PLANT SCIENCE TODAY
Vol x(x): xx–xx
https://doi.org/10.14719/pst.8682

eISSN 2348-1900

REVIEW ARTICLE

Yeast as a potential bio-control agent for managing postharvest diseases of fruits

Faeza Falha N A[1], T Anand[1]*, G Senthilraja[1], V Babu Rajendra Prasad[2] & R Umarani[3]

[1]Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[2]Department of Plant Physiology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[2]Seed Centre, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

*Correspondence email - barathiana@yahoo.com

Received: 04 April 2025; Accepted: 04 June 2025; Available online: Version 1.0: 22 July 2025

Cite this article: Faeza Falha NA, Anand T, Senthilraja G, Babu Rajendra Prasad V, Umarani R. Yeast as a potential bio-control agent for managing postharvest diseases of fruits. Plant Science Today (Early Access). https:/doi.org/10.14719/pst.8682

Abstract

Phytopathogen-induced postharvest fruit diseases can result in losses of up to 50 % of the world's total production. The impact on the use of conventional synthetic fungicides on human health and eco-toxicological risk has raised concern all over the world and strategies have been made to limit their use in disease management. The development of various antagonistic microbes as potential bio-control agents has increased due to the need for sustainable agriculture and climate change arising globally. Yeast, a unicellular fungus, is a good substitute for synthetic chemicals and it could grow in various ecological niches. Commercially, yeast and its products are used in the food industry, medicine, and biotechnological research, but it can also provide a range of bio-controlling and growth-promoting properties for plants. Yeast is harnessed as a biocontrol agent as they are known for host surface colonization, host resistance induction, production of antifungal compounds, no production of toxic antibiotics as other antagonists and is considered safe for the final food product. Hence, they are extensively harnessed as a potential antagonist in efficiently managing the post-harvest diseases of fruit throughout the world. Their application to fruit postharvest diseases enables a sustainable substitute for synthetic fungicides, enhancing food safety and prolonging shelf life. This review article focuses on the mode of action and their role in post-harvest protection of fruits.

Keywords: biological control; fruits; post-harvest diseases; yeasts

Introduction

Fruits are being devoured and acknowledged by more individuals due to their unique taste and flavor, high nutritional content and effects on human health (1). It is rich in a variety of a range of vitamins like A, B1 B2, B6, C and folate and minerals such as calcium, iron, magnesium, iodine, manganese, selenium, etc which reduces malnutrition in the growing population (2). A study by World Health Organization (WHO) proclaims that including fruit in our diet is linked to have a healthy lifestyle. Over the past ten years, there has been a steady increase in fruit production worldwide. In 2019, the estimated global fruit output was 883.4 metric tons (MT), with Asia producing 512.6 MT, or 58.0 % of the total. China leads the world in fruit production, followed by United States, Mexico, Brazil, and India (3). In 2023-2024 the production of fruits in India reached 112978000.02 metric tonnes, with an area of 7138000 ha under fruit crop cultivation. The highest productivity was recorded in Uttar Pradesh (23.50 million tonnes per ha) followed by Tamil Nadu (22.67 million tonnes per ha) (Ministry of Agriculture and Farmers Welfare, Govt of India, 2024). However, owing to the postharvest losses, which are mainly triggered due to storage conditions and physiology of the products, multiple studies have indicated that between 30 % and 50 % of horticulture products never reach the final customers (4). Reducing or eliminating these losses would lessen the demand for horticulture output, which would ease the strain on the environment. In horticulture production, where natural resource availability has been declining while human population growth continues, this is essential for maintaining sustainability.

Postharvest diseases comprise the primary contributor to postharvest losses. Fungal pathogen-induced postharvest illnesses provide serious problems for the fruit sector, resulting in large financial losses between 10 % and 50 % and jeopardizing food security. They present a serious challenge to disease control due to their high genetic flexibility and diversity, which allow them to swiftly infiltrate new hosts, disrupt gene-mediated resistance, and even develop fungicide resistance (5). The most destructive pathogens affecting after harvesting in fruits are *Penicillium digitatum*, *P. italicum* which is the incitant of green and blue mold in citrus, stone and pome fruits, followed by *Botrytis cinerea* which causes grey mold in grapes and berries; *Alternaria* spp which causes rot in pome fruits and stone fruits, *Colletotrichum* spp. which causes anthracnose and rot in many tropical fruits and *Monilia fructiocola* in temperate fruits (6). Apart from quality deterioration and financial losses, fruits infected with fungal pathogens like *Aspergillus*, *Pencillium*, *Fusarium*, etc pose an imminent health concern due to the production of potential mycotoxins, which underscores the need for effective control. Fungicides, together with cold chain management practices like packaging, cold storage, and hygiene, have long been the most crucial tools in the fight against postharvest infections. However, these existing disease management strategies have been curtailed due to (i) pathogen resistance to numerous fungicides; (ii) the emergence of novel pathogen biotypes; (iii) the absence of efficient substitute fungicides; (iv) rising fungicide residue levels in agricultural products; (v) toxicological issues pertaining to human health and (vi) adverse environmental effects (7). As a result, people became more conscious of agrochemicals worldwide and scientists focused on developing more environmentally and humanely friendly alternatives.

Yeast is a unicellular eukaryotic fungus, which has been widely exploited in the food and brewing industries. Yeasts reproduce by budding or fission asexually and sexual reproduction is not known. They also contribute to the production of biofuel (8). *Saccharomyces cerevisiae*, the first genetically manipulated eukaryote, is widely used for decades in various industries for wine, beer, and bread production (9). However, many species of yeast remain largely unexplored for their potential benefits in basic research and industries.

Both generatively (sexually) and vegetatively (asexually) yeast can reproduce. Budding, the earliest type of asexual reproduction in yeast, depends on favorable environmental factors including temperature and food availability. This kind of procreation is a feature of *Rhodotorula*, *Pichia*, *Saccharomyces* and *Candida*. The daughter cells, or buds, are smaller versions of the parent cells. Cells may merge to create a pseudomycelium, like in the genus *Candida*, or they split off from their parent cell to become a new individual. Another mode of asexual reproduction is fission where the size of daughter cell and parent cell is the same. Yeasts sporulate when they are under stress, such as when they are not getting enough nutrition (10). Pathogenic fungi multiply very quickly, known to have a short generation time and since they are target specific, the use of fungal antagonists has significantly increased (11). Yeast is an excellent antagonist against plant pathogens because it satisfies all the requirements for an effective antagonist, including the ability to quickly colonize plant surfaces, the capacity to use a variety of component sources and the ability to withstand and grow in a broad range of temperature. Also, they do not produce any detrimental metabolites and absence of detrimental effects on the finished food product. While many yeasts are beneficial and have been explored for their biocontrol potential, some species, such as those belonging to the *Candida* genus, are also known to act as opportunistic human pathogens (12). This dual nature underscores the importance of careful selection and risk assessment when considering yeasts for postharvest applications.

Major post-harvest pathogens and associated losses

***Penicillium* spp.**

Penicillium digitatum causes fruit to rot in citrus fruits. According to reports, *P. digitatum* is responsible for 90 % of the citrus sectors' overall post-harvest losses (13). Fungal infections are the primary cause of postharvest loss in citrus fruit during storage and transit. *Penicillium digitatum*, which causes green mold, is the most common pathogen globally, followed by *Penicillium italicum* (14). One of the most hazardous postharvest pathogens is *P. digitatum*, which can cause significant harm to commercial and citriculture initiatives. It has been determined that *P. digitatum* accounts for up to 90 % of all postharvest losses in citrus fruit cultivation in tropical sub climate and desert zones (15). A survey was conducted on post-harvest *Penicillium* mold infection on sweet oranges in Tamil Nadu in 2015-16. The results showed that, for locally grown fruits, losses from *Penicillium* mold were 6 % at the wholesale market, 24 % at the retail level, 20 % at the farmers market, and 2 % at the consumer level. In the rainy season, the percentage increased to 50% (16).

Botrytis cinerea

Necrotrophic fungus *Botrytis cinerea* is known worldwide which incites the disease grey mold in many fruits and is known to produce toxins. They degrade the quality of the fruit and result in significant yield losses (17). It is also challenging to combat because of its broad host range, multiple assault mechanisms, high genetic diversity, and adaptive stages that allow it to survive in hostile conditions (18). The main pathogen of harvested strawberries is *B. cinerea*, which causes large financial losses. If precautions are not followed, *B. cinerea* will damage over 80 % of strawberry fruits and blossoms (13).

