

Review

Yeast Warriors: Exploring the Potential of Yeasts for Sustainable Citrus Post-Harvest Disease Management

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Abstract: Citrus fruits stand as pivotal and extensively cultivated fruit crops on a global scale, boasting substantial economic and nutritional significance. Despite their paramount importance, citrus growers and the industry face a formidable obstacle in the form of post-harvest losses caused by plant pathogens. Effectively addressing this challenge has become imperative. The predominant approach to tackle these pathogens has traditionally involved the use of chemical fungicides. However, the escalating environmental concerns associated with chemical interventions, coupled with a growing consumer preference for pesticide-free produce, have catalyzed an earnest quest for alternative methods of disease control in the citrus industry. The antagonistic yeasts hold great promise as biocontrol agents for mitigating post-harvest fungal diseases in citrus. In this regard, this review summarizes the current state of knowledge regarding the study of yeast strains with biocontrol potential. Thus, the various modes of action employed by these yeasts and their effectiveness against prominent citrus pathogens such as *Penicillium digitatum*, *Penicillium italicum* and *Geotrichum citri* were discussed. Additionally, the review delved into the challenges associated with the practical implementation of yeast-based biocontrol strategies in citrus post-harvest management and investigated the potential of yeast-based approaches to enhance the safety and quality of citrus produce, while reducing the reliance on chemical fungicides and contributing to the sustainable and environmentally responsible future of the citrus industry.

Keywords: antagonistic yeast; citrus; biocontrol; *Penicillium digitatum*; *Penicillium italicum*; *Geotrichum citri*

1. Introduction

Citrus fruits hold a position of profound significance in the world, both economically and culturally. The citrus fruits include oranges, lemons, limes, grapefruits, tangerines and various hybrids and cultivars; they are grown in more than 130 countries and throughout six regions: Africa, North America, South America, Asia, Europe (Mediterranean) and Oceania [1].

The global citrus industry expanded rapidly, making citrus the largest fruit crop by production and planting area. In this context, statistical data reported that citrus fruits

were the second most produced fruit worldwide in 2021, accounting for 161.8 million tons produced in more than 10.2 million hectares [2]. Oranges dominate the global citrus production landscape with a commanding share of 55%, trailed by mandarins at 25%, lemons at 13% and grapefruits at 7%. Nowadays, citrus is one of the most important emerging fruit crops in Morocco, cultivated from north to southwest with an overall production during the campaign (2021–2022) reaching 2.67 million tones on a surface area of 128,000 ha, up 14% on the previous campaign (2020–2021) [3].

However, citrus production has encountered several biotic and abiotic stresses that impact the fruit quality [4]. During post-harvest handling and citrus agroindustry, numerous problems, including issues related to harvesting, transportation, packaging, storage and stocking have made citrus fruits susceptible to mechanical injuries. Consequently, these injuries facilitate the infiltration of fruit-decaying microorganisms, ultimately leading to spoilage, reduced shelf life, underscoring the significance of latent infections during the growing season, and economic losses [5,6]. In particular, the citrus fruit rot ranges from approximately 10% to 30%, although, it has been known to escalate to 50% under severe conditions [7,8]. Alternatively, Bhatta [5] revealed that the economic losses of untreated citrus fruits due to fungal decay have been associated with estimated losses as high as 90% during post-harvest handling and marketing. Therefore, *Penicillium italicum* accounts for approximately 5–10% of the total citrus diseases caused by *Penicillium* spp. While this may seem less significant, it still translates to considerable economic losses for citrus producers, especially considering the high value of the fruit [5]. Further, among all the post-harvest diseases documented in the citrus fruits industry, the green and blue mold caused respectively by *P. digitatum* and *P. italicum* stand out as two major and serious challenges [9,10].

Traditionally, the control of *Penicillium* rot, a common post-harvest disease affecting citrus fruits, has relied upon the utilization of synthetic fungicides such as prochloraz, thiabendazole, pyrimethanil, fludioxonil, and imazalil [11–13]. However, the extensive use of chemical fungicides has adverse effects on human health, contributes to environmental pollution and fosters the development of resistance in fungi, rendering them less effective over time [14,15]. Therefore, at the intersection of food security, sustainability and health-conscious consumer demands, it has become imperative to explore alternative methods for preserving the quality and safety of citrus fruits to meet these evolving needs and priorities [16]. Alternative strategies and substances derived from non-chemical sources are typically far less harmful to human health, environmentally friendly and safer in comparison to conventional synthetic fungicides. In light of this circumstance, the utilization of antagonistic yeasts, naturally present on the surfaces of vegetables and fruits, emerges as a promising and eco-friendly alternative to chemical fungicides in the control of post-harvest diseases [13,17]. The simple nutritional needs, capacity to persist on fruit surfaces for extended periods, competitive aptitude for space and nutrients, tolerance to certain pesticides and the rapid proliferation of the yeasts make them one of the crucial biological control agents (BCAs) of post-harvest disease management [18].

Therefore, this review investigated the utilization of antagonistic yeasts for biocontrol in mitigating fungal post-harvest diseases afflicting citrus fruits. The discourse was intricately woven with insights drawn from the latest literature, concentrating on various facets. This encompassed an exploration into preventing post-harvest diseases in citrus, the biocontrol paradigm against fungal diseases during storage, the application of antagonistic yeasts in citrus post-harvest disease management, the beneficial properties that render yeasts advantageous for potential biocontrol systems, a comprehensive understanding of their mechanisms of action, and a glimpse into future trends in their application.

In this review, bibliometric data were retrieved from 1602 published articles on the use of yeasts as a biological control agents against post-harvest fungal diseases in the citrus industry, based on the Scopus database, the keywords “Antagonistic Yeast,” or “*Metschnikovii pulcherrima*,” or “*Candida oleophila*,” or “*Pichia guilliermondii*,” and “Biocontrol,” and “citrus,” or “Citrus Fruit,” or “Orange,” or “Lemon,” and “Blue Mold,” or “*Geotrichum citri*,” or

“Green Mold,” or “*Penicillium digitatum*,” or “*Penicillium italicum*” were specifically used to gather bibliometric data from the database of SCOPUS (<https://www.scopus.com/>, accessed on 8 October 2023) (Figure 1). The VOSviewer processing software (v1.6.9, Leiden University, Leiden, the Netherlands) was used to create the bibliometric analysis. The network analysis displayed the worldwide distribution of related articles. In Figure 1A, the colors represent groups of linked terms, the label size of a term represents the number of publications, and the distance between two terms represents the degree to which they are associated. For Figure 1B, each node is a country and the links between countries represent co-authorship relationships.

