

Endophytic fungi in postharvest disease management in fresh produce

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4.1 Introduction

The world population does not stop growing. In 2021, we have reached 7.9 billion people worldwide ([Worldmeters.info](https://www.worldometers.info/), 2021) and estimates suggest that by 2050 we could reach 9.7 billion people ([United Nations](https://www.un.org/), 2019). This growth would translate into an increase in demand for food. Therefore increasing food security and access to nutritious and healthy diets is a priority ([FAO](https://www.fao.org/), [IFAD](https://www.ifad.org/), [UNICEF](https://www.unicef.org/), [WFP](https://www.wfp.org/), & [WHO](https://www.who.int/), 2020). Currently, there is growing inequality in access to basic resources, around a tenth of the population is undernourished ([FAO et al.](https://www.fao.org/), 2021). On the other hand, in countries where food security is assured, there is a growing awareness of the “costs of diets.” Mainly healthcare-related costs that are associated with unhealthy diets and environmental impacts such as CO₂ emissions, climatic change, and the abuse of agrochemicals ([Springmann](https://www.springer.com/), 2020). There is growing public concern about the risks to human and environmental health posed by agrochemicals in fresh produce, as well as the potential resistance that pathogens can develop after continued use ([Wisniewski](https://www.wisniewski.com/), [Droby](https://www.droby.com/), [Norelli](https://www.norelli.com/), [Liu](https://www.liu.com/), & [Schena](https://www.schena.com/), 2016).

This panorama leads us to the conclusion that we must increase the accessibility of healthy foods and reduce our environmental impact. Among these aliments, fresh, unprocessed products such as fruits and vegetables stand out. One strategy to ensure the availability of fresh produce is through the control of postharvest diseases, which are a major

cause of fresh produce losses. By reducing postharvest losses, the crop yield per hectare is increased without increasing the cultivated land or the productive pressure on the soil. This is an indispensable objective, considering that we are losing arable land due to population growth and the consequent demand for residential and industrial spaces. For now, the problem is solved with the conversion of forest land into arable land (Tong & Qiu, 2020). In addition, the quality of the products after harvest is very important, as it will influence the entire production chain and affect their storage capacity, transport and, above all, shelf life, a characteristic highly valued by consumers (Mahajan, Caleb, Singh, Watkins, & Geyer, 2014). If the product has not correctly preserved all its organoleptic characteristics or does not have a good appearance, it may be rejected by the end consumer or intermediaries (Makhal, Robertson, Thyne, & Miroso, 2021). Fruits and vegetables losses caused by postharvest diseases can be around 50%–55% of total production, while fungal spoilage is responsible for 20%–35% of the losses that occur during handling in postproduction, storage, and shipping of fresh produce (Dukare et al., 2019; Dukare, Singh, Jangra, & Bhushan, 2020; Nunes, 2012; Zhang, Mahunu, Castoria, Apaliya, & Yang, 2017).

In addition to multimillion dollar losses, some microorganisms can pose a threat to health as they generate mycotoxins (Dukare et al., 2019; Huang, Ren Li, Feng, Dong, & Ren, 2021). Because of that, for many years, strategies have been carried out to reduce or prevent infections. Among the most popular treatments are chemical treatments, followed by heat or radiation (Mahajan et al., 2014). However, the application of several agrochemicals against certain postharvest diseases has been banned or reduced due to a lack of efficient and novel active compounds, the establishment of resistant pathogens, the high levels of agrochemical residues in fresh produce, negative environmental impacts, and toxicological problems related to human health (Droby, 2006).

Chemical treatments are known to be effective and, for now, necessary. However, agrochemicals can pose a health risk. Especially when they are applied postharvest and the product is consumed raw in a short period of time after treatment (Lawal, Wong, Tan, Abdula'Uf, & Alsharif, 2018). Furthermore, many of these products degrade very slowly, and their persistence in the environment represents an additional problem (Mari, Di Francesco, & Bertolini, 2014). As a result, regulation is increasingly strict. Therefore although the use of pesticides is the main strategy to treat postharvest diseases, there is a growing interest in new approaches that do not harm the biosphere and the ecosphere. One of these nondestructive and green approaches to postharvest handling of fresh produce is the use of endophytic fungi. They act as biological control agents (BCAs) for postharvest diseases in fresh products, both by direct application and by the use of their secondary metabolites.

4.2 Main pathogen-diseases of postharvest fresh produce

Vegetables and fruits are rich in nutrients, high in moisture, and low in pH, being the perfect niche for microbial growth (Droby, Chalutz, Wilson, & Wisniewski, 1992). However, due to the diversity of postharvest pathogens, the colonization process of these niches differs from one pathogen to another. Some require a wound to penetrate, but

others can enter by directly damaging healthy tissue or through natural openings (stomata, lenticels, stems, etc.) (Prusky & Lichter, 2007). Regardless of their route of entry, they usually remain quiescent until the fruits begin to ripen.

4.2.1 *Botrytis cinerea*

B. cinerea is a necrotrophic airborne fungus and the causative agent of the disease known as gray mold (Poveda, Barquero, & González-Andrés, 2020; Van Baarlen, Woltering, Staats, & Van Kan, 2007). This fungus is one of the most important plant and postharvest pathogens in the world (Dean et al., 2012; Zhang, Qin, Li, & Tian, 2014). The pathogens cause serious losses in more than 200 crop species worldwide, causing rot in fruits and aerial parts of plants (Wan et al., 2021; Williamson, Tudzynski, Tudzynski, & Van Kan, 2007). However, the total damage caused by this pathogen cannot be accounted for, because it occurs at all stages of production and retailing and in a broad host range. Even though the infection can occur at any stage, most commonly occurs when the tissues are young. This confronts the fact that the symptoms usually appear after harvesting, during transport, or storage of healthy crops (Abdel-Rahim & Abo-Elyousr, 2017). This phenomenon is due to the ability of *Botrytis* to remain quiescent until the conditions for development are favorable and changes are observed in the environment and/or in plant physiology (Williamson et al., 2007).

Some of the crops in which *B. cinerea* is known as an important postharvest pathogen are: pome fruit (Wenneker & Thomma, 2020), tomato (Liu, Gao, et al., 2020), nectarines (Tahmasebi, Golmohammadi, Nematollahzadeh, Davari, & Chamani, 2020), peach (Suktawee et al., 2019), strawberries (Lafarga et al., 2019), blueberry (Kumar, Baghel, Yadav, & Dhakar, 2018), eggplant, cucurbits, bulbs, leafy vegetables, green beans, carrots, onions and peppers (Cole, Jarvis, & Schweikert, 2003; Lugauskas, Repečkienė, & Novošinskas, 2005).

4.2.2 *Penicillium* spp.

The fungal genus *Penicillium* contains more than 150 species. It belongs to the phylum Ascomycota and is ubiquitous, being present in soil, vegetation, air, and indoor environments (Visagie et al., 2014). The genus *Penicillium* occurs recurrently on fruits and vegetables after harvest (Huang et al., 2021). However, only a few species are considered as relevant plant pathogens (Samson & Pitt, 2003). The three most important postharvest pathogen species within the *Penicillium* genus are *Penicillium digitatum*, the causative agent of the disease known as gray mold, *Penicillium italicum*, responsible for generating blue mold rot, and *P. expansum*, responsible for blue mold. As an example, in citrus, 90% of the losses are caused by these fungi (Brasil & Siddiqui, 2018; Macarasin et al., 2007). They are pathogens that enter the plant through wounds during growth in the field as well as in the postharvest stages (Wan, Kahramanoğlu, & Okatan, 2021). Furthermore, this genera produces mycotoxins such as ochratoxin A, citrinin or patulin, which are potentially carcinogenic, mutagenic, and can cause nephrotoxicity and hepatotoxicity (Prencipe et al., 2018; Qi et al., 2014).

Some of the crops in which *Penicillium* spp. is recognized as important postharvest pathogen: pome fruit, tomato (Liu, Gao, et al., 2020), stone fruit (Zhang et al., 2016), citrus

fruit (Costa, Bazioli, de Moraes Pontes, & Fill, 2019), onion, garlic, cabbage, sugar beet and yam (Chávez-Magdaleno, González-Estrada, Ramos-Guerrero, Plascencia-Jatomea, & Gutiérrez-Martínez, 2018).

