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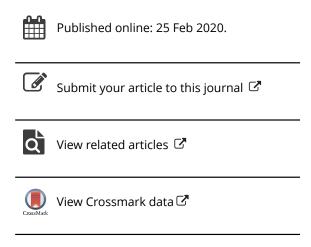
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Non-Fungicides-Based Promising Technologies for Managing Post-Production *Penicillium* Induced Spoilage in Horticultural Commodities: A Comprehensive Review

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ABSTRACT

Post-harvest commodities wastage due to decay caused by the pathogenic fungi generates a huge amount of economic losses worldwide. Different species of Penicillium spoil various foodstuffs and produce mycotoxins, alkaloids and other harmful cellular metabolites in the food. Presently, synthetic fungicides, mainly used for fungal diseases control, are associated with harmful impacts on the environment and consumer health. Hence, non-fungicide based eco-friendly and commercially viable alternative is proposed for ensuring food safety. In recent years, the safer options that have been explored include microbe mediated biological control, botanical pesticides, use of generally regarded as safe (GRAS) compounds, and innovative physical approaches including cold plasma, and pulsed light techniques. These emerging technologies could be utilized in the multiple hurdle concept of disease management for suppressing pathogens growth at different stages of spoilage development. This review, first of its kind, summarizes the exclusive information on Penicillium spp. induced spoilage, associated toxicological concerns and the potential of non-fungicide-based promising approaches for managing fungal wastage in the harvested horticultural commodities.

KEYWORDS

Penicillium decay; mycotoxins; biocontrol; antimicrobial botanicals; GRAS compounds; cold plasma

Introduction

The pathogenic decay of fruits and vegetables during the post-harvest storage and distribution stages causes a significant amount of losses and also limits their shelf-life. According to an estimate of various intergovernmental agencies, more than one-third part of fruit and vegetables produced is wasted globally. Even in developing countries, fungal decay is accountable for about 20–25% wastage of the total produce during post-production handling, storage, and shipment. The huge amount of food wastage is due to fruit rotting, induced by a fungal infection, initiated either in a farm or after harvest that further develops into decay during the food supply chain. Harvested fruits bearing enough moisture and nutrients, acidic pH, and reduced intrinsic resistance become prone to fungal spoilage. Numerous fungal species within the genera of *Penicillium*, *Botrytis*,

Rhizopus, Monilinia, Aspergillus, Alternaria, Geotrichum, Fusarium, and Gloeosporium are responsible for some of the important storage rots of produce.^[5]

Among the many pathogens, different species of *Penicillium* are accountable for some of the economically important storage decays of fruits. Penicillium are ubiquitous fungal genera that effectively colonizes wide natural habitats including soil, vegetation, several foodstuffs, air, and indoor environments. [6] The Penicillium genus includes about more than 150 species of anamorphic fungi in the Ascomycota division; however, only a small number of them are economically significant phytopathogens.^[7] Worldwide, this fungal genus have a great impact in the agriculture and fruit industry due to large amount of qualitative and quantitative losses imposed to fruit growers by them. For example, postharvest green mold (Penicillium digitatum) and blue mold rot (Penicillium italicum) of citrus fruits and blue mold (Penicillium expansum) spoilage of pome fruits are well notorious penicillium driven diseases resulting into huge monetary losses. Green decay of citrus fruits may account for about 90% of overall post-harvest losses. [8,9] Identically, almost 50% losses of total production have been reported in apple fruits due to blue mold spoilage incited by the cold-loving fungi P. expansum^[10] In addition to the economic wastage, they have been recognized as potent producer of many toxic secondary metabolites such as various mycotoxins (including patulin, citrinin, and chaetoglobosins, etc.), antibiotics, alkaloids, and allergens, which are potentially carcinogenic, mutagenic and has a certain other negative impacts on human health.[11]

Traditionally, storage fungal decays are being managed through the pre- and after harvest use of chemical fungicides such as sodium thiabendazole, ortho-phenylphenate, and imazalil. [12] These fungicides effectively curb pre-existing, established or any new pathogen infections taking place in the storehouse. However, in recent years, the exploit of many synthetic chemicals for making food safe from such pathogens has been restricted mainly due to: (i) appearance of pathogen resistance towards many important fungicides, (ii) emergence of new pathogen races, (iii) paucity of an effectual, alternative, and suitable fungicide, (iv) concern over presence of toxic residues on commodities, (v) toxicological concerns of harmful fungicides to human, animal, and ecosystem health. [13] Due to all these concerns, more scientific attention has been given for the development of non-fungicide based safer and eco-friendly alternative strategies for managing Penicillium as well as other fungal decay/rots.