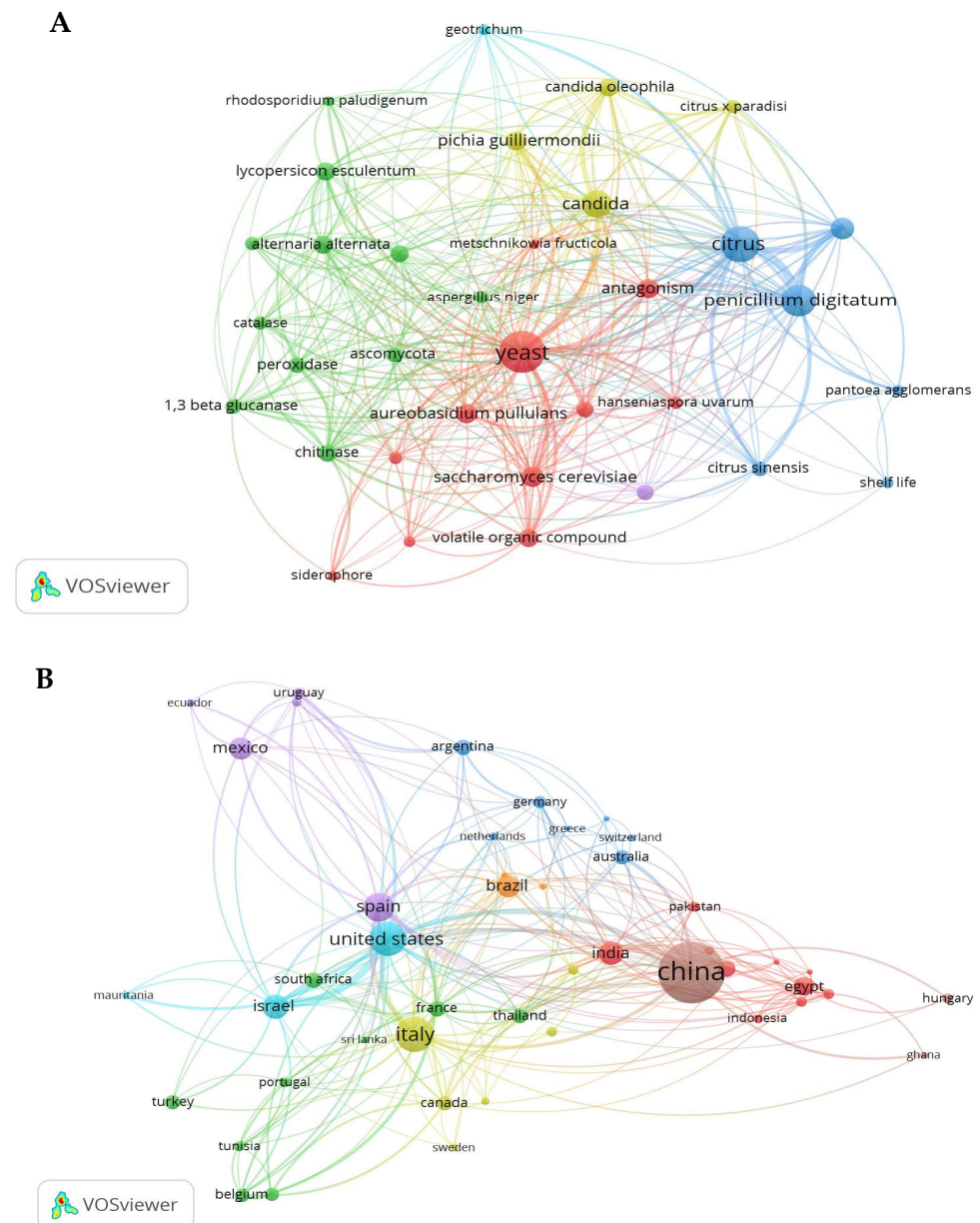


Figure 1. Bibliometric analysis of 1602 published articles about control and management of post-harvest diseases in citrus fruit production according to the Scopus database from the years 2022 to 2024 using specific keywords such as “Antagonistic Yeast,” or “*Metschnikovii pulcherrima*,” or “*Candida oleophila*,” or “*Pichia guilliermondii*,” and “Biocontrol,” and “citrus,” or “Citrus Fruit,” or “Orange,” or “Lemon,” and “Blue Mold,” or “*Geotrichum citri*,” or “Green Mold,” or “*Penicillium digitatum*,” or “*Penicillium italicum*.” (A) The network analysis of their worldwide distribution. (B) The larger the circle, the more intense the scientific activity.

2. Post-Harvest Diseases Affecting Citrus

2.1. Fungal Diseases Affecting Post-Harvest Citrus Worldwide

Fungal diseases represent a formidable menace to global post-harvest citrus production, resulting in considerable economic setbacks while adversely affecting the quality and market appeal of citrus fruits. These diseases, instigated by diverse fungal pathogens, manifest a spectrum of symptoms, ranging from evident fruit rot to latent infections that may only become apparent during post-storage and transportation [5,6]. Fungal pathogens such as *Penicillium* spp., *Alternaria* spp., *Geotrichum candidum* and *Colletotrichum* spp. are among the primary culprits responsible for post-harvest citrus diseases. *Penicillium* spp., notably *P. digitatum* and *P. italicum* are notorious for causing green and blue mold, respectively, resulting in fruit decay during storage and transit [13]. *Alternaria* spp., on the other hand, contributes to citrus black rot, causing both pre- and post-harvest losses [14]. The fungus *G. candidum citri-aurantii* is responsible for the sour rot of citrus fruits during the post-harvest period [19]. *Colletotrichum* spp. cause anthracnose, manifesting as dark, sunken lesions on the fruit's surface, which can lead to fruit deterioration and losses [20]. The frequency and severity of these fungal diseases are influenced by a combination of factors, including environmental conditions (cold, wind, hail and insects) during the citrus fruit development, storage conditions (humidity and temperature), cultural practices and the development of fungal resistance to chemical fungicides [21].

To understand the global scope of the issue, it is imperative to consider statistics and data related to fungal diseases affecting post-harvest citrus. While the specific figures may vary from year to year, the overarching trend is a persistent and substantial impact on citrus production [5]. In relation to this situation, the FAO's statistical database (FAOSTAT) offers a wealth of information on citrus production, including disease-related losses, by region and country [22]. These data reveal the extent of fungal disease outbreaks and their influence on citrus production volumes and marketability. Furthermore, several scientific researchers have investigated the efficacy of various post-harvest treatments and control measures, shedding light on the ongoing efforts to manage fungal diseases in citrus [23,24].

Fungal diseases have long posed a significant challenge to the post-harvest citrus industry in Morocco, threatening fruit quality, shelf life and economic viability [25]. As with the majority of the countries producing citrus fruits, the most common fungal diseases affecting post-harvest citrus in Morocco include *P. digitatum*, *P. italicum*, *Botrytis*, *Gloeosporium*, *Rhizopus*, *Alternaria* and *Mucor* species [26,27]. The diverse environmental conditions and agro-ecological factors in Morocco create an ideal habitat for the proliferation of the citrus fungal pathogens [28]. These pathogens can lead to fruit decay, loss of market value and economic hardship for citrus growers and exporters [9,26]. Synthetic fungicides such as pyrimethanil, imazalil, fludioxonil and thiabendazole are currently used to control these diseases [29]. However, alternative methods for controlling post-harvest citrus diseases have been explored, including the use of plant extracts such as *Anvillea radiata*, *Thymus leptobotrys*, *Ighermia pinifolia*, *Asteriscus graveolens*, *Halimium umbellatum*, *Bubonium odorum*, *Hammada scoparia*, *Inula viscosa* [29], aqueous extracts of Moroccan medicinal plants [28], non-chemical treatments [27] and antagonistic yeasts [30–33]. These alternative methods have shown antifungal activities against *P. digitatum* and *P. italicum* [34].

2.2. Types of Post-Harvest Fungal Diseases of Citrus

More than twenty distinct post-harvest diseases have been documented in citrus, constituting the primary catalyst for fruit deterioration and subsequently, resulting in massive economic losses (Figure 1) [23]. Some post-harvest afflictions affecting citrus fruits arise from infections occurring during the growing season, while others result from injuries sustained during harvest and subsequent fruit-handling processes [35]. However, the foremost and most detrimental post-harvest diseases exerting a profound impact on citrus crop productivity include green mold, blue mold and sour rot. These are attributed to the wound pathogens *P. digitatum*, *P. italicum* and *Geotrichum citri-aurantii*, respectively [36,37].

2.3. Description of the Main Fungal Diseases of Citrus Fruit in Storage

2.3.1. Green Mold

Green mold is one of the most economically impactful post-harvest diseases of citrus fruit, especially oranges and lemons worldwide, which, not only reduces the quality and marketability of citrus fruits but also contributes to food waste and increased production costs [21]. Several pieces of research have revealed that untreated fruits can experience decay from green mold, with estimated losses reaching as high as 90% during post-harvest handling and marketing [5].

P. digitatum is a common post-harvest pathogen that affects citrus fruits, causing a range of symptoms. Initially, small, water-soaked lesions appear on the fruit's surface, often surrounded by a green or yellow halo. These lesions rapidly expand, becoming soft and spongy, with a characteristic green mold growth that causes a powdery texture [38]. As the infection progresses, the citrus fruit can become completely covered with green spores, leading to decay and spoilage [1]. In addition to the visible mold growth, the affected fruit may emit a musty or earthy odor, indicating advanced decay [24].

The observation and characterization of *P. digitatum* colonies on a culture medium are essential for studying its growth, morphology, physiology and potential interactions with other microorganisms [39]. In this context, several scientific studies indicate that the *P. digitatum* colonies typically manifest by a velvety or powdery texture and vivid green color, owing to the production of conidial spores [40,41]. The mycelium radiates outward from a central point, forming a circular or irregular pattern and often exhibits septate hyphae with branching structures [42]. Under optimal growth conditions, the colonies develop rapidly and produce an abundance of conidiophores bearing conidia at their termini, resulting in a strikingly green and flourishing appearance [43]. The distinct growth pattern and pigmentation exhibited by *P. digitatum* are pivotal characteristics crucial for its precise identification in laboratory settings. These traits play a central role in recognizing *P. digitatum* as a prevalent post-harvest pathogen affecting citrus fruits [44]. However, it is noteworthy that the appearance of *P. digitatum* colonies can exhibit variations based on factors such as the specific strain, the composition of the culture medium, as well as temperature and humidity conditions [45].

