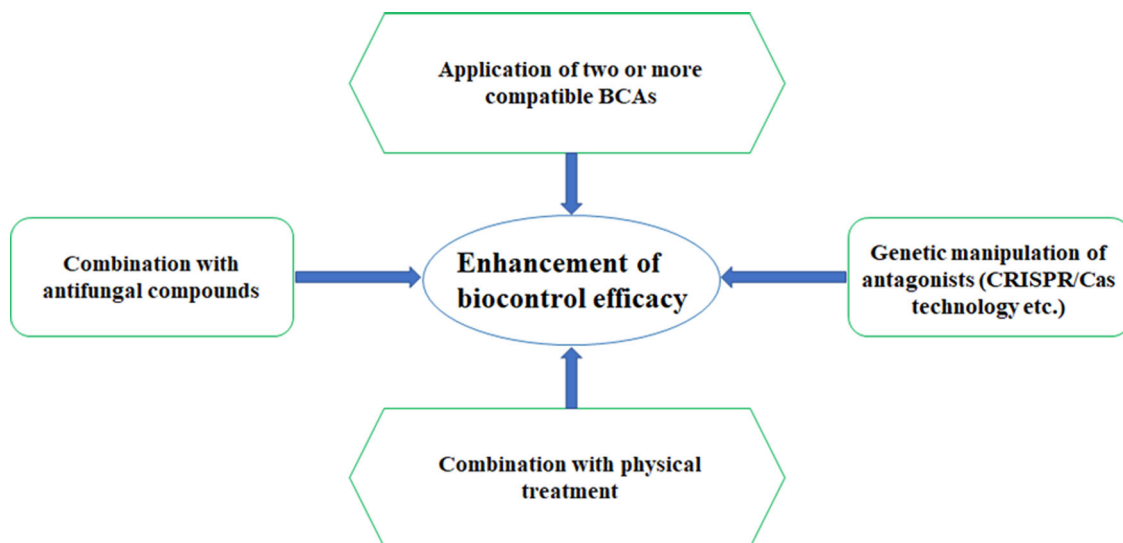
The ability to colonize host tissues is a basic attribute of an active BCA, allowing it to successfully compete with a decay pathogen for nutrients and space. It is a key factor that enables BCAs to suppress postharvest pathogens (Francesco, Martini, and Mari 2016; Nunes 2012; Spadaro and Droby 2016). Zhu et al. (2019) observed that the antagonistic yeast, *Yarrowia lipolytica*, had a greater ability than *P. digitatum* and *P. italicum* to adapt to the mandarin wound

environment at both storage temperatures of 20 and 4 °C. The yeast also induced a resistance response in mandarin fruit which contributed to decay control and biocontrol efficacy. Wang, Ruan, et al. (2020) in an analysis of population dynamics using scanning electron microscopy (SEM), reported that the antagonistic yeast, *Metschnikowia citriensis*, rapidly colonized wounds and tightly adhered to the cell surface in wound sites, enabling it to compete against *G. citri-aurantii* for nutrients and space. Importantly, depletion of nutrients and colonization in wounds during the first 48 hours after yeasts are administered is critical as it could impose a direct impact on the germination of fungal spores (Nie et al. 2019). Antagonistic bacteria can also be used to compete for nutrients and space against fungal pathogens and thus provide protection from postharvest decays (Lastochkina et al. 2019). For instance, Scuderi et al. (2009) found that the mechanisms of action by which *Burkholderia gladiol* controlled green mold of orange and lemon fruits included both competition for nutrients and space, and the production of antifungal metabolites. Recently, Wang et al. (2018) also proposed that competition for nutrients and space played a crucial role in the biocontrol properties of *Pseudomonas fluorescens* for controlling green mold of orange fruit. Collectively, these reports have provided support for the premise that competition for nutrients and space is a fundamental mechanism of action underlying the ability of BCAs to suppress postharvest decay.