Among the safer options, antagonistic microbes (bacteria, yeast, and yeast-like fungi), obtained from diverse sources of plant surface, rhizosphere, agricultural soil, sea, and extreme niche have been explored for storage disease control in last few decades. The biological control via such microbial antagonists is a promising and ecological sound option for controlling fungal rotting.^[14] The bio-control approach is more advantageous owing to non-residual toxicity, eco-friendly, safe for application, cheaper to produce, and have wider public acceptance. [15] Another biological alternative is use of botanical extracts, essential oils, and antimicrobial compounds having biodegradable and non-toxic nature, as botanical pesticides for managing fungal decays. [16] Apart from these, the perspectives of novel physical treatments including cold plasma and pulse light processing technology^[17] and importance of produce sanitation in reducing rot pathogens inocula, [18] as both a separate practice and in combination have been also demonstrated. In recent past, machine vision approaches including hyperspectral imaging have been used in the safety evaluation of horticultural produce bearing nonvisible microbial incited spoilage.[19-21]

The ultimate aim of such practices is to prevent the growth of pathogen so that spoilage induced by them is reduced by a large extent. These several approaches acting together additively or complementary can control the Penicillium infections to a required level (97-99%). Furthermore, multiple point hurdle approach, being used for managing foodborne pathogens in the food industry, can be similarly used for the controlling spoilage and ensuring produce safety during the food supply chain. [22] As a result, such manifold technologies, capable of suppressing pathogen at different stages in the disease development, could be explored in the multiple interventions/hurdle concept of disease management. Here, the present review with latest studies summarizes the exhaustive literature information on Penicillium-induced fungal decays, myco-toxicological concerns and nonchemical based safer and potent emerging approaches especially focused on curbing its infection in the harvested commodities.

Significance of *Penicillium* mold in the post-harvest and storage environment

Penicillium is one of the most frequently occurring fungal genera mainly during postharvest handling, storage, and shipment stages of fruits and vegetables. The genus Penicillium is r-strategic fungi with the ability of rapid multiplication and thriving in sparsely populated and resourceful environments.^[23] Depending on the pathogen-host interaction and specificity, fungal growth may occur as an epiphytic that eventually affect the export perspective and market potential of the fruit. [24] The pathogen produces many hydrolytic enzymes that enable them to pierce into host tissue. The rapidly occurring cross-contamination of healthy fruits from infected and spread of inoculum into the surrounding environment signify the economic importance of Penicillium spoilage during the food supply network. Penicillium is an aggressive pathogen and capable to spread, invade, and colonize the various environments under the right set of growth conditions. The pathogen can directly penetrate fruits through the wound or injuries present on the fruit surface. The colonization of fruit wounds may often keep other parts of fruit devoid of infection even if it is delimited by a lot of contaminated fruits. [25] In humid storage, fruiting bodies of *Penicillium* spp. appears as blue-green coloration on the infected fruits, which subsequently develop into decay. The infected fruits emit earthy and musty odor, mainly due to the compound named to as "geosmin, produced by the blue mold fungus, P. expansum as well as other few species of Penicillium. [26]

The most common encountered *Penicillium* rots in fruits predominantly includes green mold and blue mold spoilage. They are the most ubiquitous and catastrophic of all postharvest fungal spoilage of many fruit and vegetables. Green and blue molds are the principal fungi nearly accounting for up to 90% of fruits spoilage during the phases of storage, transit, and marketing. The decay inflicting fungi are necrotrophic pathogens and produces several hydrolytic enzymes, particularly pectinase, polygalacturonases, and cellulases, all of which macerates fruit tissue during the process of disease expansion. [27] Following the invasion, fungi utilize host nutrients for spore germination, growth, and metabolism. The pathogens extensively produce spore that ensures its all over presence in the field, packing house, equipment, storage room, transit containers, and in the marketplace too. Their spores are airborne, hence, can spread from infected fruit to healthy and surrounding environment in the packing house. The stem end or even sound parts of the rind also mediate the pathogen infection and its further spread. In general, long time coldstored fruits deteriorate and spoil rapidly, as a consequence of loss in intrinsic decay resistance of fruits.