P. digitatum can be identified under the microscope by its branching mycelium composed of septate hyphae and the characteristic brush-like clusters of conidia produced at the tips of conidiophores [46]. Recently, Wang et al. [47] revealed that the mycelium of *P. digitatum* is composed of a network of branching and filamentous hyphae. These hyphae are typically septate, meaning they are divided into individual cells by septa or cross-walls. Thus, the mycelium is usually colorless or pale in appearance and the hyphal diameter is relatively uniform. On the other hand, a study by Platania et al. [46] revealed that *P. digitatum* produces conidiophores that bear conidia (asexual spores) and that these conidia are typically single-celled and oval-shaped, often appearing in chains resembling a paintbrush or a broom, which is a characteristic feature of this genus. Additionally, Ferreira et al. [14] reported that the color of the spores can vary, but they are often green, reflecting their propensity to produce pigments, thus, these conidia are essential for the dispersal and colonization of new substrates, making them a critical component of *P. digitatum*'s life cycle and its role in causing citrus fruit decay.

P. digitatum is characterized as a necrotrophic pathogen of citrus fruits and its infection is exclusively initiated through wounds present on the surfaces of fruits (Figure 2) [48]. A study by Yang et al. [49] reported that the development cycle of this pathogen begins when airborne conidia, the asexual spores of the fungus, land on the surface of a susceptible citrus fruit. These spores germinate and grow rapidly with a formation of specialized structures called germ tubes, which penetrate the fruit's peel. Within the confines of the fruit, the fungus initiates the formation of mycelium—an intricate network of fungal threads—and embarks on the colonization of the fruit's tissues. This process results in the distinctive growth of greenish mold on the fruit's surface. As the mycelium matures, it gives rise to conidiophores, which, in turn, generate new conidia. These newly formed conidia are

released into the surrounding environment, where they have the potential to infect other citrus fruits, completing the infectious cycle. Environmental variables, particularly temperature and humidity, wield significant influence over the development and progression of *P. digitatum* infections. The production of ethylene, indole alkaloids and the secretion of enzymes that induce softening in adjacent fruits contribute to the swift spread of infection. This rapid dissemination leads to complete rotting within approximately 4–5 days, facilitated via easy transmission through contact [50,51].

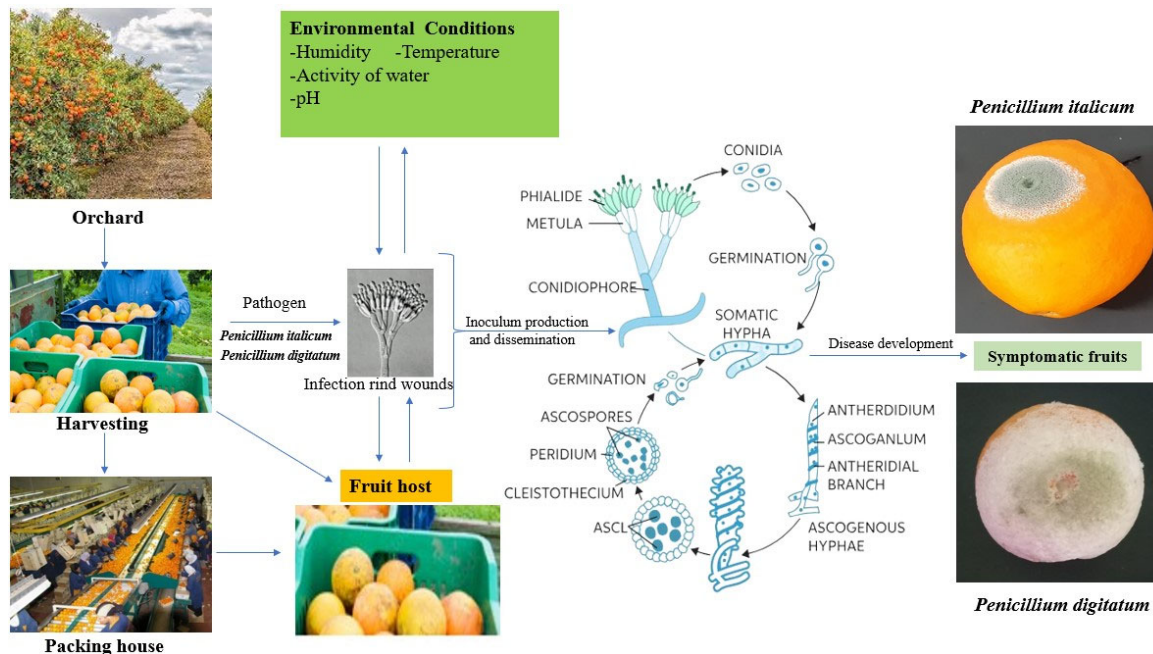


Figure 2. Life cycle and steps of green and blue mold dissemination in the citrus productions.

2.3.2. Blue Mold

P. italicum is a common post-harvest pathogen that affects citrus fruits, particularly lemons and oranges and is responsible for the blue mold disease, which results in significant economic losses for citrus growers and the fruit industry [5]. These losses can be attributed to various factors, including reduced fruit quality, increased production costs, market rejection and overall decreased profitability [36]. The extent of losses caused by the blue mold on citrus fruits during the post-harvest period can vary depending on factors such as the prevalence of the pathogen, environmental conditions and post-harvest practices. Indeed, infected fruits develop characteristic blue-green mold, sunken lesions and a shriveled appearance, making them unattractive to consumers [5]. Thus, blue mold-infected citrus fruits are less marketable due to their unappealing appearance and compromised taste and texture [52]. The *P. italicum* infections can facilitate other infections by other pathogens, such as bacteria and molds which can increase the degree of economic losses of the citrus industry [53]. Additionally, increased production costs, including the expense of fungicides and post-harvest management practices further compound the economic burden [5].

The symptoms of *P. italicum* infection on the citrus fruits typically begin as small, water-soaked lesions on the fruit's surface, often near wounds or damaged areas. As the infection progresses, these lesions expand and develop a characteristic blue mold, which can cover the entire fruit [54]. In the same way, infected fruits may also produce white mycelia and greenish conidia, which are characteristic symptoms of green mold [55]. *P. italicum* is a nesting-type pathogen that spreads rapidly in packed containers to infect adjacent fruits. Thus the pathogen can infect fruits even at lower temperatures in cold storage, leading to substantial economic losses [55].

Under microscopic examination of *P. italicum*, the mycelium appears as a network of slender, branching and septate hyphae that collectively form a dense mat [5]. These

hyphae typically measure 2–4 μm in diameter and are characterized by a distinctive septum at regular intervals, separating the individual cells [36]. As for the spores of *P. italicum*, they are typically produced on specialized structures called conidiophores responsible for the conidia production, which are the asexual spores of the fungus [56]. The conidia of *P. italicum* appear spherical to ellipsoidal in shape, measuring about 2.5–3.5 μm in diameter [56]. They are often characterized by smooth or slightly roughened surfaces and possess a distinctive coloration ranging from pale green to blue-green, which is a hallmark feature of this species [10].

The development cycle of *P. italicum* on citrus can be broken down into several stages. Firstly the *P. italicum* spores are introduced to the citrus fruit through various means, such as contaminated equipment, air or contact with infected fruit [57]. Secondly, the spores of *P. italicum* land on the surface of the citrus fruit and attach themselves to the fruit's skin and under favorable environmental conditions (such as high humidity and suitable temperature), the spores germinate, forming germ tubes, which penetrate the citrus fruit's protective outer layer, which is the peel or rind [53]. This process can be facilitated by wounds or injuries on the fruit's surface, such as those caused during harvesting or handling [53,58]. Thirdly, once inside the fruit, *P. italicum* hyphae grow and colonize the fruit's internal tissues and it starts producing asexual spores called conidia, which are typically green at first but can turn blue-green as they mature, giving the characteristic appearance of blue mold [43]. Finally, the conidia are released from the infected fruit, often aided by air currents or physical disturbances and can land on nearby healthy fruits, facilitating the spread of the disease to other citrus fruits [59]. The cycle repeats itself as the newly infected fruits become a source of spores, leading to further infection of healthy fruits [24].

2.3.3. Sour Rot

Sour rot caused by *G. citri-aurantii* is one of the most troublesome post-harvest diseases of citrus fruits, which greatly deteriorates the fruit quality, leading to massive economic losses in the citrus industry [60]. Additionally, the infection results in the development of sour odors and unsightly mold growth on affected fruits, rendering them unappealing to consumers [61]. As the fungus progresses, it causes the fruit to become soft, mushy and prone to collapsing, ultimately leading to substantial post-harvest losses [62]. Moreover, *G. citri-aurantii*-induced decay often results in off-flavors, making the affected citrus fruits unfit for sale or processing [61]. These losses not only impact the economic viability of citrus production but also contribute to food waste, emphasizing the importance of effective management strategies to mitigate the detrimental effects of this fungal disease on citrus crops [63].