#### Biofilms

A fundamental change at physiological and molecular levels under specific conditions can lead to the biofilm formation of some BCAs (Pandini et al. 2017). This biochemical shift and morphological change represents an attribute that may contribute to the ability of some BCAs to inhibit postharvest decays by reducing the amount of physical space available for pathogen development and interfering with the flow of nutrients and/or germination signals from the host to the pathogen spores (Francesco, Martini, and Mari 2016; Liu et al. 2013; Spadaro and Droby 2016). Liu et al. (2014) reported that the quorum-sensing molecule, phenylethanol, could promote adhesion and biofilm formation by *Kloeckera apiculata* in wounded orange fruit which contributed to the control of *P. italicum*. Liu et al. (2019) hypothesized that biofilm formation, along with hyphal adhesion and iron depletion, were the





**Figure 2.** Diagram of promising approaches/additives for enhancement of biocontrol efficacy.

main mechanisms of action of *Metschnikowia citriensis* against *P. digitatum* and *P. italicum*. Klein and Kupper (2018) reported that biofilm formation by the yeast-like, antagonistic fungus, *Aureobasidium pullulans*, improved its biocontrol efficacy against *G. citri-aurantii* in orange. It is more common for bacteria than yeast to form a biofilm. In this regard, 50 µg/mL tea saponin enhanced biofilm formation and stimulated the growth of *Bacillus amyloliquefaciens* in mandarin fruit wounds, contributing to an improvement in biocontrol efficacy against green and blue molds, and sour rot (Hao et al. 2011). Wang, Mei, et al. (2020) reported that the potential mechanisms of action underlying the ability of *P. fluorescens* to control blue mold included competition for nutrients and space, siderophore production, biofilm formation, and production of antifungal VOCs, all of which inhibited growth and infection of *P. italicum*. Biofilm formation also increases the tolerance of microbial antagonists to abiotic stress (Chi et al. 2015; Li et al. 2016). The ability of microbial antagonists to enhance abiotic stress tolerance in host tissues has also been reported (Timmusk et al. 2015; Wang et al. 2019). Therefore, it may be worthwhile to investigate if BCAs have a similar effect on citrus fruits.

## ROS

Macarasin et al. (2010) proposed a new role for ROS (mainly  $H_2O_2$  and  $O_2^-$ ) in postharvest biocontrol system of citrus and apple fruit. They investigated ROS production when the antagonistic yeasts, *Metschnikowia fructicola* and *Candida oleophila*, were applied to citrus and apple fruits. Their results indicated that *M. fructicola* and *C. oleophila* yeast cells generated greater amount of super oxide anion ( $O_2^-$ ) on intact fruit surfaces than on a nutrient-poor agar medium. Application of *M. fructicola* and *C. oleophila* in citrus and apple fruit wounds was correlated with  $H_2O_2$  accumulation in fruit host tissues. They proposed that the yeast-induced oxidative response in fruit host was associated with the ability of yeasts for control of postharvest decays. Since then, several other studies have elucidated the role of ROS-

related mechanisms in the postharvest biocontrol system of citrus. Luo, Zhou, and Zeng (2013) confirmed the observation of Macarasin et al. (2010) using another biocontrol yeast species, *Pichia membranaefaciens*. They found *P. membranaefaciens* enhanced the level of  $O_2^-$  and  $H_2O_2$  in citrus peel tissues and inhibited the infection fruit by *P. digitatum* and *P. italicum*. Liu et al. (2010) observed that *Cryptococcus laurentii* and *Rhodosporidium paludigenum* enhanced peroxidase and superoxide dismutase (SOD) activity in fruit host, which contributed to the control of sour rot in mandarin fruit. Similarly, the biocontrol bacterium, *Pantoea agglomerans* CPA-2, was reported to induce  $H_2O_2$  production, and catalase and SOD enzyme activity in oranges potentially contributing to the mechanism of action against green mold (Torres et al. 2011). Hershkovitz et al. (2012) and Liu et al. (2016), using an Affymetrix Citrus Gene Chip, identified the upregulation of ROS-related genes in grapefruit and navel orange, that were associated with biocontrol activity. Inevitably, new roles for ROS in the biocontrol activity of BCAs will be identified at the molecular level.