As reported in Table 1, diverse species of Penicillium causes decay in several harvested fruits and vegetables. Among them, green mold rot caused by P. digitatum is most destructive after harvest disease mostly reported in citrus family fruits worldwide. However, other fruits such as papaya, apple, pear, tomato, persimmon, beet, Arabian coffee, melon, abisin, iris, golden berry, and tamarind have also been reported as its hosts. Moreover, the fungus has been occasionally isolated from other foods such as pistachio, hazelnuts, kola nuts, peanuts, soybeans, rice, and sorghum. [53] This fungus can grow at 5° C and as high as at 37°C. Growth of fungus is slow at low temperature while it multiples rapidly at slightly higher temperatures (25-30°C), growth is fast. Therefore, decontamination of orchard and packinghouse is often required to restrict its sporulation and dissemination on adjacent fruits during the phase of storage and shipment. Likewise, P. expansum is a broad spectrum pathogen largely known for inciting blue mold spoilage in several harvested fruits of the deciduous tree including apples and pome.^[54] It is the only Penicillium sp., capable of showing pathogenicity in pome fruits, stone fruits, citrus, and grapes. The fungus may also induce spoilage in avocados, mangoes, strawberries, and tomatoes, nectarines, plums, kiwifruits, and even citrus fruits. Though unusual, it even infects certain vegetables like onions, carrot, and cabbages. [33] The pathogen spores from

Table 1. Different species of Penicillium reported as etiological agents of decay occurring in several fruits and vegetables during post-production handling and storage.

Penicillium species	Post-harvest disease	Host fruit(s)/vegetable(s)	References
Penicillium digitatum	Green mold	Citrus family fruits including citrus,	[28, 29]
Penicillium italicum	Blue mold	lemon, mandarin and orange Citrus family fruits including citrus,	[30 31]
renicinani italicani	blue Illoid	orange, mandarin, and lemon	[30 31]
Penicillium expansum	Blue mold	Apples, pears plums, peaches,	[32–37]
		apricots, cherries, kiwifruits,	
		blackberries, melons, strawberries, citrus fruits, jujube and certain	
		vegetables such as onions, garlic	
		and cabbages	
Penicillium crustosum,	Blue mold	Pears and apples	[38, 39]
Penicillium solitum	Blue mold	Pears and apples	[38, 39]
Penicillium glabrum	Post-harvest decay	Strawberries and pomegranate	[40]
Penicillium chrysogenum	Post-harvest rot	Grapes and tomatoes	[41]
Penicillium claviforme	Post-harvest storage rot	Sugarbeet	[42]
Penicillium herquei, Penjcillium implicatum, Penicillium glabrum,	Post-harvest decay	Pomegranate	[43–46]
Penicillium minioluteum, Penicillium purpurogenum, and			
Penicillium sclerotiorum			
Penicillium adametzioides	Fruit decay	Pomegranate	[47]
Penicillium juntculosum	Fruitlet core rot	Pineapple	[48]
P. olsonii P. solitum and P. polonicum	,	Tomato	[49]
P. bialowiezense, P. citrinum, P. echinulatum, P. expansum,	Blue Mold	Grape	[50]
P. solitum			
Penicillium commune	Fruit decay	Litchi	[51]
Penicillium bialowiezense	Reported as pathogenic	Chestnut	[11]
Penicillium sclerotigenum and P. polonicum	Blue mold	Yam	[52]



the soil, diseased fruits, surrounding air, washing water, and drenching solutions also cause infection in the harvested fruits. The fungus has significant socio-economic impacts and several concerns for international trade. *P. italicum* is another important wound-obligate pathogen responsible for economically important blue bold decay in citrus fruits.^[31] Both green and blue mold pathogens have a comparatively small disease cycle of 3 to 5 days at 25°C and, on a particular fruit, can produce 1 to 2 billion conidial spores. The pathogen occurrence is more common on fruit held at low-temperature storage. Furthermore, it can spread in packed cartons more rapidly than green mold and thus become more harmful to fruits held in the box. On the contrary, green mold pathogen does not spread by nesting; thus, if a single fruit is affected it remains as such without contaminating adjacent fruit.