The infected fruits often develop a sour odor due to the production of acetic acid by the fungus, and the fruit surface becomes soft and white and may collapse and become completely rotten [60]. Additionally, *G. citri-aurantii* can also cause brown lesions or decay on citrus fruits, which often start as small, water-soaked spots on the fruit surface and then expand and turn brown and the affected areas may become sunken and can have a rough texture [19]. The infected citrus fruits may develop off-flavors including a sour or musty taste and lose their firmness and become mushy, which reduces their marketability [61].

The microscopic examination of *G. citri-aurantii* reveals distinctive characteristics of its mycelium and spores. In this sense, Liu et al. [64] reported that the mycelium of *G. citri-aurantii* appears as a network of branching, septate hyphae, which are typically hyaline and thin-walled, form a dense and intricate mat, spreading across the substrate. The spores of *G. citri-aurantii* are a key diagnostic feature and are typically spherical or ellipsoidal in shape, measuring from approximately 5 to 15 μm in diameter [65]. The spores of *G. citri-aurantii* are produced in abundance and can be seen both as individual units and in clusters or chains [66]. They have a characteristic creamy to pale brown coloration, often with a granular or rough surface texture, imparting a distinctive appearance [67]. The arrangement of spores can vary, sometimes forming spore-bearing structures resembling conidia [65].

These microscopic features, including the septate hyphae and the distinctive morphology of the spores, are essential for the identification and differentiation of *G. citri-aurantii* from other fungi in the *Geotrichum* genus [68].

The development cycle of *G. citri-aurantii* in citrus fruits typically begins when the spores of the fungus come into contact with the fruit's surface [69–71]. These spores can be introduced through various means, including contaminated equipment, water or airborne particles. Upon landing on the fruit, the spores germinate and produce hyphae that penetrate the fruit's peel. When the *G. citri-aurantii* thrives in the moist and humid conditions of the fruit's microenvironment, it secretes enzymes to break down the fruit's cell walls and extract nutrients, leading to characteristic decay symptoms. Over time, the fungus produces conidia, asexual spores, which are released onto the fruit's surface, further spreading the infection.

2.3.4. Other Fungal Diseases Affecting Citrus Fruits

Citrus fruits are susceptible to a range of post-harvest diseases beyond the well-known green mold, blue mold and sour rot. These diseases encompass a diverse spectrum of pathogens, including maladies. *Alternaria* rot is a common fungal disease that affects citrus fruit, particularly in warm and humid climates [72]. It is caused by various species of the *Alternaria* genus, with *A. citri* being one of the most common pathogens involved [73]. This disease can result in significant economic losses for citrus growers, especially, in the case of over-ripe oranges or mandarins and when affecting fruits subjected to prolonged storage [72]. In this sense, Khan et al. [74] revealed that the *A. citri* initiate as a dormant infection at the button or stylar-end of the fruit, subsequently advancing across the fruit's surface and culminating in the formation of a black-colored core within the fruit. They also reported that this symptom is frequently observed in Nagpur mandarins when they are stored for extended durations under refrigerated conditions.

Phytophthora brown rot is a devastating post-harvest disease that afflicts citrus fruits, posing a significant threat to their quality and shelf life [75]. This disease generally thrives in humid conditions, making it a particularly concerning issue in regions with high humidity [76]. Fruit infections typically occur within three feet of the soil surface on the tree, however, fruit higher up in the tree can also become infected due to wind-driven rains or in groves with a heavy cover crop [75]. Once the disease takes hold, it manifests as dark, water-soaked lesions on the fruit's surface, leading to rapid decay and rendering the affected citrus fruits unfit for consumption or marketing [75]. The citrus fruits afflicted by *Phytophthora* brown rot emit a distinct, unpleasant odor that immediately distinguishes this disease from the stem-end rots of the other citrus maladies [77]. However, the major serious aspects of *Phytophthora* brown rot is that fruits infected prior to harvesting can undergo inspection and grading without exhibiting visible disease symptoms [78]. Consequently, these infected fruits become mixed with uninfected fruits during storage or packaging for market distribution.

Anthraxnose, caused by the fungus *Colletotrichum gloeosporioides*, is another significant post-harvest disease affecting citrus fruits [79]. The symptoms of anthracnose on citrus include twig dieback, premature leaf drop, dark staining on fruit and post-harvest fruit decay [80]. During wet or foggy weather, anthracnose spores drip onto fruit, where they infect the rind and leave dull, reddish to green streaks on immature fruit and brown to black streaks on mature fruit (tear stains). On the other hand, there are several factors that affect the post-harvest development of *C. gloeosporioides* in citrus fruits, including temperature, relative humidity and fruit maturity [77].

3. A Comprehensive Global Survey on Yeast-Based Strategies for Fruit Disease Management

The development of the use the biocontrol treatments using antagonistic agents is the result of the multiple negative effects of the chemical products used for the treatment of post-harvest fruit diseases which have been expressed via several negative effects [81]. Firstly, over-reliance on these chemicals can lead to the development of resistant strains

of pathogens, rendering them less effective over time and necessitating the use of even more potent and potentially harmful chemicals [82]. Additionally, the residues of these chemicals on fruits can pose serious health risks to consumers if not properly regulated and monitored, potentially causing various health issues [83]. Moreover, the environmental impact of these chemicals includes soil and water pollution, harm to non-target species and disruption of ecosystems [84]. Lastly, the financial burden on farmers can be substantial, as they must often invest in expensive chemicals and equipment, while also dealing with fluctuating market prices, ultimately affecting their profitability and sustainability [85]. Therefore, to deal with this problem, a balanced and integrated approach to post-harvest disease management that reduces reliance on chemical products is crucial for the long-term preservation of human health and the environment [22]. While biocontrol commercial products for post-harvest disease management have indeed been developed, the quest for novel antagonists continues, aiming to enhance the efficacy of biocontrol solutions suitable for integration into sustainable crop management practices, particularly within the context of fruit production. In relation to this situation, antagonistic yeasts are a promising and eco-friendly tool in the post-harvest treatment of citrus fruits which, can help reduce the incidence of post-harvest diseases, extend the shelf life of citrus fruits and minimize the need for chemical fungicides [47,86].

3.1. Advantageous Yeast Properties for Potential Biocontrol Applications

Amongst all the myriad microorganisms, yeasts have been employed in the venerable crafts of bread, wine and beer production since ancient times [87]. The first microscopic identification of the yeast species was by Antonie van Leeuwenhoek in 1680, while the yeast's pivotal role in the fermentation process was identified by Pasteur [88]. However, in recent years, the use of yeast has evolved into a ubiquitous practice across diverse fields, encompassing the food industry, research, medical science and agriculture [89].

Worldwide, a multitude of yeast species have been evaluated for their effectiveness in managing post-harvest fruit pathogens [90]. Several studies reported the use of the yeast on the fruit post-harvest disease protection (Table 1).

Table 1. Application of yeast in post-harvest disease management against different pathogens and different fruits during the 2020 to 2023 season.

Yeast Species	Pathogen	Fruit	Disease	Country	Reference
<i>Pichia guilliermondii</i>	<i>Rhizopus stolonifer</i>	Peach	Soft rot	China	[91]
<i>Meyerozyma guilliermondii</i>	<i>Alternaria brassicicola</i>	Broccoli	Black spot	China	[92]
<i>Torulaspora indica</i>	<i>Alternaria arborescens</i>	Tomato	Tomato rot	Brazil	[93]
<i>Aureobasidium pullulans</i>	<i>Erwinia amylovora</i>	Apple	Fire blight	Turkey	[94]
<i>Debaryomyces hansenii</i>	<i>Botrytis cinerea</i>	Strawberry	Gray mold	China	[95]
<i>Debaryomyces nepalensis</i>	<i>Alternaria</i> sp., <i>Penicillium</i> sp., <i>Fusarium</i> sp. and <i>Botrytis</i> sp.	Jujube	-	China	[67]
<i>Debaryomyces hansenii</i>	<i>Botrytis cinerea</i>	Blueberry	Gray mold	Spain	[96]
<i>Wickerhamomyces anomalus</i>	<i>Botrytis cinerea</i>	Cherry tomatoes	Gray mold	China	[97]
<i>Torulaspora indica</i> , <i>Torulaspora indica</i> <i>Pseudozyma hubeiensis</i>	<i>Lasiodiplodia theobromae</i> <i>Colletotrichum gloeosporioides</i>	Mango	Fruit rot and anthracnose	Thailand	[98]
<i>Saturnispora diversa</i>	<i>Colletotrichum gloeosporioides</i>	Loqua	Anthracnose	China	[99]

Table 1. Cont.