4.2.3 *Colletotrichum* spp.

Colletotrichum spp. is an ascomycete belonging to coelomycetes asexual genus, with an hemibiotrophic lifestyle (Dean et al., 2012). It is an important phytopathogen, almost every crop is susceptible to one of its 200 species (Marin-Felix et al., 2017). It shows a characteristic damage pattern with leaf spots of anthracnose and blight and postharvest fruit rot. Symptoms may appear on fruits, flowers, leaves and branches of various horticultural crops, causing great losses in important crops, especially fruits, vegetables, and ornamentals (Dean et al., 2012). *Colletotrichum* is a quiescent fungus, that can cause losses of 80% of production during storage, transportation, or marketing (Damasceno et al., 2019). Some of the crops in which *Colletotrichum* spp. is known as an important postharvest pathogen are: blueberries (Liu, Zheng, et al., 2020), grapes (Solairaj, Guillaume Legrand, Yang, & Zhang, 2020; Solairaj, Yang, Guillaume Legrand, Routledge, & Zhang, 2021), citrus fruit (Boubaker et al., 2016), beans, onions, avocado (Chávez-Magdaleno et al., 2018) and pome fruit, where it is one of the two most prevalent postharvest pathogens (Wenneker & Thomma, 2020).

4.2.4 *Monilinia* spp.

Monilinia is an important ascomycete fungal pathogen genus belonging to the Helotiales order. There are more than 30 species of this genus. Among them, three species (*Monilinia fructicola*, *M. fructigena*, and *M. laxa*) stand out for being particularly aggressive, generating important economic losses in postharvest (Huang et al., 2021). These pathogens are capable of infecting a wide variety of tissues and organs, generating different symptomatologies, depending on the plant host (Holb, 2008). The infection usually starts on the tree and it is translated into soft decay in fruits, when the sugar content increases (Wan et al., 2021). These pathogens cause diseases that include twig canker, blossom blight, and brown rot (Bellamy, Xu, & Shaw, 2021). *Monilinia* causes significant losses because it is the main disease present in stone fruit. In fact, brown rot is responsible for more than half of postharvest losses in peaches worldwide (Obi, Barriuso, & Gogorcena, 2018) and 1.7 M€/year are lost due *Monilinia* for peach and nectarine alone (Martini & Mari, 2014). Another crop in which *Monilinia* is recognized as an important postharvest pathogen is pome fruit (Wenneker & Thomma, 2020).

4.2.5 *Alternaria* spp.

Alternaria spp. belongs to the division Ascomycota and to the Pleosporales order. It is an opportunistic pathogenic fungus that is responsible for being the main cause of black rot. The symptoms of this disease are black spots on fruit and vegetables (Wan et al., 2021). In particular, *Alternaria alternata* is widely distributed being the main postharvest disease that occurs on tomatoes (Xu et al., 2014). *Alternaria* is the most relevant disease in tomato and is

responsible for large losses on *Brassicaceae* crops (Nowicki, Nowakowska, Niezgoda, & Kozik, 2012). Some of the crops in which *Alternaria* spp. is known as an important postharvest pathogen are: pome fruit (Weber, Dralle, Jork, & Niedersachsen, 2013), citrus fruit (Boubaker et al., 2016), strawberries (Lafarga et al., 2019), grapes (Solairaj et al., 2020, 2021), cucumber, carrots, cabbages, cauliflowers, and peppers (Chávez-Magdaleno et al., 2018).

4.2.6 Other fungal pathogens

Rhizopus, *Aspergillus*, *Geotrichum*, and *Botryosphaeria* have a major implication on several postharvest crops of fruit and vegetables (Dukare et al., 2020). *Rhizopus* is the causative agent of soft rot in plums, nectarines and grapes. It causes significant losses in peach, and is one of the most pathogenic microorganisms in tomato (Kong et al., 2019). *Aspergillus* causes black rot in grapes, with special relevance in tropical climates (Solairaj et al., 2020). *Geotrichum* causes acid rot in citrus fruits, the second most important disease after those generated by the genus *Penicillium* (Boubaker et al., 2016). *Botryosphaeriaceae* spp. are the causal agents of diseases such as leaf spot, fruit and root rot, dieback, and trunk canker on different fruits such as avocado, guava, and persimmon (Navarro, Edwards Molina, & Nogueira Júnior, 2021).

4.2.7 Bacterial pathogens

In vegetables and fruits, postharvest fungal pathogens are responsible for 80%–90% of total losses due to microbial diseases (Gomes, Queiroz, & Pereira, 2015; Anthracnose, 2014). However, it is worth mentioning some bacteria that cause significant losses as postharvest pathogens. The most important ones are *Erwinia* spp., *Pseudomonas* spp. and *Xanthomonas* spp. *Erwinia* spp. causes bacterial soft rot in bulbs (onion and garlic), crucifers (cabbage), cucurbits, roots tubers (carrots, potato), solanaceous (tomato, pepper, eggplant), pome fruit, asparagus, celery, and lettuce. *Xanthomonas* spp. is the causative agent of the diseases known as bacterial canker in citrus, bacterial blight in legumes (peas and beans) and bacterial rot in lettuce. Lastly, *Pseudomonas* spp. is responsible for soft rot in lettuce, celery, and asparagus, bacterial speck in solanaceous, bacterial blight legumes, black pit in citrus and warts in cucurbits (Antunes & Cavaco, 2010).

4.3 Postharvest disease management in fresh produce

To avoid the proliferation of pathogenic microorganisms in postharvest, fresh products are usually treated before or after harvest. Depending on the nature of the process, they are classified as chemical, physical, or biological treatments, although they may appear in combination.

4.3.1 Chemical control

Chemical control is the usual treatment to control postharvest diseases. Specifically, fungicides are the most common postharvest agrochemicals (Gomes et al., 2015). These fungicides have different mechanisms of action, for example, acting on respiration, osmoregulation,

microtubule assembly, sterol biosynthesis, etc. (Leroux, 2007). Therefore they are a very effective tool, whose use is widespread. However, it increasingly presents more detractors, due to the residual toxicity, environmental pollution, long degradation period, the appearance of resistant strains, and the side effects on humans (Antunes & Cavaco, 2010). In contrast to these products, new low-toxicity chemicals commonly known as GRAS are emerging. These have a minimal impact on humans and the environment. Currently, new synthetic treatments are being developed, including the use of nanomaterials that control the development of diseases (Roberto, Youssef, Hashim, & Ippolito, 2019) and organic and inorganic salts that are cheap, accessible, and can be used as synthetic edible coatings (Palou, 2018). They can be an alternative to the classical chemical treatment, among other emerging strategies such as physical treatments and/or biocontrol agents.

4.3.2 Physical treatments

Physical treatments are usually divided into those that make use of a heat treatment and those that do not. However, the most widespread physical treatment to reduce postharvest pathogen losses is to keep the product at a low temperature and control the storage atmosphere. Often it is not considered a treatment per se because the main purpose is to slow down the processes of maturation, senescence, and respiratory rate, but this leads to a reduction in the development of microorganisms (Wan et al., 2021).

Thermal treatments include air, steam, or hot water treatments. These methods are very effective but, they can alter organoleptic characteristics such as texture, taste, smell, or color, as well as reduce vitamin or mineral content (Zhang et al., 2017).

Conventional nonthermal physical technologies are microwaves and radio frequencies, hyperbaric and hypobaric pressures, and far ultraviolet radiation (Wenneker & Thomma, 2020). In addition, there are new technologies that are currently being applied such as different packaging systems, pulsed light (PL), high hydrostatic pressure, ionizing radiation, cold plasma, high-power ultrasound, and dense phase carbon dioxide (Pinela & Ferreira, 2017). These treatments, unlike the previous ones, do not modify the final products. Even so, they do have drawbacks, in some cases they are quite expensive. They also reduce the microbiota present in vegetables and fruits, eliminating both beneficial and pathogenic microorganisms, leaving a free niche after treatment, allowing a secondary infection. To increase the stability of the treatment, it could be combined with a subsequent biological treatment that repopulates the surfaces of the products with beneficial endophytes (Zhang et al., 2017).