Penicillium mycotoxins and related issues

Penicillium mycotoxins and factors affecting their biosynthesis in the infected foodstuffs

In addition to commodities spoilage, certain species of *Penicillium* are involved in the production of different mycotoxins, antibiotic compounds, alkaloids, and allergens that are potentially lethal to human and animal health.^[11] Some of the toxic secondary metabolites secreted by them are citrinin, chaetoglobosin, cyclopiazonic acid, penicillic acid, communesin B, expansolides, and roquefortine C. The mycotoxins, being major harmful compounds in foodstuffs, produced by different *Penicillium* species include (1) patulin, penicillic acid, ochratoxin A, cyclopiazonic acid, and roquefortine C produced by *P. chrysogenum*; (2) citrinin, penicillic acid, ochratoxin A, cyclopiazonic acid, viomellein, xanthomegnin, and viridicatin secreted by *P. viridicatum* and; (3) paspalinines, janthitrems, and paxillines mycotoxins of *P. tularense*. ^[55,56]

P. expansum is a major spoilage pathogen accountable for patulin production in stored fruits, principally in pome fruits and their processed products.^[57] Patulin is the most prevalent and dangerous mycotoxin of pathogenic Penicillium. It is a water-soluble, comparatively non-complex and lactone containing toxin. White et al.^[58] demonstrated that the patulin biosynthesis process is facilitated at the gene transcription level. They revealed inclusion of several enzymatic steps in the metabolic pathway of patulin synthesis from the polyketide, and 6-methylsalicylic acid. Further, they observed enhanced expression status of all the five metabolic pathways cloned genes including isoepoxydon dehydrogenase (IDH) gene, and fragments of the 6-methyl salicylic acid synthase gene, putative ATP-binding cassette transporter gene, and two putative cytochrome P450 monooxygenase genes in pathogen under patulin favorable situations, signifying their probable involvement in patulin biosynthesis. Recent advances in genomic studies of P. expansum have aided in the identification of several genes concerned with the patulin biosynthesis. These are patulin cluster genes including, patE, patG, patH, patI, patK, and patL, [54-59-61] the LaeA, gene credited for the global regulator of secondary metabolism, [62] PeSte12, the transcription factor, [63] LysM effectors, [64] and the SdnB, subunit of respiratory complex II. [65] Although P. expansum inflict blue mold decay in numerous fruits, however, the main source of patulin contamination is found in the decayed apples. The quantity of patulin produced and accumulated in fruit varies with the Penicillium strain concerned.

The biological function of fungal secondary metabolites including numerous mycotoxins is still vague. However, the most prevalent notion is that mycotoxin production allows fungi a better protection against other organisms inhabiting the same ecological niche. Certain mycotoxins may have a role fungal aggressiveness and pathogenicity during the process of host exploration. For example, the extracellular patulin production by *P. expansum* aids in the effective host tissue colonization. Many authors have investigated the probable role of secondary fungal metabolites, mainly of patulin, in pathogen virulence. More recently, an investigation by Barad et al. [67] showed the possible cytotoxic effect of patulin accumulation on the host cell, which indicated patulin dependent pathogenicity of *P. expansum*. In another study, patulin production by pathogen and its direct association with blue mold incidence on apples have been reported. [68]