Yeast Species	Pathogen	Fruit	Disease	Country	Reference
<i>Candida oleophila</i>	<i>Botrytis cinerea</i> and <i>Alternaria alternata</i>	Kiwi	Gray mold and black rot	China	[100]
<i>Meyerozyma caribbica</i>	<i>Colletotrichum gloeosporioides</i> , <i>Colletotrichum</i> sp., <i>Fusarium</i> sp.	Avocado	-	Mexico	[101]

3.2. Characteristics of Antagonistic Yeasts

Post-harvest biocontrol systems exhibit complexity, with multiple parameters influencing their effectiveness. Indeed, biocontrol yeasts are administered to fruit within commercial environments by drenching, dipping and spraying which are also commonly employed for the application of chemical fungicides. However, comprehending the mechanisms that grant biocontrol efficacy serves as the cornerstone for the knowledgeable and effective advancement and utilization of yeasts as agents for safeguarding plants [102]. In this way, the use of highly efficient genomic-based technologies has significantly enhanced the comprehension of the microbial antagonist-host and pathogen interactions, as well as the mechanisms underlying their relationship [24]. In a tritrophic interaction system, numerous potential mechanisms exist to inhibit pathogen infection (Figure 3). Nevertheless, the integration of antagonistic yeasts into the control of post-harvest diseases in fruits has been subject to the influence of various environmental factors. Factors such as pH, temperature, water activity and oxidative stress can significantly affect the viability of these yeasts and, consequently, impact their overall effectiveness [103,104]. In the treatment of post-harvest diseases in citrus using yeast, the predominant mechanisms employed by these antagonists include competition for nutrients and space, mycoparasitism, toxin production, induction of host resistance, secretion of antifungal volatile compounds and the utilization of cell wall lytic enzymes. These mechanisms collectively constitute the primary biocontrol strategies demonstrated by antagonistic yeasts in the context of citrus post-harvest disease management [105–108].

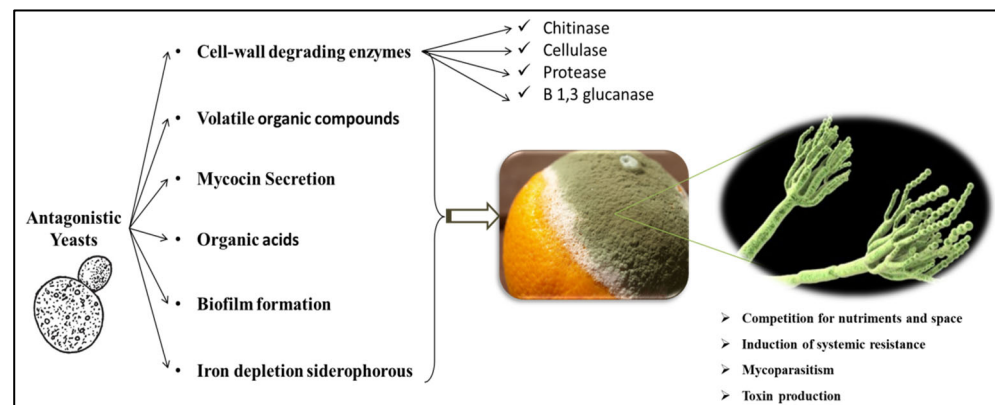


Figure 3. Antifungal mechanisms of action of antagonistic yeasts.

3.2.1. Competition for Nutrients and Space

The competition for space and nutrients stands as a primary mechanism of action by which yeasts exert their antagonistic action in inhibiting pathogenic fungi [17]. In the context of nutritional resource competition, the impact of yeasts stems from their ability to swiftly colonize host fruits, primarily through initiating growth in wounds upon initial contact. This colonization process leads to nutrient consumption, depleting resources and hindering the spore germination of pathogenic agents. Consequently, this reduces infection levels and mitigates the progression of fruit diseases [109,110]. Generally, this mechanism is related to the fact that the antagonistic yeasts deplete the nutrients found in host fruits, such as carbon and nitrogen, resulting in pathogenic fungi being unable to access crucial

nutrients necessary for their viability and proliferation [111]. In the same way, during the period of nutrient scarcity, the antagonists reduce the available nutrients in the wound site and render them inaccessible to pathogens for the processes of germination, growth and infection [24]. This mechanism has been elucidated in numerous biocontrol investigations involving antagonistic organisms such as *Yamadazyma mexicana* [112], *Coniochaeta euphorbiae* and *Auerobasidium mangrovei* [113], *Wickerhamomyces anomalus* [114], *Metschnikowia citriensis* [115], *Metschnikowia pulcherrima* [116,117] and *Debaryomyces hansenii* [95].

Carbon, nitrogen, and iron ions are the fundamental building blocks and catalysts that drive microbial proliferation and metabolic processes [82]. Indeed, several results reported that compared with carbohydrates, nitrogen is regarded as a pivotal factor that restricts the proliferation of post-harvest fruit pathogens, which are related to the fact that the fruits are abundant in sugar but have limited nitrogen sources, such as amino acids [82,118]. Similarly, the yeast *Metschnikowia pulcherrima* produces iron chelators to sequester essential iron resources required by pathogens, effectively inhibiting their growth [119,120]. Thus, the synthesis of siderophores by *Aureobasidium pullulans* plays a pivotal role in yeast development and the inhibition of pathogens, particularly under conditions of iron deficiency [121,122].

In the context of spatial competition, it is imperative that antagonistic yeast strains demonstrate the capacity to effectively establish residence on the host fruit's surface, with particular consideration for the augmentative role of biofilm formation in enhancing this colonization process [123]. The rapid growth kinetics of the yeasts and their capacity to establish biofilm matrices across the wounded fruit substrate is one of the most important mechanisms used by these antagonistic agents to inhibit the fungi distribution during the first 24 h of the fruit colonization [102,105]. However, after 24 h, other modes of action can assume a substantial role and become determining for the success of the control of the fruit's post-harvest disease [124]. In correlation with these data, Liu et al. [125] reported that the biofilm formation of *Metschnikowia citriensis* was directly related to its biocontrol effect against *P. digitatum* and *P. italicum* on citrus fruit. Similar results were revealed using the *Kloeckera apiculata* for the biocontrol of the blue mold of the citrus fruits in the post-harvest period [126].

3.2.2. Mycoparasitism

Mycoparasitism refers to the capacity of antagonistic microorganisms to bind to the hyphae of fungal pathogens, leading to the production of extracellular cell wall lytic enzymes that cause destruction of the fungal structures [127]. This phenomenon is more pronounced during the nutritional deficiencies period, in which the antagonistic yeast absorbs nutrients from pathogenic cells, resulting in the demise of these cells. Generally, yeast disintegration of fungal cell walls serves to access carbon sources and amino acids crucial for their survival [128]. In the process of mycoparasitism, a range of enzymes participate in the degradation of the fungal pathogen cell wall, with particular emphasis on glucanase, chitinase, cellulase and proteases [102]. These secreted enzymes play a crucial role in biocontrol [105]. The enzymatic degradation of fungal pathogen hyphae leads to various cellular deformities, such as cytological damage, mycelial distortion, lysis, changes in cell membrane permeability and the leakage of cytoplasmic contents [105]. The primary indication of mycoparasitism [129] was the attachment of yeast antagonist *Pichia guilliermondii* on the biocontrol of *B. cinerea*. Indeed, the results deduced that the destruction of the fungal cell wall was caused by the extracellular b-(1–3) glucanase enzyme activity. In correlation with these results, the antagonistic properties of *Pseudozyma aphidis* on the biocontrol of the post-harvest diseases caused by *B. cinerea* was based on the secretion of bioactive compounds that negatively affect the hyphae of these species, leading their morphological alterations, including hyphal curliness, vacuolization and branching and presumably affects the colonization ability and infectivity of *B. cinerea* [130].

3.2.3. Induction of Systemic Resistance

The strategy of enhancing resistance using biocontrol agents, such as yeasts has garnered growing interest as an environmentally sustainable approach for addressing post-harvest decay in fruits and vegetables [131]. The induction of resistance to biotic or abiotic stresses in the host involves the accumulation of structural barriers and the activation of various biochemical and molecular protective mechanisms. These include initiating mitogen-activated protein kinase signaling, enhancing reactive oxygen species production, synthesizing terpenoids and phytoalexins via the phenylpropanoid pathway, generating PR-proteins and phytoalexins through the octadecanoic pathway, increasing phenolic compound levels, reinforcing lignification at infection sites, and strengthening the host cell wall by producing lignin, callose, glycoproteins, and other phenolic polymers [118,132]. The variation of the mechanisms induced by the antagonistic yeasts in the resistance induction of the host was related to several factors including the yeast type and environmental conditions [133]. The induction of resistance was generally correlated with a single mechanism, such as the activation of the antioxidant enzymes [134], host cell deformation [135] or activation of the pathogenesis-related proteins [136]. However, the data reported by researchers [102,118,131] using *Rhodospiridium paludigenum*, *Ryptococcus laurentii*, *Starmerella bacillaris* and *Pichia membranefaciens* respectively, reported that the resistance induced by these yeasts in fruits was related to the activation of both defense-related enzymes and antioxidant enzymes.