***Colletotrichum* spp.**

Anthracnose disease incited by *Colletotrichum gloeosporioides* significantly lowers fruit quality and commercialization; it results in post-harvest losses of roughly 35-40 % and is a serious post-harvest disease of mangoes (19). Over 50 % of disease-related damages in fruits and vegetables during the post-harvest period are caused by *Colletotrichum* species, such as *C. gloeosporioides*. In rainy conditions, the incidence of anthracnose in mango fruit approaches 100 % (20). Fungi-related postharvest losses in papaya fruit can range from 50 % to 100 %. Of these, anthracnose is by far the most serious papaya disease (21). A significant obstacle to the marketing of fruit meant for both local and international markets is banana anthracnose, which is caused by *C. musae*. It results in crown and finger rots, as well as lesions on the fruit peel when it ripens. It has a major negative impact on fruit quality and causes large economic losses in many tropical regions (22).

***Lasiodiplodia* spp.**

One of the potentially significant plant pathogen, *Lasiodiplodia theobromae* (Syn. *Botrydiplodia theobromae*), is known to cause significant post-harvest losses in a variety of crops that are grown on more than 500 hosts (23). One of the most harmful postharvest diseases affecting several tropical and subtropical fruits is stem-end rot (SER). Numerous fungal pathogens, such as species of Botryosphaeriaceae, are responsible for the postharvest diseases (24). Mango postharvest disease causes significant losses and lower fruit quality, rendering the fruit entirely unmarketable. One of the most significant diseases affecting mangoes, SER poses a serious risk to the sector and results in financial losses (25).

***Aspergillus* spp.**

Aspergillus species complex has been linked to postharvest degradation of many fresh fruits and vegetables, according to multiple authors, even though *Aspergillus*' primary substrate is soil. These fungi are among the most prevalent ones that cause food spoilage (26). It has been reported that *Aspergillus niger* produces a large range of hazardous metabolites, one of which being ochratoxins, a class of secondary metabolites that may cause cancer in humans (27). Other significant post-harvest pathogens include *Phomopsis*, *Stilbella cinnabarina*, *Erwinia carotovora*, *Verticillium* spp., *Acremonium* spp., *Alternaria* spp., *Monilinia* spp., *Cladosporium* spp., etc.

Role of yeast in post-harvest protection

Fruits constitute a major part of human dietary consumption as they include a plethora of vital elements that are good for the body. But pathogen infections, mostly from fungi such as *Aspergillus*, *Penicillium*, *Alternaria*, *Botrytis*, *Fusarium*, *Geotrichum*, *Gloeosporium* and *Monilinia* can cause these nutrient-dense crops to lose a significant amount of their quality and cause losses (28). Because pathogenic fungi produce mycotoxins, postharvest diseases of fruits can also pose a health risk to humans (29). Since *Bacillus subtilis* was initially used to fight citrus fruit diseases, the capacity of microorganisms to bio-control postharvest degradation has garnered a lot of interest (30). Recently, more than 12 genera of yeasts have shown exhibited antagonistic activity to control various post-harvest diseases infection in fruits (31) (Fig. 1).

Antagonistic activity of yeast on post-harvest pathogens

Penicillium spp.

Members of the genus *Penicillium* comprises of many post-harvest fungi which infect large numbers of fruits and affect their fruit quality, appearance and shelf life. It is known to produce mycotoxins such as patulin and citrinin. In citrus, *P. italicum* and *P. digitatum*, which cause blue mold and grey mold gained momentum using yeast as a biological control which led to the commercialization of the yeast strain C. *oleophila* under the trade name of Aspire (32). But recently, killer yeast *Clavispora lusitaniae* was reported to have vigorous antagonistic activity against green mold of citrus, *P. digitatum*, than that of the commercial product which contains *C. oleophila*. This strain is also compatible with minor doses of fungicides (33).

In a set of *in vitro* antibiosis tests, the strain of *Aureobasidium* spp. was evaluated for its ability to inhibit *P. expansum* and patulin synthesis. Both volatile and non-volatile metabolites slowed *P. expansum* growth by 50 % on average. The concentration of 1×10^8 cells/mL, was found to be most effective and totally suppressed the symptoms of apple fruits blue mold. On “Golden Delicious” and “Fuji” apples, *Aureobasidium* strain UC14 decreased patulin by 98.1 % and 96.2 % with respect to the control, demonstrating good efficacy as a good antagonist (34). *Wickerhamomyces anomalus*, counteracts the proliferation of *P. digitatum* by producing lytic enzymes and killer toxins (35). When compared to the control *in-vivo*, *W. anomalus* dramatically lowers the disease incidence and lesion diameter of blue mold on pears. When *W. anomalus* was utilized to treat *P. expansum* of pears, the disease incidence decreased from 5.56 % to 100 % in the control group.

Lasiodiplodia theobromae

Lasiodiplodia theobromae is the cause behind one of the most significant post-harvest diseases affecting mangos fruit rot. *Cryptococcus albidus*, *Pichia guilliermondii* and *Debaryomyces hansenii* had shown good efficacy against *L. theobromae* (36). The yeast species *Talaromyces tratensis* has shown the capacity to manage stem end rot caused by *L. theobromae* on the Thailand mango cultivars Nam Dok Mai. Mango cultivars treated with *T. tratensis* spore suspension at 10^6 spores/mL shown a noteworthy ($P<0.05$) reduction in lesion development, reaching up to 85 % and 77 %, respectively (37).

Not only the conventional yeast species but also many marine yeasts have the potential to control post-harvest diseases of mango such as anthracnose and stem rot. *Meyerozyma guilliermondii* and *Pichia kudriavzevii* showed the strongest suppression of mycelial development along the radial direction. According to *in vivo* experiments, *P. kudriavzevii* decreased the severity of stem-end rot by 61 ± 3 %, while *M. guilliermondii* reduced the severity of anthracnose disease by 71 ± 3 % (38).

Colletotrichum spp.

The anthracnose pathogen causes high yield loss in both field and

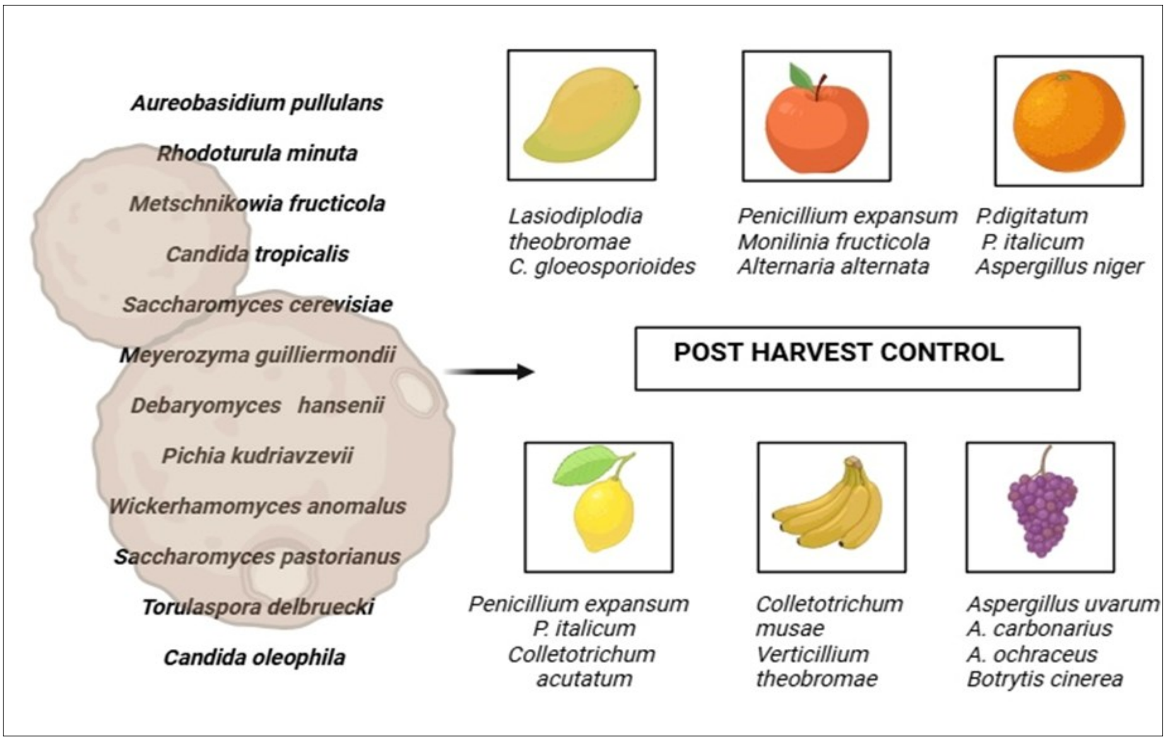

Fig. 1. Major yeast antagonists used for management of post-harvest fungal pathogens of fruits. (This image was generated using Bio-render).

storage conditions in many fruits and are attacked by the pathogen in the field, in cold storage, and during long-distance transportation, which reduces their shelf life (39). The ability of the pathogen to cause latent infection makes it difficult to identify the disease while harvest. Fungal growth inhibition and germination of spores, the bio-control mechanism of antagonistic yeast strains was studied in papaya. Based on the molecular characterization, *Trichosporon asahii* was found to be the best strain against *Colletotrichum* (40). Mango is severely affected by anthracnose which reduces its fruit quality, yield and affects export. The antagonistic activity of yeast has proven to be excellent when supplied with various chemical treatments in mango. Applications of salicylic acid (SA) (50 mg/L) or calcium chloride ($CaCl_2$) solution (1.0 g/L) and *M. pulcherrima* (1.0×10^8 cfu/mL) yeast inhibited the growth of the *C. gloeosporioides* in mango. Nevertheless, it reduced the decay index and inhibited the softening of the fruit (41). In banana, anthracnose was found to be controlled by the treatment of *S. cerevisiae* and *Candida tropicalis* (42).