The mycotoxin production in an infected produce is affected by numerous environmental factors that significantly affect the growth rate, metabolism, and development of fungi. [69] The storage temperature, ambient pH, humidity, and water activity are among the main factors influencing pathogen growth and toxin secretion. [70] The production and accumulation of extracellular patulin are also reliant on a range of multifarious interactive factors including the geographical location of fruits growing, the variety and fruit type, harvesting, maturity status, and other physiological attributes of fruits, quantum of pathogen inoculums on fruit, and fungal species concerned. The patulin production in apples, stored under controlled atmosphere conditions of 3% CO₂ and 2% O₂ was reduced consistently with time.^[71] The pH levels modulate the toxin accrual during the process of fruit colonization. Many authors have positively correlated the continuous buildup of patulin concentration with the acidic conditions. [59-72] The pH range and patulin accumulation are conversely linked and patulin is found to be unstable at higher pH level. [73] However, the elevated expression level of pePatN, the gene coding for IDH at neutral pH compared to acidic suggest the alkaline regulated transcription factor, PacC, might have an influence on pePatN. [74] In fact, P. expansum, owing to reduced available carbon sources in media, releases a large amount of ammonia, which may regulate the activation of PacC and thus patulin accretion in apples. The patulin production has been recorded at all temperature range (0-30°C) essential for optimum growth, development, and metabolic activities of P. expansum. [75]

Myco-toxicological concerns and prevailing government's regulations

The patulin accumulation is found in both organic and conventional produced fruit and its derived products. However, a significantly higher level of patulin concentrations was detected in organically produced foodstuff than do conventional produce. More recently, a survey performed by Sarubbi et al. (2016) on baby foods revealed considerably higher amounts of patulin occurrence in organically grown products compared to traditional ones. This has raised the call for stricter pre-processing control of fruits cultivated under organic agriculture. Occasionally, even if apple products are free from patulin contamination, they may contain other toxic secondary metabolites, herein, detection of related toxin such as chaetoglobosin A, rather than patulin could be a better indication for the existence of *P. expansum*. The patulin incidence in fruit products, particularly in apple products is being recorded globally. Apple juice and cider

continue to be the main source of human patulin consumption. [78] The frequency of patulin and related mycotoxins has been compared vis a vis in organic and conventional grown fruits, homemade and industrial prepared fruit products, and in a hazy and in clear fruit juice.

The consumption of spoiled fruits and their products, contaminated with mycotoxins poses a severe risk to consumer's health. It may have toxicological effects on human including carcinogenic, mutagenic, nephrotoxic, neurotoxic, teratogenic, hepatoxic, and genotoxic. Although there is no apparent proof about human carcinogenicity, however, it has shown some immunotoxic and neurotoxic effects in animals.^[79] Therefore, the European Union Commission has regulated (Regulation No. 1881/2006) and established the maximum permissible levels of patulin in foodstuffs. Further, joint expert committee of Food and Agriculture Organization (FAO) and World Health Organization (WHO) has kept an interim daily upper limit of patulin intake of 0.4 mg per kg body weight. [80] On a similar line, the US Food and Drug Administration has restricted patulin amount to 50 mg L⁻¹ in single-strength and restored apple juices. [81]

Emerging technologies for the management of post-harvest Peniciilium incited diseases/decay

Biological control of Penicillium spoilage using antagonistic microorganisms

Antagonism is the process whereby activities of one organism impede the growth, metabolism, and development of pathogen present in their vicinity. Such organisms are termed as "Biological Control Agents (BCAs)" and are fitting candidates for managing economic pests and diseases of crops. [82] Among the non-chemical-based approaches, antagonistic microbes mediated disease suppression is an emerging and more eco-friendly option. [83] Numerous microbes, possessing inhibitory attributes against pathogens, are utilized in controlling fungal decay during commodities storage. In biological control, the suppression of pathogen activities is achieved through actions of antifungal metabolites produced by the BCAs. The BCAs explored for fungal decay control belong to taxonomic groups of yeast, bacteria, and filamentous fungi.

In recent past, several different kinds of microbial antagonists, isolated from fruits and vegetable surface, phyllosphere, root, rhizosphere, orchard soil, Antarctic soil, and ocean, have been used in the biological control of Penicillium and related fungal pathogens occurring on harvested fruits. [14] Some desirable features of biocontrol strains for their use as effective post-harvest biocontrol agent must include; (1) genetic stability and effective at low concentrations, (2) need for simple growth factors, (3) longer storage life and ease of application, (4) tolerance to generally used post-harvest fungicides, (5) non-pathogenic to human, (6) ability to survive under adverse conditions and better adaptability under given set of environment, and (7) user-friendly with other chemical and physical methods. [14-84] Furthermore, higher cell viability of biocontrol microbes is also required for their use on the commercial scale.