Based on all these results, the conclusive correlation between the stimulation of host defense and the suppression of pathogenic growth remains incompletely established, while the use of molecular tools can uncover distinct gene profiles involved in the intricate interplay between antagonistic microbes, the host and pathogenic agents during the induction of host resistance.

3.2.4. Toxin Production

As one of the most important components of biocontrol agents, the yeasts possess the ability to synthesize and secrete various antimicrobial metabolites, including toxins, which can effectively inhibit the growth and development of pathogenic fungi responsible for post-harvest fruit diseases [137]. Numerous toxins have been documented as effective agents for managing post-harvest pathogens, with proteinaceous killer toxins emerging as the foremost antifungal compounds generated by yeast [138]. Lukša et al. [139] initially reported these proteins in the study of the biocontrol of the post-harvest fruit using *Saccharomyces cerevisiae* yeasts. These toxins have primarily received attention in research for their applications in controlling spoilage yeasts within the beverage and food industry, as well as in various medical contexts [140–142]. Additionally, Mannazzu et al. [142] reported that killer toxins bestow a competitive edge on yeasts, as they possess the capability to eliminate fungi through a diverse range of mechanisms. These mechanisms encompass the hydrolyzation of the cell wall, disruption of the cell's structural integrity and inhibition of DNA synthesis. In correlation with the use of these toxins as a biocontrol agent [120], researchers [143] revealed the use of the *D. hansenii* and *W. anomalus* against *M. fructigena* and *B. cinerea*, *P. digitatum*, *P. italicum*, *M. fructigena*, and *M. fructicola*. On the other hand, environmental factors play a significant role in modulating the antifungal efficacy of these killer toxins. In this regards, researchers [144] deduced that the killer toxins generated by *D. hansenii* have been documented to inhibit the pathogenic *Candida* yeasts, but only within a specific temperature and pH conditions. Nevertheless, additional research is needed to determine the yeast toxins' specificity and their impact on beneficial microorganisms, such as those in the phyllosphere, soil microbiota, and in the context of edible products, the human gastrointestinal system.

3.2.5. Volatile Organic Compounds

In general, microorganisms including fungi, bacteria and yeast, generate volatile organic compounds (VOCs) as part of their primary and secondary metabolic processes [145].

The VOCs typically consist of small molecules (usually <300 Da) exhibiting limited water solubility and demonstrating high vapor pressure [138]. They exhibit species specificity and play a crucial role in intercellular communication, as well as in either promoting or constraining the proliferation of other microorganisms [146]. The VOCs include a wide array of molecular categories, comprising alcohols, heterocyclic compounds, benzene derivatives, aldehydes, cyclohexanes, thioalcohols, hydrocarbons, derivatives, phenols, ketones and thioesters [138]. However, the chemical content of these compounds referred to as the volatilome blend, is heavily influenced by both the surrounding environment and the specific pathogen being countered [147].

Several scientific studies evidence the crucial role of the yeast VOCs in yeast-pathogen interactions, encompassing the pathogens fungi of the citrus post-harvest fruits [148,149]. In this regards, the researchers [150] deduced that the volatile compounds produced by *Pichia galeiformis* exhibited a high antagonistic capacity against citrus green mold caused by *P. digitatum*. Moreover, the findings indicated that via gas chromatography-mass spectrometry, a total of eight VOC compounds produced by *P. galeiformis* efficiently inhibited *P. digitatum*. Similar results were reported by other researchers [151,152] using *Pichia kudriavzevii* and *Meyerozyma guilliermondii* yeast in the biocontrol of the green mold in citrus fruits during the post-harvest period. Pereyra et al. [153] proved for the first time that the volatile organic compounds produced by *Clavispora lusitaniae* have a high antagonistic activity for the biocontrol fungal diseases of the lemon fruits. Thus, a study by Toffano et al. [154] revealed that the antagonist yeast *S. cerevisiae* generates volatile compounds capable of inhibiting the growth of plant pathogens, such as the filamentous fungus *Phyllosticta citricarpa*, which is responsible for causing citrus black spot. Therefore, with all these benefits of the use of these molecules in the biocontrol of the post-harvest diseases, it is imperative to conduct comprehensive assessments of volatile organic compound safety in forthcoming research endeavors.

4. Applications of Yeasts against Post-Harvest Pathogenic Fungi in Citrus

The infections by post-harvest decaying fungi, such as *P. digitatum*, *P. italicum*, *A. niger*, *A. flavus* and *G. citri-aurantii*, lead to considerable declines in both product quality and marketable yield [47]. To manage these issues, synthetic fungicides have traditionally been the predominant choice. However, their widespread utilization often leads to the development of resistant strains, coupled with concerns regarding their toxic repercussions and environmental contamination, resulting in growing restrictions on their application, combined with trade barriers to international markets [34]. To deal with these problems, efforts are underway to explore eco-friendly management approaches, including the utilization of antagonistic species such as yeasts for the biocontrol of fungal post-harvest diseases of the citrus fruits (Table 2) [24,153,155].

Table 2. Application of yeast in post-harvest disease management against different citrus fruits pathogens during the 2020–2023 season.

Yeast Species	Pathogen	Disease	Inhibition Range (%)	Country	Reference
<i>Pichia fermentans</i> <i>Clavispora lusitaniae</i>	<i>P. digitatum</i>	Green mold	70–96.67%	Argentina	[86]
<i>Pichia galeiformis</i>	<i>P. digitatum</i>	Green mold	85% in-vitro 75% in vivo	China	[150]
<i>Meyerozyma guilliermondii</i> <i>Pseudozyma</i> sp. <i>Saccharomyces cerevisiae</i>	<i>Penicillium</i> sp., <i>Fusarium</i> sp., <i>Colletotrichum</i> sp.	Green/blue mold Fusarium rot Anthracnose	85% in vitro	Mexico	[17]
<i>Aureobasidium pullulans</i> <i>Rhodoturula minuta</i> <i>Candida tropicalis</i>	<i>Aspergillus</i> sp.	Fruit rot	22.5–42.2%	Indonesia	[156]
<i>Metschnikowia citriensis</i>	<i>Geotrichum citri-auranti</i>	Sour rot	30–50%	China	[115]

Table 2. Cont.

Yeast Species	Pathogen	Disease	Inhibition Range (%)	Country	Reference
<i>Candida orthopsilosis</i> <i>Aureobasidium pullulans</i>	<i>Aspergillus flavus</i> <i>Aspergillus niger</i>	Citrus mold	25–60%	Indonesia	[157]
<i>Candida peltata</i>	<i>P. digitatum</i>	Green mold	85.7%	Brazil	[6]
<i>Clavispora lusitaniae</i>	<i>P. digitatum</i>	Green mold	86–95%	Argentina	[155]
<i>Metschnikowia</i> aff. <i>Pulcherrima</i> <i>Hanseniaspora uvarum</i> <i>Meyerozyma guilliermondii</i>	<i>P. digitatum</i>	Green mold	73.85–85.64%	Turkey	[152]
<i>Metschnikowia</i> sp.	<i>P. digitatum</i> <i>P. expansum</i>	Green and blue mold	83.63–100%	Turkey	[158]
<i>Candida oleophila</i> <i>Debaryomyces hansenii</i>	<i>P. digitatum</i> and <i>P. italicum</i>	Green and blue mold	20–32%	Tunisia	[18]
<i>Meyerozyma guilliermondii</i>	<i>P. italicum</i> <i>P. digitatum</i>	Green and blue mold	70 and 72%	México	[159]
<i>Saccharomyces cerevisiae</i>	<i>P. digitatum</i> <i>P. italicum</i>	Green and blue mold	22.5–70% of <i>P. digitatum</i> 21.1–68.5% of <i>P. italicum</i>	Egypt	[160]
<i>Candida</i> spp.	<i>Penicillium</i> sp. <i>Alternaria</i> sp.	Green mold and Alternaria rot	-	Indonesia	[81]
<i>Schwanniomyces vanrijiae</i>	<i>P. digitatum</i>	Green mold	55%	Egypt	[161]
<i>Metschnikowia citriensis</i>	<i>Geotrichum</i> <i>citri-aurantii</i>	Sour rot	43.66%	China	[47]
<i>Pichia galeiformis</i>	<i>P. digitatum</i>	Green mold	-	China	[162]
<i>Saccharomyces cerevisiae</i> <i>Candida stellimalicola</i>	<i>P. digitatum</i>	Green mold	>80%	Brazil	[84]
<i>Meyerozyma guilliermondii</i>	<i>P. italicum</i>	Blue mold	57.5%	China	[163]

4.1. Challenges of Using Yeast as BCAs against Post-Harvest Diseases of Fruit

The application of antagonistic yeasts in the biocontrol of post-harvest fungal diseases is a promising strategy to reduce the use of synthetic chemical fungicides and improve food safety. In this sense, several studies reported the positive effect of the use of the antagonistic yeast in the biocontrol of the post-harvest fungal diseases, but only a limited number have successfully transitioned into the realm of commercial antifungal products [118]. However, numerous commercial factors pose constraints on the development and marketability of antagonistic yeasts, including the underdevelopment of the commercialization technologies and the application of antagonistic yeasts for post-harvest decay control; this is a burgeoning industry [164]. Furthermore, research regarding yeasts for biocontrol uses remains incomplete and still needs some clarifications about the exact mechanisms that these organisms use to express their antagonistic property. Opulente et al. [165] deduced that there are several constraints and considerations that need to be taken into account when using antagonistic yeasts for this purpose. Firstly, there are fewer studies related to the biosafety of the antagonistic yeasts which are considered as the most important properties of the antagonistic yeast in the biocontrol of the post-harvest diseases compared to chemical fungicides [118]. Some yeasts can serve as the source of human infections under exceptional situations [166].