Botrytis cinerea

Raisins, wine and table grapes are affected by phytopathogenic fungi like *Penicillium*, *Botrytis* and *Aspergillus* during the post-harvest stages. It is a necrotroph, with filamentous fungus and causes high degrees of postharvest losses since it is ubiquitous in nature. Mycotoxin, botcinic acid is produced by the pathogen during infection. *Pichia membranifaciens*, *P. anomala* and *Debaryomyces hansenii* has the most significant antagonistic activity against *Botrytis* strains. In some yeasts, or their toxins, like the deadly toxin *P. membranifaciens* CYC 1106, may be useful as novel agents to manage *B. cinerea* (43). Calcium ascorbate enhance *P. kudriavzevii*'s environmental adaptation and, consequently, the bio-control impact in cherry tomato trials conducted against *B. cinerea* has been shown in the study (44). The study investigated potential processes and the impact of calcium ascorbate on *Pichia kudriavzevii*'s bio-control efficacy. The findings showed that 0.15 g/L of Ca ascorbate greatly increased the bio-control activity of *P. kudriavzevii*, leading to higher rates of yeast cell growth both *in vitro* and *in vivo*. Ca ascorbate increased the activity of antioxidant enzymes in *P. kudriavzevii,* such as peroxidase, catalase and superoxide dismutase which peaked at 48, 96 and 72 hr, respectively.

***Aspergillus* spp.**

The study investigated biological control of *Aspergillus flavus* by few yeast strains of *Aureobasidium pullulans* on tomato fruit *in vitro* (45). The results showed that the two most efficient strains were *A. pullulans* PP4 and *A. pullulans* ZD1. ZD1 and PP4 strains suppressed spore germination by 68.97 % and 79.66 %, respectively, and reduced mycelial development by 53.61 % and 63.05 % *in vitro* conditions. Furthermore, the production of chitinases and glucanases by both strains was verified as their mechanism of action. The effectiveness of *Meyerozyma caribbica* pretreatment with phytic acid (PA) in reducing sour rot in table grapes by regulating the formation of reactive oxygen species (ROS) to evaluate the biocontrol of this mycotoxigenic fungus has been examined (46). The most effective method for minimizing sour decay in grape berries was to pretreat *M. caribbica* with 10 μmol/mL PA (YE). This was demonstrated by an 81 % decrease in disease incidence and a 1.5 mm lesion diameter by the third day.

The efficiency of *M. caribbica* isolated from soils was tested against *Aspergillus ochraceus*. *M. caribbica* showed remarkable resilience in harsh conditions and was able to clearly prevent *A. ochraceus* from growing and producing ochratoxin A (OTA) by destroying mycelium and suppressing the expression of genes necessary for OTA synthesis. Furthermore, the incidence of disease was decreased in grapes infected with *A. ochraceus* by both *M. caribbica* and the volatile organic compounds (VOCs) it produced (47). Yeast strains show excellent results when two compatible yeasts are mixed. The mixing enables compatible yeasts to improve their viability and effectiveness in controlling the radial growth of fungi in *in vitro* assays and on stored lemon fruits (48). The combination of *M. guilliermondii* and *Pseudozyma* sp. was found the best effective for citrus. Combined applications of yeast were also found effective in mandarin. *Hansenia sporauvarum, Meyerozyma guilliermondii* and *Metschnikowia pulcherrima* isolates exhibited antagonistic activity alone and in combinations. Yeast cultures alone showed 73.85-80.64 % reduction in the mycelial growth of green mold *in vitro*, whereas combinations showed 78.40-83.18 % reduction (49). Some of the major yeast species involved in biocontrol of post-harvest diseases of fruits are given in Table 1.

Mechanism of action

Yeast as an antagonist can outcompete the phytopathogens through various mechanisms. A more thorough description of the impact of yeasts on plants and their diseases is lacking compared to other microbes such filamentous fungi or bacteria. They have favorable effects on agricultural plant development and protection both directly and indirectly. They exert beneficial effects on plants such as bio-stimulants and biopesticides, preventing the development and after effect of pathogens. It is essential to comprehend the mechanisms underlying yeasts' interactions with plants and plant diseases to effectively use them as plant-protection agents. These antagonists mostly use the following mechanisms: mycoparasitism, toxin generation, promotion of host resistance, release of volatile antifungal chemicals, competition for nutrients and space and usage of cell wall lytic enzymes and biofilm formation (Fig. 2).

Nutrient competition

This is the major and most crucial mode of action used by yeast during its action (48). The most important and common mechanism is competition for nutrients, space and oxygen. Fruits that have been harvested after harvesting can sustain physical harm that could serve as a gateway for bacteria that cause spoilage. Yeast species during competition can occupy infected areas, compete with the pathogenic fungi for resources and decrease the nutrient availability at the injury site and finally restrict the germination, growth and infection of spores (70). Competition is used for preventing most of the post-harvest fungal pathogens, as they compete for carbohydrates, nitrogen and oxygen. Yeast, due to its high surface colonization capacity, can primarily initiate growth in wounds. Carbon and nitrogen are the nutrients necessary for survival and proliferation of pathogens, and yeast is known to deplete these vital nutrients from the surface of the host fruits (72). Competition is more prominent when the yeast is present in sufficient concentration at the right time and injury site and has the capability to make use of limited resources more quickly and effectively than the

Table 1. Yeast species involved in bio-control of post-harvest diseases of fruits

Fruit crop	Target pathogen	Antagonistic yeast	References
Citrus	*Pencillium digitatum*	*Schwanniomyces vanrijiae*	(50)
		Pichia galeiformis	(51)
	Aspergillus flavus	*Candida orthopsilosis*	(52)
Orange	*Aspergillus niger*	*Aureobasidium pullulans* *Rhodoturula minuta* *Candida tropicalis*	(53)
	Penicillium digitatum *Pencillium italicum*	*Saccharomyces cerevisiae*	(54)
		Meyerozyma guilliermondii	(55)
Apple	*Pencillium digitatum*	*Candida saitoana*	(56)
	Aspergillus niger	*Debaryomyces hansenii*	(57)
Mango	*C. gloeosporioides*	*Torulaspora indica*, *Pseudozyma hubeiensis*	(58)
	Lasiodiplodia theobromae	*Saccharomyces cerevisiae ESA45*, *ESA46*, *ESA 47 Pichia kudriavzevii*	(59)
Banana	*Colletotrichum musae*	*Saccharomyces cerevisiae Candida tropicalis*	(60)
Papaya	*Colletotrichum gloeosporioides*	*Meyerozyma guilliermondii*	(61)
		Wickerhamomyces anomalus	(61)
Grapes	*Botrytis cinerea*	*Saccharomyces pastorianus* *Torulaspora delbruecki*	(62)
	Aspergillus uvarum *Aspergillus aculeatus*	*Saccharomyces cerevisiae Wickerhamomyces anomalus* *Rhodosporidium paludigenum*, *Rhodosporidium fluviale*	(63)
Strawberry	*Botrytis cinerea*	*Aureobasidium* sp. *Saccharomyces cerevisiae Candida stellimalicola*	(64)
Blueberry	*Botrytis cinerea*	*Debaryomyces hansenii*	(65)
kiwi	*Botrytis cinerea*	*Candida oleophila*	(66)
Avocado	*Colletotrichum acutatum*	*Meyerozyma caribbica*	(67)
Litchi	*Lasiodiplodia theobromae*	*Candida tropicalis* *Saccharomyces cerevisiae*	(60)
Loqua	*Colletotrichum gloeosporioides*	*Saturnispora diversa*	(68)
Jujube	*Pencillium itallicum*	*Debaryomyces nepalensis*	(69)