4.3.3 Biological control

The term biological control refers to a compendium of postharvest disease control techniques that can be preventive and/or corrective. Its most frequent use is attributed to suppressing the pathogenicity or populations of one or more pathogens through the use of live microorganisms. The definition can be expanded to recognize the use of products derived from microorganisms or other living beings. The organism that is used as a tool is called a BCA. Formulations of BCAs can be very varied, from plant extracts to combinations of microorganisms with specific activities (Zhang et al., 2017).

One strategy that is gaining popularity is the use of edible films or coatings. They are made with natural products, derived from plants, bacteria, fungi, and even insects. They are used in the food packaging industry in a similar way to the plastic that wraps fruits and vegetables. This coating acts by preventing microbial decay, improving the quality of the product, both in terms of appearance and texture and biochemically, protecting the phytochemicals it naturally contains. They can be made from proteins, lipids, or polysaccharides (Wan et al., 2021). Another procedure that is very effective to prevent pathogenic infections is the use of plant or microbial volatile organic compounds (VOCs). These compounds have antimicrobial activity, and can be used as biopesticides (Poveda, Barquero, et al., 2020). However, not all BCA have a direct mechanism of action. Some signaling molecules, such as plant hormones, can induce a certain degree of resistance against pathogens in the plant itself or in the harvested product. These hormones such as salicylic acid (SA) or jasmonic acid (JA) can be administered exogenously and reduce the symptoms caused by postharvest pathogens (Poveda, 2020).

4.4 Endophytic fungi and agriculture

Endophytes are fungi, bacteria, protists, or archaea that live in association with the living tissues of a plant without generating symptoms of infection (Wilson, 1995). They colonize, partly or throughout their lifespan, the internal organs and tissues such as roots, stems, seeds, leaves, and fruits (Kumar et al., 2021).

Endophytic fungi are involved in some key plant functions such as growth promotion, secondary metabolite production, or disease and pest control (Kumar, Soni, Jain, Dash, & Goel, 2019; Kumar et al., 2021). To promote plant growth, these fungi have various strategies. The first is to improve the accessibility of limiting nutrients: nitrogen, phosphorus, potassium, or zinc, by directly transferring these nutrients from organic matter to the plant, improving the plant's uptake efficiency, or modifying the solubility of nutrients and increasing their bioavailability. Another strategy is based on the production of phytohormones that promote growth, such as indole acetic acid and gibberellins (Poveda, Eugui, Abril-Urías, & Velasco, 2021). The second application is to increase tolerance to abiotic stress. It can occur through two mechanisms: activation of plant stress responses or through the biosynthesis of antistress compounds. In this way, endophytic fungi can promote growth in conditions of drought, high salinity, low amounts of nutrients, or extreme temperatures (Lata, Chowdhury, Gond, & White, 2018). The last application is the reduction of the attack of phytophages and pathogens. Some endophytic fungi are capable of reducing the damage caused by biotic stresses through direct strategies such as parasitism, antibiosis, the synthesis of lytic enzymes, competition for space and nutrients, and the activation of plant defenses (Mantzoukas & Eliopoulos, 2020; Poveda, Abril-Urías, & Escobar, 2020).

4.5 Endophytic fungi as biocontrol agents in postharvest

Fungi are found as epiphytes and endophytes of fruits and vegetables, being part of their composition, forming a whole holobiont (Kusstascher et al., 2020). Thanks to the new omics

techniques, the diversity and function of the internal and external microbiome of fruits and vegetables can be quickly and accurately characterized (Droby & Wisniewski, 2018; Zhang et al., 2021). This information is an important starting point for the study of new postharvest BCAs and products for fresh produce based on endophytic fungi (Droby & Wisniewski, 2018; Nayak, Mukherjee, Sengupta, & Samanta, 2019; Sare, Jijakli, & Massart, 2021).

Endophytic fungi can play an important role as BCAs in fruits and vegetables in post-harvest, due to different mechanisms of action (Huang et al., 2021). The competition for space and nutrients (mainly iron), antibiosis, and the activation of plant defense responses stand out (Huang et al., 2021). Endophytic fungi produce a wide range of antimicrobial compounds, such as antibiotics, alkaloids, VOCs or lytic enzymes (chitinases, glucanases, etc.) (Poveda et al., 2021; Spadaro & Droby, 2016). On the other hand, the activation of plant defenses leads to the accumulation in the tissues of fruits and vegetables of pathogenesis-related proteins (PRs), phytoalexins or defense-related enzymes (catalases, peroxidases, etc.) (Poveda, 2020; Spadaro & Droby, 2016). Specifically, in recent years, the development of new BCAs based on endophytic fungi with the capacity to produce antimicrobial VOCs is gaining great development, a process known as myofumigation (Gomes et al., 2015). Table 4.1 shows all the studies on the use of endophytic fungi (yeasts and filamentous fungi) as BCAs against postharvest pathogens in fresh products. In addition, Fig. 4.1 shows an infographic as a summary of the different mechanisms of action described for these BCAs.

During the last decades, numerous studies have been conducted to find endophytic fungi with the ability to control different postharvest pathogens in fresh products, without delving into the possible mechanisms of action involved. In this way, different species have been described within the endophytic yeast genera *Aureobasidium* (Kheireddine, Essghaier, Hedi, Dhieb, & Sadfi-Zouaoui, 2018; Rathnayake, Savocchia, Schmidtke, & Steel, 2018), *Candida* (Fernandez-San Millan, Larraya, Farran, Ancin, & Veramendi, 2021; Vilaplana, Cifuentes, Vaca, Cevallos-Cevallos, & Valencia-Chamorro, 2020), *Clavispora* (Kheireddine et al., 2018; Pereyra, Díaz, Meinhardt, & Dib, 2020), *Metschnikowia* (Fernandez-San Millan et al., 2021; Spadaro, Ciavarella, Dianpeng, Garibaldi, & Gullino, 2010; Zhang, Spadaro, Garibaldi, & Gullino, 2010a), *Pichia* (Vilaplana et al., 2020), *Saccharomycopsis* (Abdel-Rahim & Abo-Elyousr, 2017; Pimenta et al., 2009), or *Wickerhamomyces* (Fernandez-San Millan et al., 2021), or filamentous endophytic fungi such as *Epicoecum nigrum* (Larena, De Cal, & Melgarejo, 2004; Mari et al., 2007), with great capacity to control pathogens such as *B. cinerea*, *M. fructicola*, *A. alternata*, *P. expansum*, *M. laxa* or *Colletotrichum musae*.

The different studies carried out in this sense have also tried to develop effective forms of application of fungi as BCAs in postharvest and to know the duration and effect on the quality of fresh products of their use. The endophytic yeast of olives *Wickerhamomyces anomalus* has been applied to “Valencia” oranges through the use of biofilms obtained from sodium alginate and locust bean gum, increasing the survival of the yeast by 85%, reducing the affectation by *P. digitatum* in 73% and improving the quality of fresh produce (reducing weight loss and maintaining firmness) (Aloui Licciardello, Khwaldia, Hamdi, & Restuccia, 2015). In the case of the filamentous fungus *Fusarium chlamydosporum*, isolated from stems and leaves of *Calotropis procera*, its application through biosynthesized silver nanoparticles has been reported to increase the ability to control *P. digitatum* in oranges (El, 2020). Other studies have determined the effect of the simultaneous application of

TABLE 4.1 Yeasts and endophytic fungi used in the control of postharvest pathogens in fresh produce, indicating the mechanisms of action involved.