The antagonistic yeasts have been more often employed for managing Penicillium infection of stored produce. Their ability of fast proliferation, rapid colonization of fruit surface under adverse environment, quick utilization of host nutrients and thus, making it

unavailable for pathogens growth and increased endurance due to extracellular matrix production make them suitable as successful post-production BCA. [85] Additionally, they are more ecological competitive due to the secretion of extracellular proteinous toxins, as observed in some yeast strains such as Hansenula, Saccharomyces, Pichia, and Kluyveromyces.[86,87]

Zhang et al. [88] showed the biocontrol efficacy of antagonistic yeast Wickerhamomyces anomalus against blue mold decay of pears and demonstrated the significant impact of yeast on the reduction of spore germination and germ tube length of the pathogen along with minimizing disease incidence on pear fruits. Authors observed a disease incidence of only 5.56% in pears treated with 1×10^8 cells mL⁻¹, as compared with 100% disease occurrence in the control. Moreover, expression levels of defense-related enzymes were drastically stimulated by W. anomalus in the host. In another recent study, results of Wang et al. [89] experiment showed bioprotection ability of novel antagonist yeast Yarrowia lipolytica against storage decay of grapes incited by Penicillium rubens. They observed a significant reduction of fungal decay and disease incidence when biocontrol strain was applied at the 1×10^9 cells mL⁻¹. Further, considerable inhibition of pathogens spore germination, germ tube elongation, and activation of pathogen defense-related gene expression, following the inoculation of the biocontrol yeast strain, was noticed in the fruits. In a similar manner, control of Penicillium rot in many other fruits have been achieved using several antagonistic strains of yeast such as Aureobasidium, Candida, Cryptococcus, Pichia, Wickerhamomyces, and Debayromyces, etc. [90–94]

Similar to yeasts, antagonistic bacteria possessing potent antifungal and antibacterial potential are also explored as natural bioagents for suppressing Penicillium proliferation. [95,96] Regarding the bacterial-mediated post-harvest biocontrol, the work of Wallace et al. [10] reported the disease suppression ability of *Pseudomonas fluorescens*, a soil rhizobacteria isolates, against P. expansum causing blue mold decay on the apple fruits. Application of this bacterium reduced decay incidence on fruits held during cold storage after 15 weeks of periods. With the aid of in vitro and scanning electron microscopy (SEM) studies, pathogen inhibition ability of strains was attributed to the mechanisms of nutrients and space competition and production of growth inhibitory metabolites, that probably targeting conidial germination and mycelia inhibition. In another work, bacterial bioagent such as Bacillus subtilis and Agrobacterium radiobacter exhibited significant antifungal activity against the green mold pathogen of lemon fruits, possibly due to the production of cell wall lytic enzymes (chitinase and glucanase). These strains caused negative impacts on the mycelial growth and spore germination of the pathogen and considerably reduced disease severity of P.digitatum on lemon fruits under in vivo conditions. [97] Similar to these works, the inhibition of *Penicillium* growth in various fruits has been obtained using different strains of bacterial antagonists such as Bacillus, Agrobacterium, Pseudomonas, Pantoea, and Streptomyces. [98-101] Among them, some of the bacterial biocontrol strains have been formulated and developed into marketed products for curbing fungal decay. In addition to yeasts and bacterial bioagent, certain fungi also protect the harvested fruits from the infections of numerous *Penicillium* spp. Within fungal genera, few species of Trichoderma, Aureobasidium, and Verticillium have received interest as post-production biocontrol agents. [99-102,103] The fungal biocontrol activities are mainly due to the nutrient competition, mycoparasitism, antifungal compounds production, and stimulation of host defenses.