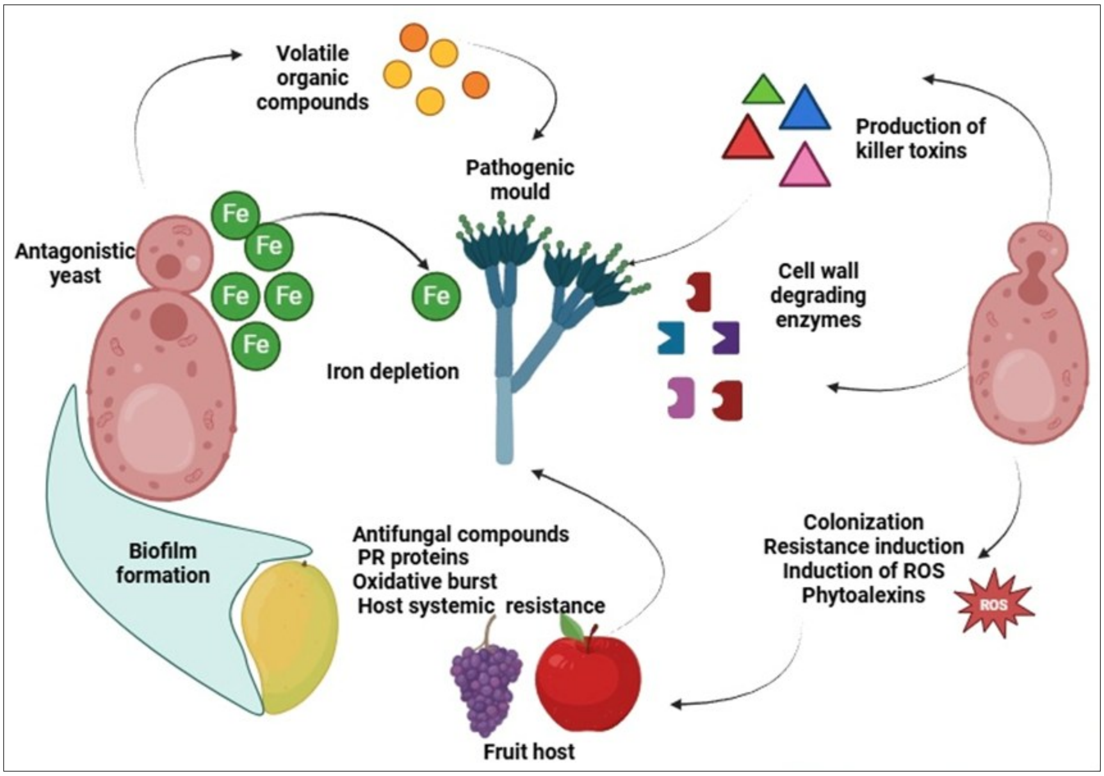

Fig. 2. The mechanism of action of yeast antagonists. (This image was generated using Bio-render).

pathogen (73).

Synthesis of siderophores

Iron is a biologically important element and is vital for the proliferation of all microbes. In nature, many microorganisms can produce siderophores, which are nothing but the relatively less molecular weight compounds which have strong attraction towards iron (74). These microorganisms play a major role in the prevention of disease and can be exploited as biological control by exhibiting iron competition with pathogens that produce relatively low quantities of siderophores with less iron affinity (75). *Metschnikowia* yeast strains employ this mechanism widely. The iron chelators produced by *Metschnikowia pulcherrima* efficiently impede the growth of infections by sequestering the necessary iron resources they require.

The mechanism of iron competition against *B. cinerea* in grapes was explained in *M. pulcherrima.* Researchers evaluated strains of *S. cerevisiae*, *Wickerhamomyces anomalus*, *M. pulcherrima* and *Aureobasidium pullulans* as bio-control agents (BCAs) against *B. cinerea*, a mold causing fungi as post-harvest disease in grapes. The biggest inhibitory halos indicated that the killer strains of *W. anomalus* and *S. cerevisiae* had the maximum antagonistic activity. The abilities to produce biofilm, compete for iron, and colonize fruit wounds have all been proposed as *M. pulcherrima*'s primary modes of action.

Production of hydrolytic enzymes

Parasitism is when the biocontrol agent feeds on the pathogen, which results in the entire devastation of pathogen vegetative structures (73). Most of the parasitism is associated with the production of certain enzymes. These enzymes are relevant as they can act on the fungal cell wall which causes lysis and death (76). The predominant component of cell wall of fungi is made up of chitin and β-1,3-glucan. Filamentous fungi contain more than 20 % of chitin. Fungal cell wall also contains some glycoproteins (20-30 %).

Chitinases

Chitinases can break down chitin, unbranched homopolymer of N-acetyl glucosamine, linked by beta-1,4 linkages (77). They are hydrolyzed by exo-chitinase or endo-chitinases. Exo-chitinases can cleave NAG residues from the one end and endo-chitinase cleaves beta-linkages randomly in the long chain of polymer (78). *Monilinia fructicola* possesses chitinase activity and the chitinase gene MfChi was found to be highly induced in the presence of cell wall of *M. fructicola*, hence MfChi plays a role in the antagonistic activity of the yeast (79).

Glucanases

The β-1,3-glucanase generated by *Pichia membranifaciens*, induces coagulation and cytoplasm leakage in *B. cinerea* hyphae (80). When the culture medium is supplemented with β-glucan at several doses to assess its impact on marine yeast *Scheffersomyeces spartinae* W9, the results showed that 0.1 % β-glucan may boost its bio-control ability against *B. cinerea* in strawberries as well as *in vitro.* It was discovered that including 0.1 % β-glucan into the culture medium facilitated the development of *S. spartinae* W9 in strawberry wounds, improved the capacity to form biofilms, and increased the amount of β-1,3-glucanase produced (81).

Bio-film formation

The antagonistic yeast strains are known to produce biofilms which are embedded in a matrix of nucleic acids, hydrated proteins, etc. Because of this ability, yeasts can adhere, colonize, and multiply on both intact and wound sites of fruits (82). Quorum sensing is often observed in the biofilm growth of yeasts (69). It was proved that carboxymethyl chitosan promotes biofilm formation of *Cryptococcus laurentii* to improve bio-control efficacy against *P. expansum.* In postharvest grapefruit, the synergistic efficacy of the yeast *C. laurentii* cultivated with carboxymethyl chitosan (CMCS) at several doses was investigated for the purpose of suppressing *P. expansum* and investigating the biofilm formation process. The findings show that *C. laurentii* treated with 0.5 % (w/v) CMCS for 72 hr was able to considerably elevate the biocontrol efficiency of *P. expansum* conidia by suppressing hyphal growth and germination of conidia *in vitro* on grapefruit (83).

The bio-control ability of *Torulaspora indica* DMKU-RP31, DMKU-RP35 and *Pseudozyma hubeiensis* YE-21 yeast strains *in vitro* were found to be due to bio-film formation along with siderophore and VOC production. These antagonists were effective against *L. theobromae* infection in mangoes (58). The mechanism of action of native yeast

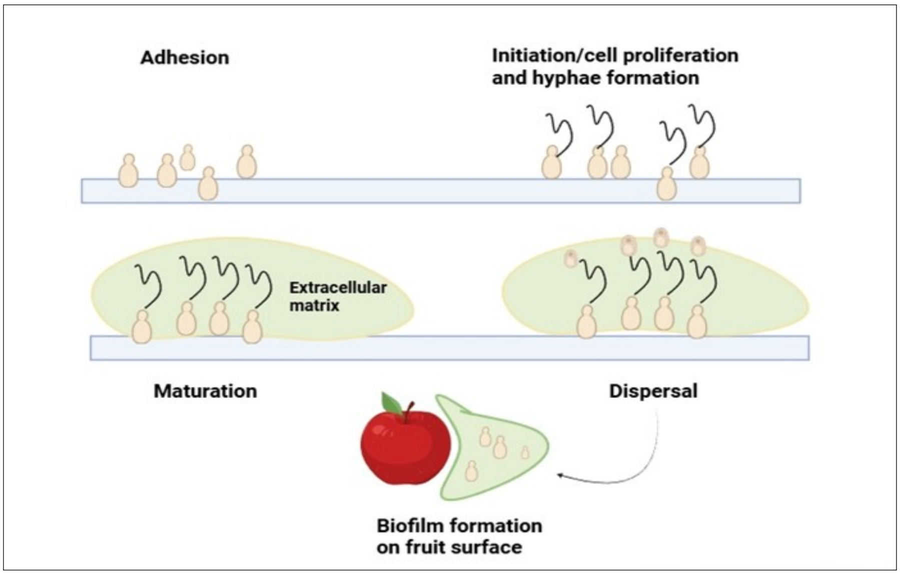

Fig. 3. Phases of *Saccharomyces cerevisiae* biofilm formation. (This image was generated using Bio-render).

Clavispora lusitaniae AgL21, was investigated along with other strains against green mold of lemon incited by *Penicillium digitatum* and the results showed that the strain has ability to form biofilms and colonize lemon wounds (84). The phases of biofilm formation in *Saccharomyces cerevisiae* are given in Fig. 3.