Group	Species	Isolation plant-organ	Use in fresh produce	Pathogen	Effect	Mechanism of action	Reference
Yeasts	<i>Aureobasidium pullulans</i>	Sweet cherries	Sweet cherries Table grapes	<i>Botrytis cinerea</i> , <i>Monilinia laxa</i>	Disease reduction	Not identified	Schena et al. (2003)
		Apples	Apples	<i>Penicillium expansum</i>	Disease reduction	Competition for nutrients	Bencheqroun et al. (2006)
		Apples	Apples	<i>B. cinerea</i>	Disease reduction	Competition for nutrients	Vero et al. (2009)
		Peaches	Peaches	<i>M. laxa</i>	Disease reduction	Not identified	Zhang et al. (2010b)
		Plums	Peaches Apples Plums	<i>M. laxa</i> , <i>B. cinerea</i> , <i>P. expansum</i>	Disease reduction	Lytic enzyme production	Zhang et al. (2010a)
		Grapes	Grapes	<i>Aspergillus carbonarius</i>	Disease reduction	Competition for nutrients and space	De Curtis et al. (2012)
		Peaches	Peaches Nectarines	<i>M. laxa</i> , <i>M. fructicola</i> , <i>M. fructigena</i>	Disease reduction	Competition for nutrients and space	Mari, Martini, Spadoni, Rouissi, and Bertolini (2012)
		Peaches	Apples	<i>B. cinerea</i> , <i>Colletotrichum acutatum</i> , <i>P. expansum</i>	Disease reduction	Production of antifungal volatiles	Mari, Martini, Guidarelli, and Neri et al. (2012)
		Plums	(<i>in vitro</i>)	<i>B. cinerea</i> , <i>M. laxa</i> , <i>P. expansum</i>	Inhibition of pathogen growth	Lytic enzyme production	Zhang et al. (2012)
		Plums	Apples	<i>P. expansum</i> , <i>B. cinerea</i> , <i>M. fructicola</i> , <i>Alternaria alternata</i>	Inhibition of pathogen growth	Lytic enzyme production	Banani et al. (2014)
		Peaches	Apples Oranges	<i>B. cinerea</i> , <i>C. acutatum</i> <i>P. expansum</i> , <i>P. digitatum</i> <i>P. italicum</i>	Disease reduction	Production of antifungal volatiles	Di Francesco et al. (2015)

(Continued)

TABLE 4.1 (Continued)

Group	Species	Isolation plant-organ	Use in fresh produce	Pathogen	Effect	Mechanism of action	Reference
		Pomegranates	Strawberries Tangerines	<i>Penicillium digitatum</i> , <i>P. italicum</i>	Disease reduction	Production of antifungal volatiles	Parafati, Vitale, Restuccia, and Cirvilleri (2017)
		Apples	Apples	<i>B. cinerea</i>	Disease reduction	Not identified	Kheireddine et al. (2018)
		Vineyard tissues	Grapes	<i>Greeneria uvicola</i>	Disease reduction	Not identified	Rathnayake et al. (2018)
		Apples	(<i>in vitro</i>)	<i>P. expansum</i> , <i>P. digitatum</i>	Inhibition of pathogen growth	Competition for nutrients and space Production of antifungal volatiles Lytic enzyme production	Agirman and Erten (2020)
		Peaches	Cherries Peaches Apricots	<i>M. laxa</i> , <i>M. polystroma</i> , <i>M. fructigena</i>	Inhibition of pathogen growth	Production of antifungal volatiles Activation of plant defenses	Di Francesco et al. (2020)
		<i>Baccharis dracunculifolia</i> tissues	<i>In vitro</i>	<i>B. cinerea</i>	Inhibition of pathogen growth	Production of antifungal nonvolatile compounds	Oki et al. (2021)
	<i>Candida guilliermondii</i>	Tomato tissues	Tomatoes	<i>Rhizopus stolonifer</i>	Disease reduction	Production of antifungal nonvolatile compounds	Celis-Zambrano et al. (2014)
	<i>C. inconspicua</i>	Pineapples	Yellow pitahayas Bananas	<i>A. alternata</i> , <i>Colletotrichum musae</i>	Disease reduction	Not identified	Vilaplana et al. (2020)
	<i>C. lusitaniae</i>	Grapes	Tomatoes Grapes Apples	<i>P. expansum</i>	Disease reduction	Not identified	Fernandez-San Millan et al. (2021)
	<i>C. maltosa</i>	Peaches	Peaches	<i>Mucor circinelloides</i>	Disease reduction	Competition for nutrients and space	Restuccia et al. (2006)
	<i>C. oleophila</i>	Tomatoes	<i>In silico</i>	–	–	Competition for nutrients and space Lytic enzyme production Activation of plant defenses	Sui et al. (2020)

	Grapes	Tomatoes Grapes Apples	<i>P. expansum</i>	Disease reduction	Not identified	Fernandez-San Millan et al. (2021)
<i>C. stellimalicola</i>	Citrus leaves	Oranges	<i>P. italicum</i>	Disease reduction	Lytic enzyme production	da Cunha, Ferraz, Wehr, and Kupper (2018)
<i>C. tropicalis</i>	Olive leaves	Olive fruits	<i>Colletotrichum gloeosporioides</i>	Disease reduction	Competition for nutrients and space Lytic enzyme production	Pesce et al. (2018)
<i>Citeromycesmatritensis</i>	Apples	Apples	<i>B. cinerea</i>	Disease reduction	Not identified	Kheireddine et al. (2018)
<i>Clavispora lusitaniae</i>	Citrus fruits	Lemons	<i>P. digitatum</i>	Disease reduction	Not identified	Perez et al. (2017)
	Citrus fruits	Lemons	<i>P. digitatum</i>	Disease reduction	Not identified	Pereyra et al. (2020)
<i>Cryptococcus albidus</i>	Olive fruits	Olive fruits	<i>Colletotrichum gloeosporioides</i>	Disease reduction	Competition for nutrients and space Lytic enzyme production	Pesce et al. (2018)
<i>C. flavescens</i>	Apples	Apples	<i>B. cinerea</i>	Disease reduction	Not identified	Kheireddine et al. (2018)
<i>C. laurentii</i>	Apples	Sweet cherries	<i>M. fructicola</i>	Disease reduction	Not identified	Qin et al. (2006)
<i>Debaryomyces hansenii</i>	Lemons	Grapes	<i>P. digitatum</i>	Disease reduction	Competition for nutrients	Droby, Chalutz, Wilson, and Wisniewski (1989)
	Apples	Apples	<i>M. fructigena</i>	Disease reduction	Lytic enzyme production	Madbouly et al. (2020)
	Grapes	Tomatoes Grapes Apples	<i>P. expansum</i>	Disease reduction	Not identified	Fernandez-San Millan et al. (2021)
<i>Galactomyces candidum</i>	Tomato leaves	Cherry tomatoes	<i>Athelia rolfsii</i>	Disease reduction	Production of antifungal volatiles	Cai, Chiu, and Chou (2021)
<i>G. geotrichum</i>	Apples	Apples	<i>M. fructigena</i>	Disease reduction	Lytic enzyme production	Madbouly et al. (2020)
<i>Hanseniaspora uvarum</i>	Strawberry fruits	Strawberries	<i>B. cinerea</i> , <i>R. stolonifer</i>	Disease reduction	Activation of plant defenses	Cai et al. (2015)

(Continued)

TABLE 4.1 (Continued)

Group	Species	Isolation plant-organ	Use in fresh produce	Pathogen	Effect	Mechanism of action	Reference
		Loquat fruits	Kiwifruits	<i>B. cinerea</i> , <i>A. alternata</i>	Disease reduction	Activation of plant defenses	Cheng et al. (2019)
	<i>Hypopichia pseudoburtonii</i>	Grapes	Tomatoes Grapes Apples	<i>P. expansum</i>	Disease reduction	Not identified	Fernandez-San Millan et al. (2021)
	<i>Metschnikowia fructicola</i>	Grapes	Grapes	<i>B. cinerea</i>	Disease reduction	Not identified	Kurtzman and Droby (2001)
		Grapes	Apples	<i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Comoclathris</i> sp., <i>Stemphylium</i> sp., <i>Nigrospora</i> sp., <i>Penicillium</i> sp., <i>Podosphaera</i> sp.	Disease reduction	Microbiota modification	Biasi et al. (2021)
		Grapes	Strawberries	<i>M. fructicola</i>	Disease reduction	Microbiota modification	Zhimo et al. (2021)
	<i>M. pulcherrima</i>	Apples	Apples	<i>B. cinerea</i> , <i>P. expansum</i>	Disease reduction	Not identified	Spadaro et al. (2010)
		Grapes	Grapes	<i>A. carbonarius</i>	Disease reduction	Competition for nutrients and space	De Curtis et al. (2012)
		Grapes	Tomatoes Grapes Apples	<i>B. cinerea</i>	Disease reduction	Not identified	Fernandez-San Millan et al. (2021)
		Loquat leaves	Loquat fruits	<i>Pestalotiopsis vismiae</i>	Disease reduction	Biofilm formation Competition for nutrients and space	Yang et al. (2021)
	<i>Metschnikowia</i> sp.	Peaches	Peaches	<i>M. laxa</i>	Disease reduction	Not identified	Zhang et al. (2010b)
	<i>Papiliotrema aspenensis</i>	Rice, corn and sugarcane leaves	Mango fruits	<i>C. gloeosporioides</i>	Disease reduction	Production of antifungal volátiles Biofilm formation Competition for nutrients	Konsue et al. (2020)