Mechanisms of microbial antagonists involved in the control of Penicillium decay

The mechanisms involved in the biological suppression of decay pathogen include nutrients and space competition, production of antibiotics and cell wall lytic enzymes, and stimulation of host defense. Furthermore, some recent studies have elucidated the important role of quorum sensing, biofilm formation, mitigation of host oxidative stress and production of biocidal volatiles in the pathogen biocontrol. These mechanisms are interlinked and operate in a tritrophic interaction system involving microbial antagonist, the fungal pathogen, and host fruit (Fig. 1). Often, simultaneously more than one mode of antimicrobial action contributes to the effective biological disease suppression.

The successful competition between antagonist and pathogen for the available nutrients such as sugar, vitamins, amino acids, and minerals, and limiting space results in pathogen biocontrol. This antifungal action is reported in many microbial antagonists. As discussed in the previous section, a microbial antagonist rapidly diminishes the available nutrients oozed from fruit wound, and hence, it became unavailable for pathogens reproduction and virulence. In fruit wounds, competition usually occurs for the amino acids, vitamins, and oxygen, when present in the low level. Bencheqroun et al. showed the importance of the competition process in the inhibition of apple blue mold pathogen, *P. expansum* by the yeast antagonist *A. pullulans*. They found that the biocontrol efficacy of yeast strain against fungi was improved increased when a concentration of amino acids was limiting in the fruit wounds. Rapid multiplication and production of extracellular sugar matrix are the most vital traits of yeast antagonists competing with the pathogen for colonizing limited space. Siderophore, a low molecular weight iron chelator compound

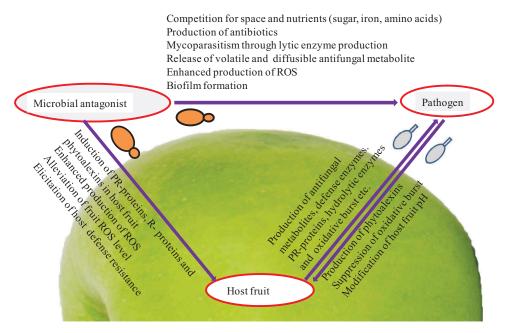


Figure 1. Schematic diagram illustrating the probable mechanisms of antagonistic microbes mediated post-harvest biological control actions involved in tritrophic interaction system, comprising the microbial antagonists, decay inflicting pathogen and host fruit. Adapted after modification from Dukare et al.^[3]

produced by biocontrol strain is also involved in retarding the pathogens growth, reproduction, and pathogenicity. Siderophore compounds make iron nonaccessible for pathogen by forming a firm complex with ferric ions of medium and bringing it into the cytoplasm. [108] The work of Saravanakumar et al. [109] related to siderophore-mediated biocontrol revealed that siderophore (pulcherrimin) producing yeast antagonists Metschnikowia pulcherrima and M. fructicola impeded conidial germination of apple rotting fungi (P. expansum, B. cinerea, and Alternaria alternate) under the limited iron concentration in the medium. Following iron depletion in the growth medium, complex and multiple physiological reactions were triggered in the pathogen hyphae resulting in the disintegration and breakdown of fungi mycelia structures.^[109] Similarly, the biocontrol potential of the bacterium, Rahnella aquatilis, against apple decay pathogens (P. expansum and *Botrytis cinerea*) is linked with its ability to produce siderophore. [110]

The production of fungal cell wall lytic enzymes is another important way by which antagonist suppresses pathogen proliferation. Such enzymes cause mycoparasitism via attaching and degrading fungal hyphae. In the process, pathogens propagules are killed and cellular structures and cellular integrity get destroyed. The fungal cell wall, composed of chitin and glucan in combination with wall protein, is disintegrated by an individual or collective actions of lytic enzymes such as chitinases, glucanases, chitosanases, cellulase, and protease produced by antagonists [105] Moreover, these enzymes adversely affect pathogens conidial germination, germ tube elongation, and reproductive structure. [111] Accordingly, several reported biocontrol strains of *Penicillium* spp. produce extracellular hydrolytic enzymes. For example, the biocontrol action of antagonist yeast C. oleophila, against P. expansum, causing blue mold decay in the apple was mediated through cell wall degrading β-1, 3-glucanase enzyme.^[91] Authors observed that the action of purified glucanase reduced pathogens conidial germination and mycelia growth. The antimicrobial actions of many species of Bacillus and Pseudomonas are credited to extracellular chitinase released by them.^[112] Detrimental effects of enzymatic actions on pathogen hyphae include cellular deformities, protoplasmic damage, mycelial distortion and lyses, leakage of cellular contents, and changes in membrane permeability. [104] Therefore, the loss of fungal cytoplasm resulting from cell wall disintegration is one of the key modes accountable for biocontrol actions of antagonists.