Production of volatile organic compounds (VOCs)

When compared with other mechanisms, VOCs have gathered relatively less focus. Volatile organic compounds produced by yeast include wide range of aldehydes, ketones, esters, lactones, cyclohexanes, terpenes, etc (85). The biocontrol potential of VOCs produced by different yeast strains like *P. kudriavzevii*, *P. occidentalis*, *Issatchenkia orientalis* and *M. quilliermondii/M. caribbica* was demonstrated in grapes against mold fungi such as *Fusarium* sp., *Mucor* sp., *Botrytis* sp., *Aspergillus* and *Penicillium* sp. (86). Yeasts isolated from figs were detected to produce volatile organic compounds through screening. It was found that VOCs emitted by Hansenia sporauvarum had potential in the control of B. cinerea infection in fruits.

Using gas chromatography-mass spectrometry, a study was carried out to identify volatile organic compounds, or volatiles, produced by *Metschnikowia pulcherrima* T 2. It also sought to ascertain the effectiveness of *Metschnikowia pulcherrima*'s volatiles in preventing *B. cinerea*'s conidial germination and mycelial growth, as well as controlling the disease that causes blueberry fruit rot. The findings demonstrated that two compounds, 1,3,5,7-cyclooctatetraene and 3-methyl-1-butanol, were among the 49 volatiles (esters, alcohols, alkenes, alkanes, alkynes, organic acids, ketones and aldehydes) that were discovered from *Metschnikowia pulcherrima* cultures capable of inhibiting growth of *B. cinerea* (87). The mechanism of action of some widely exploited yeasts is given in Table 2.

Yeast based formulations in the market

A wide range of yeast-based products are available on the market, specifically designed to manage post-harvest diseases. Commercial formulations of yeast have gained momentum in various parts of the world, due to its effectiveness and eco-friendly nature. These commercial formulations contain yeast species with antagonistic activity such as *Saccharomyces cerevisiae*, *Pichia* spp., *Candida* spp., etc in their live form. These are available as powder formulations, liquid concentrates or even ready to use formulations which make it easier on fruits.

Table 2. Mechanism of action of some widely exploited yeasts

Mode of action	Yeast species	Origin	Target pathogen	References
Competition for nutrients and space	*Candida stellimalicola* ACBL-07	Citrus leaves	*Penicillium italicum*	(88)
	Debaryomyces nepalensis	Soil of unsprayed mango orchards	*Colletotrichum gloeosporioides*	(89)
Biofilm formation	*Candida oleophila* L12, *Debaryomyces hansenii* L16	Fruits of several citrus varieties	NA	(90)
	Metschnikowia aff. fructicola 1-UDM	Green grapes blackberry		(91)
Volatile organic compounds (VOCs)	*Wickerhamomyces anomalus* BS91	Naturally fermented olive brine	*Monilinia fructigena, Monilinia fructicola*	(92)
	Galactomyces geotrichum JYC549	Cherry tomato	*Fusarium proliferatum*	(93)
Killer toxin	*Candida stellimalicola* ACBL-07	Citrus leaves	*Penicillium italicum*	(88)
Secretion of lytic enzyme	*Aureobasidium pullulans* GE17, *Meyerozyma guilliermondii* KL3	Golden Delicious apple	NA	(94)
Mycoparasitism	*Pichia kudriavzevii* S2C, *Yarrowia lipolytica* S4A	kimchi	*Penicillium digitatum*	

Table 3. Yeast based commercial formulations

Antagonist	Product	Pathogen	Use	Manufacturer	References
Candida oleophila I-182	Aspire	*Penicillium, Botrytis*	Citrus, apple, pear	Ecogen Inc. USA	(96)
Aureobasidium pullulans	Boni protect	*Botrytis cinerea Penicillium expansum Monilinia fructigena*	Pome fruits	BioFerm GMbH, Germany	(96)
Cryptococcus albidus	YieldPlus		Fungicide on vegetables and fruit	Anchor Bio-Technologies, Cape Town, South Africa	(97)
Candida oleophila strain O	Nexy	*Pencilllium*	Apple, pear, banana	BioNext sprl, France	(97)
A. pullulans	Blossom Protect	*E. amylovora B. cinerea*	Soft fruits Strawberry Stone fruits Table/ wine grapes	-	(10)
A. pullulans	Botector	*Botrytis cinerea*	Pear, apple, grapes	-	(10)
M. fructicola	Noli	*Botrytis cinerea*	Wine grapes, strawberry	-	(10)
S. cerevisiae (cell walls)	Romeo	*Erysiphales*	Tomato, cucumber, strawberry	-	(10)
Candida sake	Candifruit	*Penicillium expansum Botrytis cinerea Rhizopus stolonifer*	Pome fruits	Sipcam-Inaagri, SA (Valencia, Spain)	(71)
Metschniowia fructicola	Shemer	*Aspergillus niger Botrytis cinerea Rhizopus stolonifer*	Grape, Strawberry, peach, citrus	Bayer Cropscience, Israel	(96)

Some of the commercial yeast-based formulations are listed in Table 3.

Conclusion

Post-harvest diseases affect fruit quality, shelf-life and marketability, causing major financial losses worldwide. As concerns grow about toxicity, environmental impact, and resistance linked to synthetic fungicides, the search for safer, sustainable alternatives has intensified. Yeast delivers to be an effective replacement for the well-established chemical approaches towards the management of postharvest diseases of fruits. A wide range of yeast strains serve as beneficial bio-control agents that can inhibit a wide range of pathogenic microorganisms on fruits which tends to be a major threat that reduces shelf-life, questioning palatability. The successful application of yeast in post-harvest disease management could culminate in safer, environmentally sound food systems while research remains in progress to discover the most promising yeast species and how to exploit them commercially and solve constraints with large-scale production, formulation stability, regulatory approval and performance consistency under various storage conditions to go from experimental success to commercial application.

Acknowledgements

The authors would like to express their deepest gratitude to Tamil Nadu Agricultural University, Coimbatore, India for supporting them throughout the study. Special thanks are extended to the Chairman and advisory members for their valuable feedback and constructive suggestions on the manuscript. Authors like to acknowledge Anusandhan National Research Foundation (ANRF), Project no: CRG/2022/006273-G for providing financial support.

Authors' contributions

NAF made substantial contributions to the conception and design. TA was involved in drafting the manuscript or critically revising it for important intellectual content. GS assisted in collecting the data and RU contributed to editing and reviewing. All authors read and approved of the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

References

1. Semwal P, Painuli S, Jamloki A, Rauf A, Rahman MM, Olatunde A, et al. Himalayan wild fruits as a strong source of nutraceuticals, therapeutics, food and nutrition security. Food Reviews International. 2023;39(9):6500-36. https://doi.org/10.1080/87559129.2022.2121407
2. Jaglan P, Buttar HS, Al-bawareed OA, Chibisov S. Potential health benefits of selected fruits: Apples, blueberries, grapes, guavas, mangos, pomegranates, and tomatoes. In: Functional foods and nutraceuticals in metabolic and non-communicable diseases. Academic Press; 2022. p. 359-70. https://doi.org/10.1016/B978-0-12-819815-5.00026-4
3. Thiviya P, Gamage A, Kapilan R, Merah O, Madhujith T. Single cell protein production using different fruit waste: a review. Separations. 2022;9(7):178. https://doi.org/10.3390/separations9070178
4. Gunders D, Bloom J. Wasted: How America is losing up to 40 percent of its food from farm to fork to landfill. Science of Food. 2018;2:14. https://doi.org/10.1038/s41538-018-0021-9
5. Godana EA, Yang Q, Zhang X, Zhao L, Wang K, Dhanasekaran S, et al. Biotechnological and biocontrol approaches for mitigating postharvest diseases caused by fungal pathogens and their mycotoxins in fruits: A review. Journal of Agricultural and Food Chemistry. 2023;71(46):17584-96. https://doi.org/10.1021/acs.jafc.3c06448
6. Thompson AK. Fruit and vegetables: harvesting, handling and storage. John Wiley & Sons; 2008.
7. Dukare AS, Paul S, Nambi VE, Gupta RK, Singh R, Sharma K, et al. Exploitation of microbial antagonists for the control of postharvest diseases of fruits: a review. Critical Reviews in Food Science and Nutrition. 2019;59(9):1498-513. https://doi.org/10.1080/10408398.2017.1417235
8. Maicas S. The role of yeasts in fermentation processes. Microorganisms. 2020;8(8):1142. https://doi.org/10.3390/microorganisms8081142
9. Molina-Espeja P. Next generation winemakers: Genetic engineering in *Saccharomyces cerevisiae* for trendy challenges. Bioengineering. 2020;7(4):128. https://doi.org/10.3390/bioengineering7040128
10. Kowalska J, Krzymińska J, Tyburski J. Yeasts as a potential biological agent in plant disease protection and yield improvement-A short review. Agriculture. 2022;12(9):1404. https://doi.org/10.3390/agriculture12091404
11. Thambugala KM, Daranagama DA, Phillips AJ, Kannangara SD, Promputtha I. Fungi vs. fungi in biocontrol: An overview of fungal antagonists applied against fungal plant pathogens. Frontiers in Cellular and Infection Microbiology. 2020;10:604923. https://doi.org/10.3389/fcimb.2020.604923
12. Macias-Paz IU, Pérez-Hernández S, Tavera-Tapia A, Luna-Arias JP, Guerra-Cárdenas JE, Reyna-Beltrán E. *Candida albicans* the main opportunistic pathogenic fungus in humans. Revista Argentina de Microbiologia. 2023;55(2):189-98. https://doi.org/10.1016/j.ram.2022.08.003
13. Hatamzadeh S, Akbari Oghaz N, Rahnama K, Noori F. Comparison of the antifungal activity of chlorine dioxide, peracetic acid and some chemical fungicides in post-harvest management of *Penicillium digitatum* and *Botrytis cinerea* infecting sweet orange and strawberry fruits. Agricultural Research. 2024;13(1):72-84. https://doi.org/10.1007/s40003-023-00677-4
14. Ballester AR, Lafuente MT, González-Candelas L. Spatial study of antioxidant enzymes, peroxidase and phenylalanine ammonia-lyase in the citrus fruit-*Penicillium digitatum* interaction. Postharvest Biology and Technology. 2006;39(2):115-24. https://doi.org/10.1016/j.postharvbio.2005.10.002
15. Ghanei Ghooshkhaneh N, Golzarian MR, Mamarabadi M. Detection and classification of citrus green mold caused by *Penicillium digitatum* using multispectral imaging. Journal of the Science of Food and Agriculture. 2018;98(9):3542-50. https://doi.org/10.1002/jsfa.8864
16. Patil SR, Parthiban VK, Sekar G, Marimuthu K. Survey, isolation and identification of post harvest *Penicillium* mould of sweet orange.