<i>Pichia fermentans</i>	Peaches	Peaches	<i>Mucor circinelloides</i>	Disease reduction	Competition for nutrients and space	Restuccia et al. (2006)
	Citrus fruits	Lemons	<i>P. digitatum</i>	Disease reduction	Not identified	Perez et al. (2017)
<i>P. galeiformis</i>	Citrus tissues	Oranges	<i>P. digitatum</i>	Disease reduction	Competition for nutrients and space Production of antifungal volatiles	Chen et al. (2020)
<i>P. guilliermondii</i>	Lemon tissues	Oranges	<i>P. italicum</i>	Disease reduction	Competition for nutrients and space	Arras, De Cicco, and Arru (1998)
<i>P. kluyveri</i>	Blackberries	Yellow pitahayas Bananas	<i>A. alternata</i> , <i>Colletotrichum musae</i>	Disease reduction	Not identified	Vilaplana et al. (2020)
<i>P. kudriavzevii</i>	Olive fruits	Olive fruits	<i>Colletotrichum gloeosporioides</i>	Disease reduction	Competition for nutrients and space Lytic enzyme production	Pesce et al. (2018)
	Apples	Apples	<i>M. fructigena</i>	Disease reduction	Lytic enzyme production	Madbouly et al. (2020)
<i>P. membranefaciens</i>	Apples	Sweet cherries	<i>M. fructicola</i>	Disease reduction	Not identified	Qin et al. (2006)
	Peaches	Peaches	<i>R. stolonifer</i>	Disease reduction	Activation of plant defenses	Zhang et al. (2020)
<i>Pseudozyma fusiformata</i>	Peaches	Peaches	<i>M. laxa</i>	Disease reduction	Not identified	Zhang et al. (2010b)
<i>P. hubeiensis</i>	Rice, corn and sugarcane leaves	Mango fruits	<i>Lasiodiplodia theobromae</i>	Disease reduction	Production of antifungal volatiles Biofilm formation Competition for nutrients	Konsue et al. (2020)
<i>Rhodotorula glutinis</i>	Apples	Apples	<i>M. fructigena</i>	Disease reduction	Lytic enzyme production	Madbouly et al. (2020)
<i>Saccharomyces cerevisiae</i>	Olives	Oranges	<i>P. digitatum</i>	Disease reduction	Lytic enzyme production	Platania et al. (2012)
<i>Saccharomycopsis fibuligera</i>	Guava fruits	Guava fruits	<i>B. cinerea</i>	Disease reduction	Not identified	Abdel-Rahim and Abo-Elyousr (2017)

(Continued)

TABLE 4.1 (Continued)

Group	Species	Isolation plant-organ	Use in fresh produce	Pathogen	Effect	Mechanism of action	Reference
	<i>S. crataegensis</i>	<i>Acrocomia aculeata</i> fruits	Oranges	<i>P. digitatum</i>	Disease reduction	Not identified	Pimenta et al. (2009)
	<i>Saccharomyces</i> sp.	Different fruits and vegetables	Kinnow fruits	<i>P. digitatum</i>	Disease reduction	Not identified	Habiba et al. (2019)
	<i>Schwanniomycetes vanrijijae</i>	Apples	Apples	<i>M. fructigena</i>	Disease reduction	Lytic enzyme production	Madbouly et al. (2020)
		Lemons	Lemons	<i>P. digitatum</i>	Disease reduction	Activation of plant defenses	Abo-Elyousr Al-Qurashi, and Almasoudi (2021)
	<i>Trichosporon asahii</i>	Leaves, petioles and fruit of papaya	Papayas	<i>C. gloeosporioides</i>	Disease reduction	Competition for space	Hassan, Mohamed, Yusoff, Hata, and Tajidin (2021)
	<i>Torulaspota indica</i>	Rice, corn and sugarcane leaves	Mango fruits	<i>Lasiodiplodia theobromae</i>	Disease reduction	Production of antifungal volatiles Biofilm formation Competition for nutrients	Konsue et al. (2020)
	<i>Wickerhamomyces anomalus</i>	Olives	Oranges	<i>P. digitatum</i>	Disease reduction	Lytic enzyme production	Platania et al. (2012)
		Olives	Oranges	<i>P. digitatum</i>	Disease reduction	Not identified	Aloui et al. (2015)
		Pomegranates	Strawberries Tangerines	<i>B. cinerea</i> , <i>P. digitatum</i> , <i>P. italicum</i>	Disease reduction	Production of antifungal volatiles	Parafati et al. (2017)
		Olive stems	Olive fruits	<i>Colletotrichum gloeosporioides</i>	Disease reduction	Competition for nutrients and space Lytic enzyme production	Pesce et al. (2018)
		Grapes	Tomatoes Grapes Apples	<i>B. cinerea</i>	Disease reduction	Not identified	Fernandez-San Millan et al. (2021)
		Not indicated	Apples	<i>P. expansum</i>	Disease reduction	Competition for nutrients and space Activation of plant defenses	Zhao et al. (2021)

	<i>Yarrowia lipolytica</i>	Grapes	Table grapes	<i>Talaromyces rugulosus</i>	Disease reduction	Competition for nutrients and space	Yang et al. (2017)
	Not identified	Leaves and fruits of chili	Chili fruits	<i>Colletotrichum capsici</i>	Disease reduction	Not identified	Chaisensaeng, Mongkolthanaruk, and Bunyatratcata (2013)
Filamentous fungi	<i>Albifimbria verrucaria</i>	Grape leaves	Grapes	<i>B. cinerea</i>	Disease reduction	Production of antifungal nonvolatile compounds	Li et al. (2020)
	<i>Aspergillus fumigatus</i>	<i>Melia azedarach</i> steam	<i>In vitro</i>	<i>B. cinerea</i> <i>A. alternata</i> <i>A. solani</i> <i>C. gloeosporioides</i>	Inhibition of pathogen growth	Lytic enzyme production Production of antifungal nonvolatile compounds	Li et al. (2012)
	<i>Ceratocystis fimbriata</i>	Pomegranate tree tissues	<i>Peaches</i> <i>Oranges</i>	<i>M. fruticola</i> <i>P. digitatum</i>	Disease reduction	Production of antifungal volatiles	Li et al. (2015)
	<i>Daldinia eschscholtzii</i>	<i>Barleria prionitis</i> leaves	Strawberries	<i>C. acutatum</i>	Disease reduction	Production of antifungal volatiles	Khruengsai, Pripdeevech, Tanapichatsakul et al. (2021)
	<i>Epicoccum dendrobii</i>	<i>Cunninghamia lanceolata</i> leaves	Apples	<i>C. gloeosporioides</i>	Disease reduction	Production of antifungal nonvolatile compounds	Bian et al. (2021)
	<i>E. nigrum</i>	Peach twigs	<i>In vitro</i>	<i>M. laxa</i>	Inhibition of pathogen growth	Production of antifungal nonvolatile compounds	Larena, Liñán, and Melgarejo (2003)
		Peach twigs	<i>Peaches</i>	<i>M. laxa</i>	Disease reduction	Not identified	Larena et al. (2004)
		Peach twigs	<i>Nectarines</i>	<i>M. laxa</i>	Disease reduction	Not identified	Mari et al. (2007)
	<i>Fusarium chlamydosporum</i>	Stems and leaves of <i>Calotropis procera</i>	<i>Oranges</i>	<i>P. digitatum</i>	Disease reduction	Not identified	El (2020)
	<i>Fusarium</i> sp.	<i>Taxus baccata</i> bark	<i>In vitro</i>	<i>Fusarium oxysporum</i> <i>Aspergillus niger</i> <i>R. stolonifer</i> <i>F. oxysporum</i>	Inhibition of pathogen growth	Production of antifungal nonvolatile compounds	Tayung, Barik, and Jha (2010)
	<i>Hypoxylon anthochroum</i>	Leaves of <i>Bursera lancifolia</i> and <i>Gliricidia sepium</i>	Cherry tomatoes		Inhibition of pathogen growth	Production of antifungal volatiles	Medina-Romero et al. (2017)