## Other mechanisms of action

Induction of host defense is one of the mechanisms of action in the biocontrol of postharvest decay by antagonistic microbes on various fruits, including citrus (Dukare et al. 2019; Moraes Bazioli et al. 2019; Talibi et al. 2014). Induction of pathogenesis-related proteins, antioxidant enzymes, and antifungal substances in citrus fruit by various antagonistic yeasts, including *Debaryomyces hansenii* (Arras and Arru 1999), *C. oleophila* (Droby et al. 2002), *Pichia membranaefaciens* (Luo, Zeng, and Ming 2012; Wang, Zhou, et al. 2020), and *Y. lipolytica* (Zhu et al. 2019), and by bacteria, including *P. fluorescens* (Wang et al. 2018) and *Bacillus subtilis* (Waewthongrak, Pisuchpen, and Leelasuphakul 2015) have been reported. Secondary metabolites, such as cyclic lipopeptide antibiotics (Arrebola, Jacobs, and Korsten 2010; Tian et al. 2020; Waewthongrak, Pisuchpen, and Leelasuphakul 2015) are produced by antagonistic bacteria, as well as VOCs,

which are produced by both antagonistic bacteria (Arrebola, Sivakumar, and Korsten 2010) and yeasts (Tilocca, Cao, and Migheli 2020; Toffano, Fialho, and Pascholati 2017). Regarding the production of antibiotics, however, food safety issues should be taken into consideration. In contrast to bacteria, no antibiotics have been reported to be involved in the biocontrol activity of yeasts.

Other mechanisms of action have also been reported to be involved in the biocontrol of postharvest decay in citrus. These include, the production of hydrolytic enzymes and “killer proteins,” adhesion to and parasitism of fungal mycelia, iron depletion, etc. Readers are referred to the recent review articles on these aspects for more details (Moraes Bazioli et al. 2019; Papoutsis et al. 2019). In all likelihood, several mechanisms operate together and are responsible for the biocontrol activity of yeast and other biocontrol agents. Notably, biocontrol efficacy is not only determined by the interactions between the pathogen, BCA, and the host but also by environmental factors (Liu et al. 2013; Sui et al. 2015).

### Enhancement of biocontrol efficacy and commercial products

Despite the ability to inhibit postharvest decay, application of BCAs alone has not been proven to be sufficient to achieve a consistent and stable level of control efficacy. Therefore, integrated management strategies have been developed to attain the commercial levels of decay control achieved by the use of synthetic chemicals and required by industry under various environmental conditions (Romanazzi et al. 2016; Sui et al. 2016; Wisniewski et al. 2016; Zhang et al. 2017; Zhang et al. 2018). A diagram of promising approaches/additives for enhancement of biocontrol efficacy is shown (Figure 2). Panebianco et al. (2015) reported that use of a combination of *Pseudomonas* spp. and *Trichoderma* spp. represented a promising approach for control of green mold of citrus, based on the premise that improved decay control could be achieved by the combined mechanisms of action of two or more compatible BCAs that operate on different aspects or stages of fungal growth. Combining BCA with bioactive, natural compounds has also been reported to be an effective, integrated control method. The addition of glycolchitosan (El-Ghaouth, Smilanick, and Wilson 2000), chitosan oligomers (Lu et al. 2014), chitosan (Zhou, Zhang, and Zeng 2016), cinnamic acid (Li, Li, et al. 2019), and cardoon leaf extract (Restuccia et al. 2020) could effectively enhance the biocontrol performance of antagonistic yeasts, including *Candida saitoana*, *Rhodospiridium paludigenum*, *Pichia membranaefaciens*, *Cryptococcus laurentii*, and *Wickerhamomyces anomalus*, against postharvest decays of orange, lemon, and mandarin fruits, respectively. Physical treatments, such as hot water also enhance the biocontrol efficiency of yeast antagonists against infection of postharvest pathogens on citrus fruit (Porat et al. 2002; Zhou, Deng, and Zeng 2014). An eco-friendly integrated management approach may be what is needed for biocontrol to be accepted and readily used by the fruit industry.