Journal of Soils and Crops 2017;27:45-9.

17. Choquer M, Fournier E, Kunz C, Levis C, Pradier JM, Simon A, et al. *Botrytis cinerea* virulence factors: new insights into a necrotrophic and polyphageous pathogen. FEMS Microbiology Letters. 2007;277 (1):1-10. https://doi.org/10.1111/j.1574-6968.2007.00930.x

18. Raynaldo FA, Xu Y, Wang Q, Wu B, Li D. Biological control and other alternatives to chemical fungicides in controlling postharvest disease of fruits caused by *Alternaria alternata* and *Botrytis cinerea*. Food Innovation and Advances. 2024;3(2):135-43. https://doi.org/10.48130/fia-0024-0014

19. Jeevanantham S, Praveen A, Livitha R, Balamurugan K. Post harvest anthracnose of mango caused by *Colletotrichum gloeosporioides*: a review. Archives of Current Research International. 2024;24(2):106-15. https://doi.org/10.9734/acri/2024/v24i2637

20. Wang QH, Fan K, Li DW, Han CM, Qu YY, Qi YK, et al. Identification, virulence and fungicide sensitivity of *Colletotrichum gloeosporioides* ss responsible for walnut anthracnose disease in China. Plant disease. 2020;104(5):1358-68. https://doi.org/10.1094/PDIS-12-19-2569-RE

21. Bautista-Baños S, Sivakumar D, Bello-Pérez A, Villanueva-Arce R, Hernández-López M. A review of the management alternatives for controlling fungi on papaya fruit during the postharvest supply chain. Crop Protection. 2013;49:8-20. https://doi.org/10.1016/j.cropro.2013.02.011

22. Panuwet P, Prapamontol T, Chantara S, Thavornyuthikarn P, Montesano MA, Whitehead Jr RD, et al. Concentrations of urinary pesticide metabolites in small-scale farmers in Chiang Mai Province, Thailand. Science of the Total Environment. 2008;407(1):655-68. https://doi.org/10.1016/j.scitotenv.2008.08.044

23. Akhtar J, Dubey SC. *Lasiodiplodia theobromae*, a potential post-harvest threat to agri-horticultural crops and its morpho-molecular diversity. Indian Journal of Plant Protection. 2021;49(2):125-30.

24. Karunanayake KO, Adikaram NK. Stem-end rot in major tropical and sub-tropical fruit species. Ceylon Journal of Science. 2020;49 (5):327-36. https://doi.org/10.4038/cjs.v49i5.7800

25. Xu L, Lan X, Chen Y, He R, Wang M, Zhang Y, et al. Identity, pathogenicity and genetic diversity of *Lasiodiplodia* associated with stem-end rot of avocado in China. Plant Disease. 2024;108(9). https://doi.org/10.1094/PDIS-09-23-1939-SR

26. Sharma R. Pathogenecity of *Aspergillus niger* in plants. Cibtech Journal of Microbiology. 2012;1(1):47-51.

27. Tian J, Wang Y, Zeng H, Li Z, Zhang P, Tessema A, Peng X. Efficacy and possible mechanisms of perillaldehyde in control of *Aspergillus niger* causing grape decay. International Journal of Food Microbiology. 2015;202:27-34. https://doi.org/10.1016/j.ijfoodmicro.2015.02.022

28. Min D, Li F, Ali M, Zhang X, Liu Y. Application of methyl jasmonate to control disease of postharvest fruit and vegetables: A Meta-analysis. Postharvest Biology and Technology. 2024;208:112667. https://doi.org/10.1016/j.postharvbio.2023.112667

29. You Y, Zhou Y, Duan X, Mao X, Li Y. Research progress on the application of different preservation methods for controlling fungi and toxins in fruit and vegetable. Critical Reviews in Food Science and Nutrition. 2023;63(33):12441-52. https://doi.org/10.1080/10408398.2022.2101982

30. Zhang X, Li B, Zhang Z, Chen Y, Tian S. Antagonistic yeasts: A promising alternative to chemical fungicides for controlling postharvest decay of fruit. Journal of Fungi. 2020;6(3):158. https://doi.org/10.3390/jof6030158

31. El-Tarabily KA, Sivasithamparam K. Potential of yeasts as biocontrol agents of soil-borne fungal plant pathogens and as plant growth promoters. Mycoscience. 2006;47:25-35. https://doi.org/10.1007/S10267-005-0268-2

32. Droby S, Cohen L, Daus A, Weiss B, Horev B, Chalutz E, et al. Commercial testing of Aspire: a yeast preparation for the biological control of postharvest decay of citrus. Biological control. 1998;12 (2):97-101. https://doi.org/10.1006/bcon.1998.0615

33. Díaz MA, Pereyra MM, Picón-Montenegro E, Meinhardt F, Dib JR. Killer yeasts for the biological control of postharvest fungal crop diseases. Microorganisms. 2020;8(11):1680. https://doi.org/10.3390/microorganisms8111680

34. Cignola R, Zucchinali S, Firrao G, Di Francesco A. Aspects of the biocontrol activity of *Aureobasidium* spp. strain against *Penicillium expansum* of apple. Annals of Applied Biology. 2024;184(3):307-13. https://doi.org/10.1111/aab.12892

35. Di Canito A, Mateo-Vargas MA, Mazzieri M, Cantoral J, Foschino R, Cordero-Bueso G, et al. The role of yeasts as biocontrol agents for pathogenic fungi on postharvest grapes: A review. Foods. 2021;10 (7):1650. https://doi.org/10.3390/foods10071650

36. Hartati S, Wiyono S, Hidayat SH, Sinaga MS. Antagonism mechanism of epiphytic yeast against anthracnose pathogen (*Colletotrichum acutatum*) on chilli. Jurnal Perlindungan Tanaman Indonesia. 2019;23(1):47-53. https://doi.org/10.22146/jpti.40951

37. Suasaard S, Eakjamnong W, Dethoup T. A novel biological control agent against postharvest mango disease caused by *Lasiodioplodia theobromae*. European Journal of Plant Pathology. 2019;155:583-92. https://doi.org/10.1007/s10658-019-01794-z

38. Kaewkrajay C, Dethoup T. Biocontrol ability of marine yeasts against postharvest diseases in mangos caused by *Colletotrichum gloeosporioides* and *Lasiodiplodia theobromae*. European Journal of Plant Pathology. 2024;168(4):709-21. https://doi.org/10.1007/s10658-023-02795-9

39. Bordoh PK, Ali A, Dickinson M, Siddiqui Y, Romanazzi G. A review on the management of postharvest anthracnose in dragon fruits caused by *Colletotrichum* spp. Crop Protection. 2020;130:105067. https://doi.org/10.1016/j.cropro.2019.105067

40. Hassan H, Mohamed MT, Yusoff SF, Hata EM, Tajidin NE. Selecting antagonistic yeast for postharvest biocontrol of *Colletotrichum gloeosporioides* in papaya fruit and possible mechanisms involved. Agronomy. 2021;11(4):760. https://doi.org/10.3390/agronomy11040760

41. Shao YZ, Zeng JK, Hong TA, Yi ZH, Wen LI. The chemical treatments combined with antagonistic yeast control anthracnose and maintain the quality of postharvest mango fruit. Journal of Integrative Agriculture. 2019;18(5):1159-69. https://doi.org/10.1016/S2095-3119(18)62128-8