(Continued)

TABLE 4.1 (Continued)

Group	Species	Isolation plant-organ	Use in fresh produce	Pathogen	Effect	Mechanism of action	Reference
		Leaves of <i>B. lancifolia</i> , <i>G. sepium</i> , <i>Hippocratea acapulcensis</i> and <i>Sapium macrocarpum</i>	Cherry tomatoes	<i>F. oxysporum</i>	Inhibition of pathogen growth	Production of antifungal volatiles	Macías-Rubalcava et al. (2018)
	<i>Muscodor albus</i>	Limbs of <i>Cinnamomum zeylanicum</i>	Apples	<i>B. cinerea</i> <i>P. expansum</i>	Disease reduction	Production of antifungal volatiles	Mercier and Jiménez (2004)
		Limbs of <i>C. zeylanicum</i>	Lemons	<i>P. digitatum</i> <i>Geotrichum citri-aurantii</i>	Disease reduction	Production of antifungal volatiles	Mercier and Smilanick (2005)
		Rye seeds	(<i>in vitro</i>)	<i>B. cinerea</i> <i>P. expansum</i> <i>Sclerotinia sclerotiorum</i> <i>Erwinia carotovora</i> pv. <i>carotovora</i> <i>Pseudomonas fluorescens</i> <i>Escherichia coli</i>	Inhibition of pathogen growth	Production of antimicrobial volatiles	Ramin et al. (2005)
		Limbs of <i>C. zeylanicum</i>	Grapes	<i>B. cinerea</i>	Disease reduction	Production of antifungal volatiles	Gabler et al. (2006)
		Limbs of <i>C. zeylanicum</i>	Peaches	<i>M. fructicola</i>	Disease reduction	Production of antifungal volatiles	Schnabel and Mercier (2006)
		Limbs of <i>C. zeylanicum</i>	Apples	<i>B. cinerea</i> , <i>P. expansum</i> <i>S. sclerotiorum</i>	Disease reduction	Production of antifungal volatiles	Ramin et al. (2007)
		Limbs of <i>C. zeylanicum</i>	Table grapes	<i>B. cinerea</i>	Disease reduction	Production of antifungal volatiles	Gabler et al. (2010)
	<i>Muscodor suthepensis</i>	Leaves and stems of <i>Cinnamomum bejolghota</i>	Tangerines	<i>P. digitatum</i>	Disease reduction	Production of antifungal volatiles	Suwannarach et al. (2016)

<i>Nodulisporium</i> sp.	<i>Cinnamomum loureirii</i>	Apples	<i>B. cinerea</i> <i>P. expansum</i>	Disease reduction	Production of antifungal volatiles	Park et al. (2010)
	Leaves and stems of <i>Lagerstroemia loudoni</i>	Tangor Tangerines	<i>P. expansum</i> <i>P. digitatum</i>	Inhibition of pathogen growth	Production of antifungal volatiles	Suwannarach et al. (2013)
	Leaves of <i>Peperomia dindygulensis</i>	Oranges	<i>P. digitatum</i>	Disease reduction	Production of antifungal volatiles	Yeh et al. (2021)
<i>Oxyporus latemarginatus</i>	Pepper tissues	Apples	<i>B. cinerea</i>	Disease reduction	Production of antifungal volatiles	Lee et al. (2009)
<i>Penicillium rolfsii</i>	Papaya leaves	Papayas	<i>Neoscytalidium dimidiatum</i>	Disease reduction	Activation of plant defenses	Wang et al. (2021)
<i>Phaeosphaeria nodorum</i>	Plums	<i>In vitro</i>	<i>M. fructicola</i>	Inhibition of pathogen growth	Production of antifungal volatiles	Pimenta et al. (2012)
<i>Phomopsis</i> sp.	<i>Gossypium hirsutum</i> roots	<i>In vitro</i>	<i>B. cinerea</i> <i>S. sclerotiorum</i>	Inhibition of pathogen growth	Production of antifungal nonvolatile compounds	Jing, Yang, Hai Feng, Yong Hao, and Jian Hua (2011)
<i>Preussia africana</i>	<i>B. dracunculifolia</i> tissues	<i>In vitro</i>	<i>B. cinerea</i> <i>C. acutatum</i> <i>P. digitatum</i> <i>Pestalotiopsis longisetula</i>	Inhibition of pathogen growth	Production of antifungal nonvolatile compounds	Oki et al. (2021)
<i>Trichoderma afroharzianum</i>	<i>Schefflera leucantha</i> leaves	Chilies	<i>F. oxysporum</i> <i>F. proliferatum</i>	Inhibition of pathogen growth	Production of antifungal nonvolatile compounds	Khruengsai, Pripdeevech, D'Souza et al. (2021)
<i>T. asperellum</i>	Muskmelons tissues	Muskmelons	<i>Fusarium incarnatum</i>	Inhibition of pathogen growth	Production of antifungal nonvolatile compounds	Intana et al. (2021)
<i>Xylaria arbuscula</i>	<i>B. dracunculifolia</i> tissues	<i>In vitro</i>	<i>B. cinerea</i>	Inhibition of pathogen growth	Production of antifungal nonvolatile compounds	Oki et al. (2021)

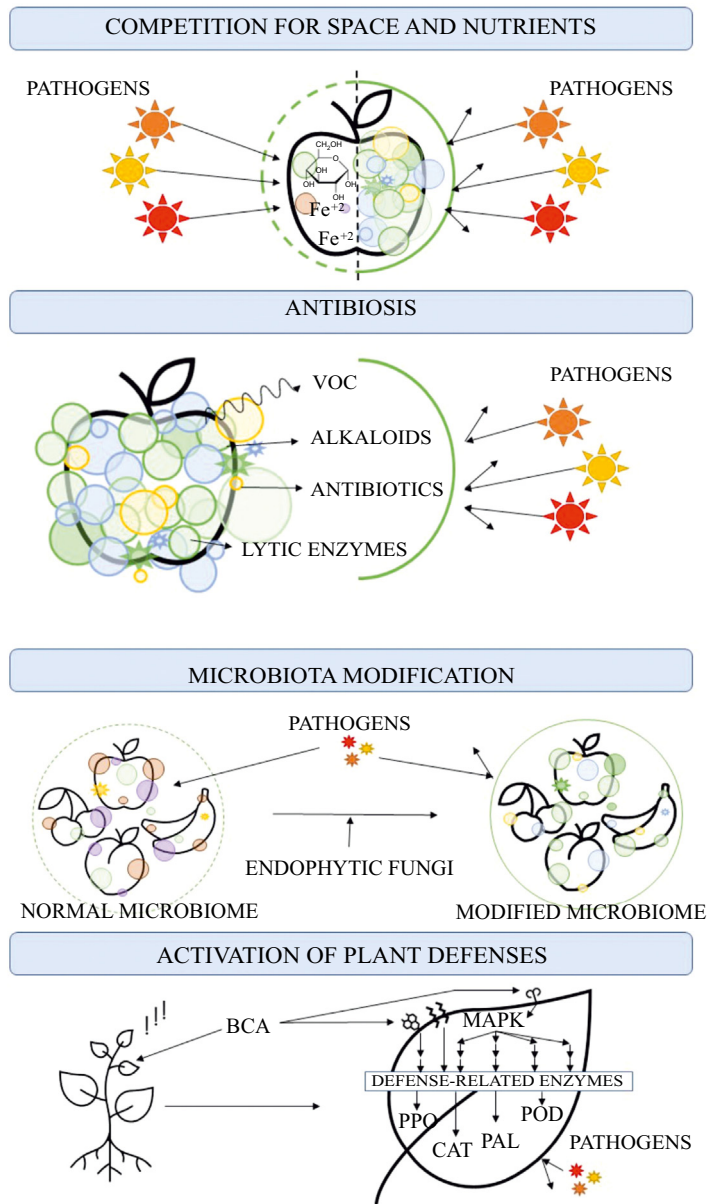


FIGURE 4.1 Summary infographic of different mechanisms of action described for endophytic fungi against postharvest diseases in fresh produce.