On the other hand, in other studies, researchers [102,167] have reported that the antagonistic yeasts may not provide consistent control of fungal diseases across different fruits and vegetables or under varying environmental conditions and the choice of the most suitable antagonistic yeast type strain for a specific post-harvest pathogen can be challenging, as the efficacy may vary among strains. Thus, the antagonistic yeasts often have specific temperature and pH requirements for optimal activity. The extreme temperature conditions or pH levels in post-harvest storage facilities can limit their effectiveness [102]. Additionally, Janisiewicz et al. [164] deduced that obtaining regulatory approvals for the use of antagonistic yeasts in post-harvest biocontrol can be time-consuming and requires

extensive data on safety and efficacy. Therefore, there is a risk of the development of resistance in fungal pathogens over time when using antagonistic yeasts, which may reduce long-term efficacy. In comparison to chemical fungicides, antagonistic yeasts require further enhancements in various aspects, which hinder their broader commercialization and acceptance in the market. Antagonistic yeasts tend to be costlier than chemical fungicides, which pose usability challenges [168].

4.2. Biocontrol Enhancement Using Mixtures of Antagonistic Materials and Implementing Yeast against Post-Harvest Diseases

Yeasts are continuously being studied as potential biocontrol agents due to their adaptability to fruit environments, long-term colonization, their easy and fast growth on bioreactors and high tolerance to temperature, pH and oxygen levels. In addition, yeast are made to produce mycotoxins, or antibiotics, as many fungi or bacteria do [102]. Since yeasts can utilize a variety of carbohydrates, including nitrogen, disaccharides and monosaccharides, they are useful microorganisms. As a result, one of the main mechanisms of post-harvest microbial biocontrol agents is competition for space and nutrients [169]. While several yeasts with antifungal qualities have been found, there are not many investigations on the antagonistic actions of mixed microorganisms. This is why regarding the compatibility aspect, mixed cultures of microbial antagonists are needed for an enhanced biocontrol property against post-harvest disease in the fruits and vegetables industry [17]. In *Citrus* spp., the most reported epiphytic yeasts are: *Pichia guilliermondii*, *Metschnikowia fruticola*, *Candida oleophila*, *Candida sake*, *Kloeckera apiculata*, *Metschnikowia pulcherrima*, *Debaryomyces hansenii*, *Candida famata* and *Candida saitoana* [17].

A study tested various yeast mixtures on Red Delicious apples to control *P. expansum* and *B. cinerea*. The study found that the mixture of *Rhodotorula* and *Cryptococcus* strains was less effective than either strain alone that is due to differences to yeast population dynamics. However, the only mixture that showed synergism against *B. cinerea* was *R. glutinis* SL 1 and *C. laurentii* SL 62 [170]. Mexico, a major citrus fruit producer, faces challenges during storage due to fungi-related problems such as green/blue mold, fusarium rot and anthracnose. Researchers have tested yeasts from lemons or fermented traditional products to protect stored lemons against these diseases. The best-performing yeasts were identified as LCBG-03, LCBG-30 and LCBG-49. These yeasts were tested against various strains of fungi. The best combinations, containing *M. guilliermondii* formulated with either *Pseudozyma* sp. or *S. cerevisiae*, showed efficacies higher than 95% in both in vitro fungal radial growth rate inhibition and on stored lemon fruits. This proves that mixing yeast improved biocontrol without increasing antagonists and contributes to the search for compatible yeast combinations to mitigate fungal losses in citrus fruits [17].

Adhering to host and pathogen cell sites, competing for nutrients or space, direct parasitism, quorum sensing, secreting lytic enzymes and antimicrobial substances, producing volatile organic compounds, biofilm formation, extracellular proteic toxins and inducing host resistance are all examples of antagonistic yeasts biocontrol activity [102]. However, an alternative for synthetic fungicides is the application of antagonistic bacteria and yeasts, which are naturally occurring on the surfaces of fruits and vegetables [37,171]. The use of compatible microbial consortia in post-harvest biocontrol systems offers a new approach to enhance biocontrol efficacy. These consortia, which can be natural or synthetic, comprise microbial populations that thrive in diverse environments. This approach offers advantages such as wider biocontrol efficacy, robustness, resilience to environmental stress and modularity [172].

The optimization of these conditions and the co-application of yeast-compatible antagonistic bacteria can ensure the yeast populations thrive and efficiently combat post-harvest fungal diseases [35,102]. On the other hand, the genetic modification of yeast strains can enable the production of antimicrobial compounds, such as killer toxins and volatile organic compounds that inhibit fungal growth [142]. The improvement of the antagonistic yeast through the incorporation of additives can lead to various benefits, including the potential

for direct pathogen inhibition, the induction of systemic acquired resistance within the host tissue and the activation of antagonistic activities [104].

Biocontrol using yeast and *Trichoderma* species has emerged, and gained too much attention for its efficiency against major plant diseases. However, the practicality of biocontrols requires effective adoption and understanding of the interactions between pathogens, plants, and the environment for sustainable agriculture [173]. A study tested 14 *Pseudomonas* spp. and three *Trichoderma* spp. strains against *P. digitatum*, the cause of citrus green mold. Bacterial and fungal strains effectively inhibited pathogen growth, with increased efficacy when applied in combination. The presence of living bacterial cells was required for a synergistic effect. The combination of *Pseudomonas* spp. and *Trichoderma* spp. strains was found to be a promising means for controlling citrus green mold decay, suggesting improved disease control through the combined action of the two agents [174].

Moreover, the inclusion of additives in the composition of antagonistic yeast formulations emerges as a critical requirement for the successful commercial viability of these biocontrol agents [175]. Palou et al. [167] revealed that the use of chitosan, a polymer consisting of poly- β -(1 $\rightarrow$ 4) N-acetyl-D-glucosamine, along with its derivatives, has been as an effective strategy for managing post-harvest diseases, through its antifungal characteristics and its ability to stimulate host defense responses. A different category of additives used alone or in conjunction with biocontrol agents comprises inorganic salts and minerals, such as sodium bicarbonate, ammonium molybdate and calcium chloride [176]. In this sense, the use of the ammonium molybdate ($\text{NH}_4\text{-Mo}$) has great potential to enhance the biocontrol efficacy of antagonistic yeasts against post-harvest diseases on pears, jujube and peach fruits [177–179]. On the other hand, several studies reported the potential positive effect of sodium bicarbonate on the enhancing of the biocontrol efficacy of antagonistic yeasts against the post-harvest disease [178,180]. Similarly, a study by Ippolito et al. [181] found that the combination of *M. pulcherrima* and sodium bicarbonate significantly reduced the incidence of *B. cinerea* in strawberries. For the biocontrol of the post-harvest diseases of the citrus fruits, the combination of antagonistic yeast and some additive product such as ammonium molybdate and sodium bicarbonate can offer a synergistic effect, as the yeast provides biological control while sodium bicarbonate creates a hostile environment for pathogens, thereby enhancing the overall efficacy of disease management. In relation to this investigation, the combined application of sodium bicarbonate with *Saccharomycopsis crataegensis*, *Rhodosporidium paludigenum* and *C. oleophila*, respectively, enhanced the control of the post-harvest diseases in citrus fruits [182–184]. However, Lu et al. [185] revealed that the combining of the ammonium molybdate and *R. paludigenum* had a significant effect in the control of the green mold caused by *P. digitatum* in satsuma mandarin (*Citrus unshiu* Marc.). Similar results were reported by Zhang et al. [110] who revealed that the crucial role of the use of the ammonium molybdate in the amelioration of the *M. pulcherrima* in the biocontrol of the citrus green mold during post-harvest.