42. Zhimo VY, Dilip D, Sten J, Ravat VK, Bhutia DD, Panja B, et al. Antagonistic yeasts for biocontrol of the banana postharvest anthracnose pathogen *Colletotrichum musae*. Journal of Phytopathology. 2017;165(1):35-43. https://doi.org/10.1111/jph.12533

43. Santos A, Sánchez A, Marquina D. Yeasts as biological agents to control Botrytis cinerea. Microbiological Research. 2004;159(4):331-8. https://doi.org/10.1016/j.micres.2004.07.001

44. Sun K, Wang Z, Zhang X, Wei Z, Zhang X, Li L, et al. Enhancement of biocontrol efficacy of *Pichia kudriavzevii* induced by Ca ascorbate against *Botrytis cinerea* in cherry tomato fruit and the possible mechanisms of action. Microbiology Spectrum. 2021;9(3):e01507-21. https://doi.org/10.1128/spectrum.01507-21

45. Podgórska-Kryszczuk I. Biological control of *Aspergillus flavus* by the yeast *Aureobasidium pullulans in vitro* and on tomato fruit. Plants. 2023;12(2):236. https://doi.org/10.3390/plants12020236

46. Foku JM, Ackah M, Qiya Y, Zhang H. Phytic acid-mediated enhancement of *Meyerozyma caribbica* biocontrol of *Aspergillus carbonarius* infection in grape berries through regulation of ROS metabolism. Scientia Horticulturae. 2024;333:113213. https://doi.org/10.1016/j.scienta.2024.113213

47. Wu Y, Ji C, Jiang Y, Hu H, Yu T, Yan F. Mechanisms of *Meyerozyma caribbica* isolated from Tibetan soil to inhibit *Aspergillus ochraceus*

on grapes. Postharvest Biology and Technology. 2024;210:112797. https://doi.org/10.1016/j.postharvbio.2024.112797

48. Edward-Rajanayagam RM, Narváez-Zapata JA, Ramírez-González MD, de la Cruz-Arguijo EA, López-Meyer M, Larralde-Corona CP. Yeast mixtures for postharvest biocontrol of diverse fungal rots on citrus Limon var eureka. Horticulturae. 2023;9(5):573. https://doi.org/10.3390/horticulturae9050573

49. Öztekin S, Karbancioglu-Guler F. Biological control of green mould on mandarin fruit through the combined use of antagonistic yeasts. Biological Control. 2023;180:105186. https://doi.org/10.1016/j.biocontrol.2023.105186

50. Abo-Elyousr KA, Al-Qurashi AD, Almasoudi NM. Evaluation of the synergy between *Schwanniomyces vanrijiae* and propolis in the control of *Penicillium digitatum* on lemons. Egyptian Journal of Biological Pest Control. 2021;31:66. https://doi.org/10.1186/s41938-021-00415-4

51. Chen O, Yi L, Deng L, Ruan C, Zeng K. Screening antagonistic yeasts against citrus green mold and the possible biocontrol mechanisms of *Pichia galeiformis* (BAF03). Journal of the Science of Food and Agriculture. 2020;100(10):3812-21. https://doi.org/10.1002/jsfa.10407

52. Sukmawati D, Family N, Hidayat I, Sayyed RZ, Elsayed EA, Dailin DJ, et al. Biocontrol activity of *Aureubasidium pullulans* and *Candida orthopsilosis* isolated from *Tectona grandis* L. phylloplane against *Aspergillus* sp. in post-harvested citrus fruit. Sustainability. 2021;13(13):7479. https://doi.org/10.3390/su13137479

53. Nasahi C, Yusuf AR, Hartati S, Kurniadie D, Subakti-Putri SN. Yeast potential in controlling *Aspergillus* sp. causing fruit rot disease in dekopon oranges (Citrus reticulata 'Shiranui'). Research on Crops. 2023;24(2):407-15. https://doi.org/10.31830/2348-7542.2023.ROC-922

54. Abdel Maksoud Elfaramawy DS, Abo Ghalia HH, Ashour SM, Mohamed AA, Zaki SS. Evaluation of the native killer yeasts against the postharvest phytopathogenic mould of balady orange fruits. Journal of Scientific Research in Science. 2022;39(2):23-48. https://doi.org/10.21608/jsrs.2022.275786

55. López-Cruz R, Segarra G, Torres R, Teixidó N, Ragazzo-Sanchez JA, Calderon-Santoyo M. Biocontrol efficacy of *Meyerozyma guilliermondii* LMA-Cp01 against post-harvest pathogens of fruits. Archives of Phytopathology and Plant Protection. 2023;56(13):1003-20. https://doi.org/10.1080/03235408.2023.2251907

56. El Ghaouth A, Wilson C, Wisniewski M, Droby S, Smilanick JL, Korsten L. Biological control of postharvest diseases of fruits and vegetables. In: Applied mycology and biotechnology. Vol. 2. Elsevier; 2002. p. 219-38. https://doi.org/10.1016/S1874-5334(02)80012-0

57. Çorbacı C, Uçar FB. Purification, characterization and *in vivo* biocontrol efficiency of killer toxins from *Debaryomyces hansenii* strains. International Journal of Biological Macromolecules. 2018;119:1077-82. https://doi.org/10.1016/j.ijbiomac.2018.07.121

58. Konsue W, Dethoup T, Limtong S. Biological control of fruit rot and anthracnose of postharvest mango by antagonistic yeasts from economic crops leaves. Microorganisms. 2020;8(3):317. https://doi.org/10.3390/microorganisms8030317

59. Carvalho Castro AP, Tavares PF, Araújo CP, da Paz CD, Gava CA. Semi-commercial field evaluation of yeast formulations for control of mango postharvest decay caused by Botryosphaeriacean fungi in organic production. International Journal of Fruit Science. 2020;20(2):207-20. https://doi.org/10.1080/15538362.2019.1613469

60. Zhimo VY, Bhutia DD, Saha J. Biological control of post harvest fruit diseases using antagonistic yeasts in India. Journal of Plant Pathology. 2016:275-83. https://doi.org/10.4454/JPP.V98I2.026

61. Lima JR, Gondim DM, Oliveira JT, Oliveira FS, Gonçalves LR, Viana FM. Use of killer yeast in the management of postharvest papaya anthracnose. Postharvest Biology and Technology. 2013;83:58-64. https://doi.org/10.1016/j.postharvbio.2013.03.014

62. Tsioka A, Psilioti Dourmousi K, Poulaki EG, Papoutsis G, Tjamos SE, Gkizi D. Biocontrol strategies against *Botrytis cinerea* in viticulture: evaluating the efficacy and mode of action of selected wine making yeast strains. Letters in Applied Microbiology. 2024;77(3):ovae026. https://doi.org/10.1093/lambio/ovae026

63. Solairaj D, Legrand NN, Yang Q, Zhang H. Isolation of pathogenic fungi causing postharvest decay in table grapes and *in vivo* biocontrol activity of selected yeasts against them. Physiological and Molecular Plant Pathology. 2020;110:101478. https://doi.org/10.1016/j.pmpp.2020.101478

64. Chen PH, Chen RY, Chou JY. Screening and evaluation of yeast antagonists for biological control of *Botrytis cinerea* on strawberry fruits. Mycobiology. 2018;46(1):33-46. https://doi.org/10.1080/12298093.2018.1454013

65. Ramos-Bell S, Hernández-Montiel LG, Velázquez-Estrada RM, Herrera-González JA, Gutiérrez-Martínez P. Potential of *Debaryomyces hansenii* strains on the inhibition of *Botrytis cinerea* in blueberry fruits (*Vaccinium corymbosum* L.). Horticulturae. 2022;8(12):1125. https://doi.org/10.3390/horticulturae8121125

66. Gao Z, Zhang R, Xiong B. Management of postharvest diseases of kiwifruit with a combination of the biocontrol yeast *Candida oleophila* and an oligogalacturonide. Biological Control. 2021;156:104549. https://doi.org/10.1016/j.biocontrol.2021.104549

67. Iñiguez-Moreno M, González-Gutiérrez KN, Ragazzo-Sánchez JA, Narváez-Zapata JA, Sandoval-Contreras T, Calderón-Santoyo M. Morphological and molecular identification of the causal agents of post-harvest diseases in avocado fruit, and potential biocontrol with *Meyerozyma caribbica*. Archives of Phytopathology and Plant Protection. 2021;54(7-8):411-30. https://doi.org/10.1080/03235408.2020.1834806

68. Yan F, Zhang D, Ye X, Wu Y, Fang T. Potential of *Saturnispora diversa* MA as a postharvest biocontrol agent against anthracnose in loquat fruit. Biological Control. 2022;173:105006. https://doi.org/10.1016/j.biocontrol.2022.105006