chemical fungicides or additives with endophytic fungi in postharvest. In lemons it was found as *Clavispora lusitaniae* and *Pichia fermentans* yeasts were able to tolerate different commonly used postharvest fungicides (thiabendazole and imazalil), allowing the simultaneous application of chemical and biological control strategies against *P. digitatum* (Perez et al., 2017). Similarly, the application of food additives, such as ammonium molybdate

and sodium bicarbonate, in peaches maintained the ability of the yeasts *Clavispora laurentii* and *Pichia membranifaciens* to control *M. fructicola* (Qin, Tian, Xu, Chan, & Li, 2006). Regarding the durability of the treatment, a study carried out over 2 years with *A. pullulans*, isolated from sweet cherries, reported how the preharvest application could be a fundamental factor to increase its population throughout the storage and to penetrate in the fruit, improving it significantly if the treatment is carried out during flowering (Schena, Nigro, Pentimone, Ligorio, & Ippolito, 2003). Furthermore, it has been possible to determine in treatments with *A. pullulans* or *Pseudozyma fusiformata* in peaches, how the use of these BCAs in postharvest does not modify the quality of the fresh produce (soluble solids, firmness, ascorbic acid content, and acidity) (Zhang, Spadaro, Garibaldi, & Gullino, 2010b).

4.5.1 Competition for space and nutrients

Endophytic fungi are very efficient at exploiting certain niches and nutrients such as minerals (Fe, N...), glucose or oxygen sources. This gives them an advantage over pathogens, which can be displaced. For example, in fruit and vegetable wounds, endophytes can establish themselves preferentially, before pathogens, preventing the establishment of pathogens that can control postharvest diseases (Huang et al., 2021).

It is important to highlight that competition for space and nutrients is a strategy currently only reported for endophytic yeasts, without having been described for filamentous fungi. Through competition for space and nutrients, different yeast species are able to control postharvest diseases implicated in direct damage to health. For example, *A. pullulans* and *Metschnikowia pulcherrima* reduce the incidence of *Aspergillus carbonarius* in grapes, preventing the accumulation of ochratoxin A in wines, one of the most toxic and widespread mycotoxins (De Curtis, de Felice, Ianiri, De Cicco, & Castoria, 2012). Furthermore, yeasts with this mechanism of action can be used in integrated control strategies, as they tolerate the fungicides most commonly used in postharvest. In this sense, *A. pullulans* effectively competes for iron against *B. cinerea* in apples, reducing the disease, being resistant to the fungicides thiabendazole, iprodione, and imazalil (Vero, Garmendia, González, Garat, & Wisniewski, 2009).

Determining the competition for space and nutrients in endophytic yeasts is done by direct observation under the microscope of the growth and/or biofilm formation, or by providing nutrients in a targeted manner. By scanning electron microscopy, it has been described how *M. pulcherrima*, isolated from loquat leaves, rapidly colonizes the wounds of loquat fruits forming biofilms, competing for space and iron with the pathogen *Pestalotiopsis vismiae* (causing gray spot rot) and reducing the incidence of disease (Yang et al., 2021). Similarly, the action of *Pichia galeiformis* against *P. digitatum* in oranges (Chen, Yi, Deng, Ruan, & Zeng, 2020), *W. anomalus* against *P. expansum* in apples (Zhao et al., 2021), or *Yarrowia lipolytica* against *Talaromyces rugulosus* on table grapes has been described (Yang et al., 2017).

The production of siderophores is a mechanism used by endophytic yeasts to chelate iron and prevent its use by pathogens. The ability to produce siderophores and compete for iron has been described in the yeasts *Papiliotrema aspenensis*, *P. hubeiensis*, and

Torulasporea indica, isolated from rice, corn, and sugarcane leaves, and used effectively as BCAs in mango fruits against the pathogen *Lasioidiplodia theobromae*, reducing the incidence of disease by 90% (Konsue, Dethoup, & Limtong, 2020). The nutrients involved in competition can be very varied. For example, in apples infected with *P. expansum*, it was reported that *A. pullulans* yeast competed for nutrients by adding apple juice and verifying how the yeast-BCA capacity disappeared (Bencheqroun et al., 2006).

4.5.2 Antibiosis

Endophytic fungi synthesize a wide range of compounds derived from their secondary metabolism that have different biological activities (Rustamova, Bozorov, Efferth, & Abulimti, 2020). Among these metabolites, VOCs stand out for their antimicrobial capacity (Poveda et al., 2021; Rustamova et al., 2020).

With regard to diffusible nonvolatile secondary metabolites, their potential use against postharvest pathogens has been described through the application of extracts generated in liquid culture media. The filamentous endophytic fungi *Albifimbria verrucaria* generate extracts capable of protecting grapes against *B. cinerea* (Li, Chang, Gao, & Wang, 2020).

The organic phase of filtrates from cultures of the yeast *Candida guilliermondii* was able to reduce the disease caused by *Rhizopus stolonifer* in tomatoes by 80% (Celis-Zambrano et al., 2014). Similarly, using the organic solvent ethyl acetate, different antifungal secondary metabolites were obtained from an *Epicoccum dendrobii* culture, effective against *Colletotrichum gloeosporioides* in apples (Bian et al., 2021). In the case of some endophytic fungi, the antifungal effect is associated with the production of an isolated metabolite, as in the protection of chilies and muskmelons against Fusarium rot by phenylethyl alcohol released by *Trichoderma afroharzianum* and *T. asperellum*, respectively (Intana, Kheawleng, & Sunpapao, 2021; Khruengsai, Pripdeevech, D'Souza, & Panuwet, 2021). However, the antifungal capacity may be due to different compounds, such as 12 β -hydroxy-13 α -methoxyverruculogen TR-2, verruculogen, fumitremorgin B or helvolic acid release by *Aspergillus fumigatus* to suppress the growth of *B. cinerea*, *A. alternata*, *A. solani* and *C. gloeosporioides* (Li, Zhang, Zhang, & Gao, 2012).

The use of endophytic fungi in the management of postharvest diseases through the production of VOCs is gaining great prominence in recent years, a process known as myofumigation (Kaddes, Fauconnier, Sassi, Nasraoui, & Jijakli, 2019). As far as yeasts are concerned, the ability of *A. pullulans*, isolated from peaches, to produce the antifungal VOC 2-phenethyl alcohol has been described. This metabolite is involved in the control of a wide variety of different postharvest pathogens (*B. cinerea*, *C. acutatum*, *P. expansum*, *P. digitatum*, *P. italicum*, *M. laxa*, *M. fructicola*, *M. polystroma*, or *M. fructigena*) (Di Francesco, Ugolini, Lazzeri, & Mari, 2015; Di Francesco, Di Foggia, & Baraldi, 2020).

In the case of endophytic filamentous fungi, numerous antimicrobial VOCs have been identified against the main postharvest diseases. For example, the endophyte of *Barleria prionitis* leaves, *Daldinia eschscholtzii*, reduces the symptoms generated by *C. acutatum* in strawberries by producing the VOCs elemicin, benzaldehyde dimethyl acetal, ethyl sorbate, methyl geranate, trans-sabinene hydrate, and 3,5-dimethyl-4-heptanone (Khruengsai, Pripdeevech, Tanapichatsakul, et al., 2021). *Phaeosphaeria nodorum* is an endophyte isolated from plums whose VOCs (ethyl acetate, acetic acid, 3-methyl-1-butanol, 2-propyn-1-ol and

2-propenenitrile) inhibit the development of the pathogen *M. fructicola*, producing a reduction in hyphal amplitude and a collapse of its internal content (Pimenta, Moreira da Silva, Buyer, & Janisiewicz, 2012). The main endophytic fungi used in postharvest mycofumigation are *Muscodor albus* and *Nodulisporium* sp. (anamorph of *Hypoxylon anthochroum*). In the case of *M. albus*, isolated from limbs of *Cinnamomum zeylanicum*, its antifungal capacity against fungi and postharvest pathogenic bacteria (*B. cinerea*, *P. expansum*, *Sclerotinia sclerotiorum*, *Erwinia carotovora* pv. *carotovora*, *Pseudomonas fluorescens*, and *Escherichia coli*) is due mainly to 2-methyl-1-butanol and isobutyric acid VOCs (Mercier & Jiménez, 2004; Ramin, Braun, Prange, & DeLong, 2005). The antifungal capacity of *Nodulisporium* sp. is related to different VOCs, depending on the isolate used, including, elemene, 1-methyl-1,4-cyclohexadiene, β -selinene, α -selinene or eucalyptol, among other VOCs (Park et al., 2010; Suwannarach et al., 2013). The antifungal effect of these VOCs has been described with foliar endophytic isolates of *H. anthochroum*, when used against *F. oxysporum* in cherry tomatoes. The different VOCs identified, mainly sesquiterpenes and monoterpenes, cause the inhibition of the pathogen's growth by blocking its respiration and altering the cell membrane permeability, which causes damage to the hyphal morphology (Macías-Rubalcava, Sánchez-Fernández, Roque-Flores, Lappe-Oliveras, & Medina-Romero, 2018; Medina-Romero, Roque-Flores, & Macías-Rubalcava, 2017).