The low success rate of postharvest biocontrol products has been attributed to several issues, like difficulty in mass production and formulation, short shelf life, and highly variable conditions in pack houses. A well-formulated biocontrol product typically consists of one (or more) microbial antagonist(s) as an active ingredient, carrier material, and adjuvants that support cell viability and provide protection from various environmental stresses. A third-party evaluation of the safety to human health and environment that meets with the criteria of specific government agencies is also mandatory for a commercial product. Specifically, in regard to postharvest biocontrol products, the regulation may be more strict as the harvested produces would directly go to the table for consumption. Four commercial biocontrol products based on microbial antagonists, “Aspire,” “Shemer,” “Pantovital,” and “Biosave,” have been available at one time or another for the control of postharvest citrus fruit (Moraes Bazioli et al. 2019). The yeast-based postharvest biocontrol product was commercialized under the trade name “Aspire” by Ecogen, Inc, and was based on *Candida oleophila* strain I-182, however, for several reasons its place in the market was not sustained (Liu et al. 2013). The potential of this yeast species is still being used, however, and is the active ingredient in a European product, Nexy. The genome of *C. oleophila* I-182 has also been recently sequenced (Sui et al. 2020). Shemer<sup>TM</sup>, based on the yeast *Metschnikowia fructicola* (Droby et al. 2009), was initially registered in Israel for both pre- and postharvest application on a variety of horticultural crops, including citrus fruit. Shemer<sup>TM</sup> was acquired by Bayer CropScience (Germany), and then sublicensed to Koppert (Netherlands) (Spadaro and Droby 2016). Two bacterial products “Pantovital” and “Biosave,” based on *Pantoea agglomerans* and *Pseudomonas syringae*, respectively, also exhibit effective control against various postharvest fungal pathogens, including *Penicillium*, *Botrytis*, *Monilinia*, and *Mucor* (Moraes Bazioli et al. 2019).

### Potential of microbiome

Microbiome-based research has started a new era in which the knowledge of postharvest biology and technology will be further explored. Based on a more comprehensive understanding of the relationship between the resident microbiota and harvested horticultural crops, it also offers new opportunities for developing novel concept and approaches of biocontrol (Kusstatscher et al. 2020; Wisniewski and Droby 2019). The structure and composition of the postharvest microbiome has been suggested to be a crucial factor in preventing postharvest diseases and has been investigated in various fruits, including strawberry (Cruz et al. 2018), cherry tomato (Liu et al. 2020), and apple (Abdelfattah et al. 2016; Angeli et al. 2019).

The carpoplane (fruit surface) of citrus fruit is colonized by a variety of microorganisms, including several species of bacteria, fungi and yeasts, which may affect its postharvest quality and safety (Gomba, Chidamba, and Korsten 2017). Their study indicated that packhouse processing markedly influenced microbial communities on the citrus carpoplane. More recently, a study of the structure and function of the citrus

rhizosphere microbiome at the global scale was reported by Xu et al. (2018), who found that the core citrus rhizosphere microbiome comprises *Pseudomonas*, *Agrobacterium*, *Cupriavidus*, *Bradyrhizobium*, *Rhizobium*, *Mesorhizobium*, *Burkholderia*, *Cellvibrio*, *Sphingomonas*, *Variovorax*, and *Paraburkholderia*, some of which represent potential beneficial microbes to citrus growth. The authors of that study also identified over-represented microbial functional traits in the citrus rhizosphere, including mediation of plant/microbe-microbe interactions, and promotion of plant growth. The collective findings of the mentioned studies suggest that there is great potential for the use of microbial consortia from different sources to control postharvest decays of citrus.

## Conclusions and future prospects

There is increasing need to develop eco-friendly, effective methods to prevent postharvest losses in citrus (Papoutsis et al. 2019). As the population of the world continues to increase, the ability to prevent the loss of harvested crops to postharvest diseases has become even more critical (Dukare et al. 2019; Wisniewski and Droby 2019). Biological control is a key component of an integrated management approach for the sustainable development of citrus industry. In addition of exploration and utilization of beneficial microbial consortia, further and deeper research about management of postharvest decays will be needed at a molecular level. Genetic manipulation of antagonists has tremendous potential for improving the biocontrol activity of antagonists. Kong et al. (2016) reported that overexpression of bivalent antibacterial peptide genes in *Pichia pastoris* could delay sour rot in citrus fruit and induce cell apoptosis in *Geotrichum citri-aurantii*. The utilization of CRISPR/Cas technology in the manipulation of biocontrol antagonists is an area that deserves greater research. CRISPR/Cas technology can be potentially used to enhance the biocontrol efficacy of BCAs, the postharvest disease resistance of harvested crops, and/or impair the virulence of pathogens (Borrelli et al. 2018; Glandorf 2019; Muñoz et al. 2019).

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