Furthermore, the use of antagonistic yeast in conjunction with calcium chloride represents a promising biocontrol strategy for mitigating post-harvest diseases in citrus fruits. This approach not only leverages the antagonistic properties of yeast to combat pathogens but also capitalizes on the fruit-strengthening capabilities of calcium chloride. Similarly, the antifungal efficacy of the antagonistic yeast strains *C. pseudotropicalis* and *P. guilliermondii* against green mold was enhanced in combination with 2% calcium chloride which induced a significant reduction in fungal diseases by 83.1 and 74.8%, respectively [160].

5. Commercial Yeast-Based Products for Phytosanitary Uses

The term “biofungicide” refers to any combination of naturally occurring substances and microorganisms that have the capacity to regulate plant diseases [102]. Biocontrol mechanisms in post-harvest diseases are not fully understood, but wound colonization and nutrient competition are significant factors. Microorganisms have potential as commercial biocontrol products due to their efficacy against fungal pathogens in field conditions. Despite research, few biofungicides are commercially available and not many yeasts or

yeast-like fungi, such as hemiascomycetes and other fungi, have made it to market for biocontrol or biopreservation. The majority of these goods have biopesticide registrations [186]. Prior to their commercialization, a regulatory process was implemented to govern the utilization of yeasts in biocontrol and biopreservation. In the sense that pre-market authorization is not necessary, the conventional use of microorganisms with a history of safety in food fermentation or as particular starter cultures in dairy products is virtually uncontrolled worldwide [187,188]. The novel foods regulation requires industry planning to market new foods and ingredients to submit a petition for approval to a national authority. It covers microorganisms as novel foods or ingredients but allows exemptions if they are similar to existing food products [189]. Several commercial biological control formulations based on *Bacillus subtilis*, *Streptomyces griseoviridis*, *Trichoderma harzianum*, *A. pullulans* and *Gliocladium virens* have been used against many plant fungal diseases [102,104] and BCA combinations that work well together may provide a fresh and efficient method for enhancing the management of plant diseases (Table 3).

Yeast-based products for phytosanitary uses can contain a variety of active ingredients tailored to their specific applications. Some examples of active ingredients found in these products include certain strains of *Saccharomyces cerevisiae* yeasts have been identified for their phytosanitary capabilities, and they can serve as active ingredients in phytosanitary compositions for their antifungal compounds production. Indeed, yeast-based products can contain antifungal compounds that help protect plants against fungal diseases. For example, yeasts that produce killer toxins and although other yeast strains cannot survive these toxins, the yeasts that produce them are usually resistant to both them and other strains in the same class [142]. Since the cell wall is one of the most often targeted sites of action for toxins, a variety of substances, including mannoproteins, chitin, β -1,3-D-glucans and β -1,6-D-glucans, can be discovered functioning as receptors for killer toxins [142]. Known yeast toxins include: (i) PMKT and PMKT2, which are produced by *Pichia membranifaciens* and bind to mannoproteins and β -1,6-D-glucans in pathogen cell walls, respectively; (ii) panomycocin, which is produced by a *P. anomala* strain and works by hydrolyzing β -1,3-glucans; and (iii) zymocin, which is produced by *Kluyveromyces lactis* and hydrolyzes chitins in the fungal cell wall that function as antifungal components [190]. Furthermore, yeasts, including *Saccharomyces cerevisiae*, can produce phytohormones such as Indole-3-Acetic Acid (IAA), which are plant growth regulators that can stimulate plant growth and development [191,192]. Yeast-based products can provide essential nutrients to plants, supporting their growth and overall health including molecular nitrogen (N₂) fixation, phosphorus (P) and potassium (K) solubilization. This nutrient supply can contribute to the biostimulant and bionutrition properties of these products. These active ingredients contribute to the diverse functions of yeast-based products in agriculture, including biocontrol, biostimulation and bionutrition, and highlight the potential of yeast in promoting sustainable and environmentally friendly farming practices [192].

The lack of field application reliability and inconsistent disease control in field conditions hinder the adoption of these approaches, contributing to their low market dissemination [102,193]. The commercialization of bioproducts based on BCA faces challenges in producing shelf-stable products with biocontrol activity similar to fresh cells. Despite biofungicides having good action against host pathogens, their effectiveness in the field is limited [17].

Table 3. Yeast based products registered and available in the market and their uses in post-harvest disease management.

Microorganisms	Product	Use	Registration	References
<i>Ampelomyces quisqualis</i> M-10	AQ10	Fungicide on grapes, vegetables and berries	Registered biopesticide in the EU 2004	[194]
<i>Pseudozyma flocculosa</i> PF-A22	Sporodex	Fungicide on roses and cucumber	Registered biopesticide in the US and Canada	[195]

Table 3. Cont.

Microorganisms	Product	Use	Registration	References
<i>Metschnikowia fructicola</i>	Shemer	Fungal rots on fruit <i>Rhizopus</i> , <i>Botrytis</i> , <i>Aspergillus</i> , <i>Penicillium</i> ,	Registered biopesticide in Israel	[196]
<i>Candida oleophila</i> I-182	Aspire	Post-harvest plants and fruit <i>Penicillium</i> , <i>Botrytis</i>	Registered biopesticide in the US. Withdrawn	[173]
<i>Cryptococcus albidus</i>	YieldPlus	Fungicide on vegetables and fruit	Registered biopesticide in South Africa	[197]
<i>Candida oleophila</i> strain O	Nexy	Post-harvest fungicide on apple and pear	Registered biopesticide in the US 2009	[197]

Numerous studies have explored bioactive compounds for citrus phytopathogens, but few products reach commercialization. The process from discovery to commercialization is complex and involves several steps. Biocontrol agent development involves two main phases: discovery and commercial development. The first phase involves testing the efficacy of lab-based compounds, evaluating microorganisms' action mechanisms and obtaining patents. The commercial phase involves scale-up production, product formulation, biosafety and registration [171,193,197]. The creation of biomolecule-based products faces challenges such as intricate workflows, high production costs, regulatory hurdles and recurring issues that require immediate attention [171,197–199]. There are now four microorganism-based commercial biofungicides available for the management of post-harvest citrus fruit. For example, the commercially produced product “Shemer” is based on the yeast *Metschnikowia fructicola*, which has been found to be an effective biological control agent of post-harvest diseases of fruits and vegetables [199]. According to reports, its effectiveness in preventing orange rot is comparable to that of oranges treated with the chemical fungicide imazalil [124]. However, only few adversaries have advanced to the point of commercial commercialization as finished goods. Based on *C. oleophila*, Aspire™ [104] has been on the market for a while, but it hasn't been successful because of the industry's and consumers' perceptions, poor and variable efficacy under commercial settings and challenges with market penetration [102]. Other products, such as Shemer™ (based on the yeast *M. fructicola*), have been more successful [124] and are being used for both pre- and post-harvest application on various fruits and vegetables, including peaches, peppers, grapes, strawberries citrus fruit and sweet potatoes [37].

Specific biofungicides are few, but in recent years, there has been a rise in the need for these products in agriculture as synthetic pesticide substitutes. Foods that are exempt from or have minimal levels of chemical residues can be produced with the adoption and broad usage of biofungicide. In terms of fungicide use, this will support the consumption of more natural, healthful and safe foods [193,200]. Therefore, to address the issues facing the biofungicide market, improvements must be made to both workflow-related processes and regulatory impediments [37].

6. Conclusions and Perspectives

In conclusion, harnessing yeasts as biocontrol agents against post-harvest pathogenic fungi in citrus represents a promising and environmentally friendly approach for managing diseases in the citrus industry. Employing diverse mechanisms, such as nutrient and space competition, antifungal compound production and the elicitation of plant defense responses, yeasts have proven their efficacy in suppressing the growth of pathogenic fungi. This not only prolongs the shelf life of citrus fruits but also mitigates the reliance on chemical fungicides, known for their adverse effects on both human health and the environment. The research and development of yeast-based biocontrol strategies exhibit significant potential, with various yeast strains demonstrating effectiveness against a spectrum of citrus post-harvest pathogens. Nevertheless, challenges persist, including the

optimization of application methods, seamless integration into existing citrus production systems and ensuring the long-term stability and efficacy of these biocontrol agents.

Furthermore, a comprehensive understanding of the ecological interactions between yeasts, citrus fruits and pathogenic fungi is imperative for the successful implementation of yeast-based biocontrol strategies. Future research endeavors should prioritize the identification and characterization of yeast strains with superior biocontrol properties, elucidating the involved mechanisms of action, and devising innovative and practical approaches for their seamless integration into the citrus industry.

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