The way in which these endophytic fungi are applied as postharvest mycofumigants involves the use of plant material where they can grow and develop. For *M. albus*, rye grains colonized by mycelium and applied in commercial fruit packaging are usually used, a strategy capable of completely reducing the disease caused by *B. cinerea*, *P. expansum* or *S. sclerotiorum* in grapes and apples (Gabler, Fassel, Mercier, & Smilanick, 2006; Ramin, Prange, Braun, & DeLong, 2007). Other culture substrates can also be used, such as bagasse for the fungus *Nodulisporium* sp (Yeh, Wang, Chen, Tsai, & Chung, 2021), or wheat bran–rice hull for *Oxyporus latemarginatus* (Lee et al., 2009). Furthermore, endophytic fungi as fumigants can be used in combination with other postharvest disease management strategies. In peaches stored at cold (1–2°C), the use of *M. albus* as a mycofumigant in closed cardboard boxes significantly reduces the decay caused by *M. fructicola* (Schnabel & Mercier, 2006). In table grapes, the simultaneous application of *M. albus* and ozone has been shown to reduce *B. cinerea* damage by up to 3% (Gabler, Mercier, Jiménez, & Smilanick, 2010).

Within the mechanism of action of antibiosis, endophytic fungi can synthesize several enzymes with hydrolase activity. These cell wall lytic enzymes, such as glucanases and chitinases, enable the fungus to degrade the cell wall of postharvest pathogens (Huang et al., 2021). In the case of endophytic filament fungi used as BCAs in postharvest, only the involvement of chitinases in the management of *B. cinerea* in grapes by *A. verrucaria* has been described so far (Li et al., 2020). On the other hand, numerous species of endophytic yeast producing lytic enzymes effective in the control of these pathogens have been described. The production of chitinases, pectinases, β -1,3-glucanases and proteases by *Galactomyces geotrichum*, *Pichia kudriavzevii*, *Rhodotorula glutinis*, *Schwanniomyces vanriijiae* or *Debaryomyces hansenii* stand out (Madbouly, Abo Elyousr, & Ismail, 2020). Other endophytic yeasts produce mainly a type of hydrolytic enzyme, such as β -glucanases by *W. anomalus* and *Saccharomyces cerevisiae* (Platania, Restuccia, Muccilli, & Cirvilleri, 2012), alkaline serine proteases by *A. pullulans* (Banani et al., 2014), or phospholipases by *W. anomalus*, *P. kudriavzevii*, *Candida tropicalis* and *Cryptococcus albidus* (Pesce et al., 2018).

To study the production of cell wall lytic enzymes by endophytic yeasts, they are usually grown in salt-poor medium, where the only available carbon source is the cell wall of pathogenic fungi (Zhang et al., 2010a).

4.5.3 Activation of plant defenses

Endophytic fungi, when colonizing plant tissues or organs, can generate a local or systemic defense state by acting as BCA (Huang et al., 2021). Indirectly, it has been described how the tissues of cherries, peaches, or apricots are able to perceive the VOCs emitted by *A. pullulans* and activate physical defensive responses, such as increasing the fruit waxes complexity (Di Francesco et al., 2020). In peaches treated with *P. membranifaciens*, activation of the mitogen-activated protein kinase pathway and signaling by ethylene, SA and jasmonate (JA) has been documented, due to plant recognition of the pathogen-associated molecular patterns (MAMPs) of the endophyte. Thanks to the activation of these signaling pathways, peaches-tissues increase the activity of defense-related enzymes against the pathogen *R. stolonifer*, including peroxidase (POD), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL) and catalase (CAT) (Zhang et al., 2020). Similarly, *W. anomalus* reduces *P. expansum* disease in apples by increasing the plant content of flavonoids and total phenols, and PPO, POD, CAT, PAL, and ascorbate peroxidase (APX) activity (Zhao et al., 2021). This mechanism of action has been reported in other endophytic yeasts, such as *Hanseniaspora uvarum* (Cai Yang, Xiao, Qin & Si, 2015; Cheng, Nie, Jiang, & Li, 2019), and filamentous fungi, such as *P. rolfsii* (Wang, Zhang, Yuan, & Chen, 2021).

4.5.4 Microbiota modification

As indicated above, the microbiota of fruits and vegetables can greatly contribute to the management of different postharvest diseases. Accordingly, the use of endophytic fungi can actively modify the microbial diversity of plant tissues, therefore, acting indirectly as BCAs. It has been reported that the endophytic yeast of grapes *Metschnikowia fructicola* is capable of increasing the diversity of beneficial bacteria (such as the genera *Methylobacterium*, *Sphingomonas*, *Rhizobium* or *Bacillus*) present in apples and strawberries, reducing fungal diversity, and improving the control of various fungal diseases (Biasi et al., 2021; Zhimo et al., 2021).

Finally, it is important to note that, under certain conditions, some of these endophytic fungi can also behave as postharvest pathogens of fruits and vegetables. For example, *E. nigrum* and *A. pullulans* can be rot producers in grapes that have suffered severe dehydration during storage (Lorenzini & Zapparoli, 2015).

4.6 Future challenges and perspectives

Endophytic fungi are a very promising postharvest tool. In addition, they allow for a wide range of solutions because they are quite versatile and can generate a wide variety of biocontrol products. Microorganisms can be applied, modifying the microbiota, and allowing a sustained response over time. Equally, by-products generated by these fungi in the

form of biopesticides, activators of the plant's defenses, etc. can be added. We must investigate in depth the mechanisms of action to establish protocols and elucidate the application window and the most effective treatment based on the characteristics of the product, other complementary treatments, and the conditions to which the product will be subjected throughout the retail chain. To achieve this, it is essential to know the possible interactions between the environment, the plant's genotype or the microbiota that may be present initially, since it can lead to changes in the effectiveness of the treatment. Therefore we must exhaustively monitor the products that are entering the market and establish the effectiveness and duration of the effect. For now, the information is limited, and it is difficult to predict when the treatment will begin to be effective after inoculation and how long it will be maintained over time. We must take into account that the conditions may change throughout harvest, transportation, or storage and that can certainly affect treatment. In turn, the industry will have to overcome challenges such as scaling the production of these compounds and finding the best format to supply them.

On the other hand, the development of techniques such as metagenomics, metabolomics, and massive sequencing, will allow us to discover new metabolites and endophytes that are difficult to cultivate or obtain in the laboratory. Access to this information can help us discover new compounds or protection tools that can be used through genetic engineering for the improvement of plants.

Finally, we must explore the perspective of how endophytes can contribute, not only to the maintenance of the health of the plant and fresh products but can also have a benefit at other deeper levels. Among them are the improvements to the quality of the postharvest products, enriching them in some way. Or a potential improvement in human health because the microbiota present in the fruits and vegetables we eat could eventually modify the human microbiota.

4.7 Conclusions

It is essential to find solutions to food waste in postharvest. Many of the strategies to combat it are dangerous for human health, the environment, consume a lot of resources, or are expensive. The incorporation of fungal endophytes as postharvest biocontrol tools may represent an improvement, as some of the commercialized products have already shown. However, they must be accompanied by other complementary processes because a single approach is not enough. Postharvest disease management is a complex problem that requires a holistic approach to find an alternative that can truly supersede current methods. Furthermore, more research is needed on their drive mechanisms and how they can affect the environment and humans.

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