69. Lei X, Deng B, Ruan C, Deng L, Zeng K. Phenylethanol as a quorum sensing molecule to promote biofilm formation of the antagonistic yeast *Debaryomyces nepalensis* for the control of black spot rot on jujube. Postharvest Biology and Technology. 2022;185:111788. https://doi.org/10.1016/j.postharvbio.2021.111788

70. Ezzouggari R, Bahhou J, Taoussi M, Seddiqi Kallali N, Aberkani K, Barka EA, et al. Yeast warriors: Exploring the potential of yeasts for sustainable citrus post-harvest disease management. Agronomy. 2024;14(2):288. https://doi.org/10.3390/agronomy14020288

71. Agirman B, Carsanba E, Settanni L, Erten H. Exploring yeast‐based microbial interactions: the next frontier in postharvest biocontrol. Yeast. 2023;40(10):457-75. https://doi.org/10.1002/yea.3895

72. Lahlali R, Ezrari S, Radouane N, Kenfaoui J, Esmaeel Q, El Hamss H, et al. Biological control of plant pathogens: A global perspective. Microorganisms. 2022;10(3):596. https://doi.org/10.3390/microorganisms10030596

73. Spadaro D, Droby S. Development of biocontrol products for postharvest diseases of fruit: The importance of elucidating the mechanisms of action of yeast antagonists. Trends in Food Science & Technology. 2016;47:39-49. https://doi.org/10.1016/j.tifs.2015.11.003

74. van Loon L. Helping plants to defend themselves: biocontrol by disease-suppressing rhizobacteria. In: Developments in plant genetics and breeding. Vol. 6. Elsevier; 2000. p. 203-13. https://doi.org/10.1016/S0168-7972(00)80123-1

75. Köhl J, Kolnaar R, Ravensberg WJ. Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. Frontiers in Plant Science. 2019;10:845. https://doi.org/10.3389/fpls.2019.00845

76. González-Estrada RR, Carvajal-Millán E, Ragazzo-Sánchez JA,

Bautista-Rosales PU, Calderón-Santoyo M. Control of blue mold decay on Persian lime: Application of covalently cross-linked arabinoxylans bioactive coatings with antagonistic yeast entrapped. LWT-Food Science and Technology. 2017;85:187-96. https://doi.org/10.1016/j.lwt.2017.07.019

77. Wang F, Deng H, Wu Q, Sun H, Zhang J, Li Z, et al. Biocontrol of black rot of sweet potato by *Pichia pastoris* recombinant strain expressing chitinase IbChiA. Scientia Horticulturae. 2024;329:112979. https://doi.org/10.1016/j.scienta.2024.112979

78. Stoykov YM, Pavlov AI, Krastanov AI. Chitinase biotechnology: production, purification, and application. Engineering in Life Sciences. 2015;15(1):30-8. https://doi.org/10.1002/elsc.201400173

79. Banani H, Spadaro D, Zhang D, Matic S, Garibaldi A, Gullino ML. Biocontrol activity of an alkaline serine protease from *Aureobasidium pullulans* expressed in *Pichia pastoris* against four postharvest pathogens on apple. International Journal of Food Microbiology. 2014;182:1-8. https://doi.org/10.1016/j.ijfoodmicro.2014.05.001

80. Masih EI, Paul B. Secretion of β-1,3-glucanases by the yeast *Pichia membranifaciens* and its possible role in the biocontrol of *Botrytis cinerea* causing grey mold disease of the grapevine. Current Microbiology. 2002;44:391-5. https://doi.org/10.1007/s00284-001-0011-y

81. Chen X, Wei Y, Zou X, Zhao Z, Jiang S, Chen Y, et al. β-Glucan enhances the biocontrol efficacy of marine yeast *Scheffersomyeces spartinae* W9 against *Botrytis cinerea* in strawberries. Journal of Fungi. 2023;9(4):474. https://doi.org/10.3390/jof9040474

82. Freimoser FM, Rueda-Mejia MP, Tilocca B, Migheli Q. Biocontrol yeasts: mechanisms and applications. World Journal of Microbiology and Biotechnology. 2019;35(10):154. https://doi.org/10.1007/s11274-019-2728-4

83. Wu HY, Wang F, Yang L, Chen L, Tang JR, Liu Y, et al. Carboxymethyl chitosan promotes biofilm-formation of *Cryptococcus laurentii* to improve biocontrol efficacy against *Penicillium expansum* in grapefruit. Advanced Composites and Hybrid Materials. 2024;7(1):23. https://doi.org/10.1007/s42114-023-00828-9

84. Pereyra MM, Díaz MA, Vero S, Dib JR. Enhancing biological control of postharvest green mold in lemons: Synergistic efficacy of native yeasts with diverse mechanisms of action. PLoS One. 2024;19(4):e0301584. https://doi.org/10.1371/journal.pone.0301584

85. Morath SU, Hung R, Bennett JW. Fungal volatile organic compounds: a review with emphasis on their biotechnological potential. Fungal Biology Reviews. 2012;26(2-3):73-83. https://doi.org/10.1016/j.fbr.2012.07.001

86. Choińska R, Piasecka-Jóźwiak K, Chabłowska B, Dumka J, Łukaszewicz A. Biocontrol ability and volatile organic compounds production as a putative mode of action of yeast strains isolated from organic grapes and rye grains. Antonie van Leeuwenhoek. 2020;113:1135-46. https://doi.org/10.1007/s10482-020-01420-7

87. Li Z, Liu Q, Wu C, Yuan Y, Ni X, Wu T, et al. Volatile organic compounds produced by *Metschnikowia pulcherrima* yeast T-2 inhibited the growth of *Botrytis cinerea* in postharvest blueberry fruits. Horticultural Plant Journal. 2024. https://doi.org/10.1016/j.hpj.2023.12.003

88. da Cunha T, Ferraz LP, Wehr PP, Kupper KC. Antifungal activity and action mechanisms of yeasts isolates from citrus against *Penicillium italicum*. International Journal of Food Microbiology. 2018;276:20-7. https://doi.org/10.1016/j.ijfoodmicro.2018.03.019

89. Zhou Y, Li W, Zeng J, Shao Y. Mechanisms of action of the yeast *Debaryomyces nepalensis* for control of the pathogen *Colletotrichum gloeosporioides* in mango fruit. Biological Control. 2018;123:111-9. https://doi.org/10.1016/j.biocontrol.2018.05.014

90. Hammami R, Oueslati M, Smiri M, Nefzi S, Ruissi M, Comitini F, et al. Epiphytic yeasts and bacteria as candidate biocontrol agents of green and blue molds of citrus fruits. Journal of Fungi. 2022;8(8):818. https://doi.org/10.3390/jof8080818

91. Oztekin S, Karbancioglu-Guler F. Bioprospection of *Metschnikowia* sp. isolates as biocontrol agents against postharvest fungal decays on lemons with their potential modes of action. Postharvest Biology and Technology. 2021;181:111634. https://doi.org/10.1016/j.postharvbio.2021.111634

92. Grzegorczyk M, Żarowska B, Restuccia C, Cirvilleri G. Postharvest biocontrol ability of killer yeasts against *Monilinia fructigena* and *Monilinia fructicola* on stone fruit. Food Microbiology. 2017;61:93-101. https://doi.org/10.1016/j.fm.2016.09.005

93. Chen RY, Jiang W, Fu SF, Chou JY. Screening, evaluation, and selection of yeasts with high ammonia production ability under nitrogen free condition from the cherry tomato (*Lycopersicon esculentum* var. *cerasiforme*) rhizosphere as a potential bio-fertilizer. Rhizosphere. 2022;23:100580. https://doi.org/10.1016/j.rhisph.2022.100580

94. Agirman B, Erten, H. Biocontrol ability and action mechanisms of *Aureobasidium pullulans* GE17 and *Meyerozyma guilliermondii* KL3 against *Penicillium digitatum* DSM2750 and Penicillium expansum DSM62841 causing postharvest diseases. Yeast. 2020;37(9-10):437-48. https://doi.org/10.1002/yea.3501

95. Delali KI, Chen O, Wang W, Yi L, Deng L, Zeng K. Evaluation of yeast isolates from kimchi with antagonistic activity against green mold in citrus and elucidating the action mechanisms of three yeast: *P. kudriavzevii*, *K. marxianus*, and *Y. lipolytica*. Postharvest Biology and Technology. 2021;176:111495. https://doi.org/10.1016/j.postharvbio.2021.111495

96. Leyva Salas M, Mounier J, Valence F, Coton M, Thierry A, Coton E. Antifungal microbial agents for food biopreservation-A review. Microorganisms. 2017;5(3):37. https://doi.org/10.3390/microorganisms5030037

97. Anuagasi CL, Okigbo RN, Anukwuorji CA, Okereke CN. The impact of biofungicides on agricultural yields and food security in Africa. International Journal of Agricultural Technology. 2017;13(6):953-78.

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.