Some bioagents prevent pathogens development by releasing growth-retarding antibiotic compounds. The antibiotics producing species of bacterial genera, predominantly Bacillus and Pseudomonas are well recognized for their antifungal potential. For example, the antibiotic "pyrrolnitrin" producing bacterium, Pseudomonas cepacia controlled P. digitatum on lemon and P. expansum and Botrytis cinerea on apples. [104] Similarly, an antibiotic, syringomycin producing Pseudomonas syringae managed citrus green mold disease, inflicted by P. digitatum. [106] The antibiotic compounds restrain pathogen development through the cell membrane damages, prevention of cell wall biosynthesis and disruption in the protein assimilation process.^[113]

The external application of BCAs often induces systemic resistance (ISR) to invading pathogens in the host tissue. [114] The ISR process involves the accretion of structural barriers and stimulation of various biochemical and molecular responses including mitogen-activated protein kinase signaling, production of reactive oxygen species (ROS), phytoalexins and PR-proteins, synthesis of terpenoid and phytoalexin, increased synthesis of phenolics, cellular lignifications, glycoproteins, and callose. [115] The induction of host

defenses against Penicillium spp. following BCAs application had been shown. For example, peach fruits, when treated with antagonistic yeast, C. laurentii in combination with methyl jasmonic acid triggered the elevated activities of several defense proteins such as chitinase, glucanase, phenylalanine ammonia-lyase, and peroxidase, which further reduced disease lesion diameter of P. expansum and Monilia fructicola. [116] Differential changes in gene and protein expression levels in response to BCAs application have been also demonstrated in both antagonists and host tissue. These changes contributed to augmented host defense to attacking fungal pathogens.[117]

Apart from these, other reported mechanisms of post-harvest biological disease control, though minor in action, are the production of antifungal volatile metabolites.^[118] This mode of action is implicated in the growth inhibition of Penicillium spp. on several fruits and has shown in certain bacterial, fungal, and yeast BCAs. [119-120] The undesirable effects of fungicidal volatiles on the pathogen, as revealed by SEM studies, included several cellular deformities like negative changes in cell vacuolation and membrane permeability, swelling and breakdown of hyphae, reduced conidial germination, and formation of aspersoria. [121] Likewise, biocontrol strain mediated production reactive oxygen species (ROS), oxidative stress mitigation, and biofilm formation are some other modes documented in the control of *Penicillium* spp. and other fungal pathogens.^[3] The list of microbial antagonists and their reported mechanisms of biocontrol action against postharvest Penicillium induced diseases/decay on several fruits have been shown in Table 2.

Use of plant-derived botanicals for controlling fungal spoilage

Plant-derived botanical compounds of antifungal nature also have a potential for the controlling fungal decay of storage commodities in an eco-friendly manner. Presently, considerable attention is being given towards developing the botanical fungicides for controlling the diseases of harvested fruits. More than thousands of plant species and ten thousands of its secondary metabolites are a vast depository of different antimicrobial compounds. [140] The antifungal botanical compounds Essential oils (EOs), natural products, and crude plant extracts are biodegradable, non-toxic, and are regarded as GRAS to mammal's health; hence, they have a huge potential for their use in integrated disease management.[141]

Essential oils (EOs) are naturally occurring complex and volatile compounds having antimicrobial, medicinal, and anti-oxidative potential. [142] They are regarded as GRAS by the U.S. Food and Drug Administration. [143] In the last decade, plant EOs have been used in food and pharmaceutical industry as antifungal, anti-mycotic, and pest control agents. [144] Their use in fungal spoilage control is more preferred mainly due to (1) more volatile, biodegradable, and of ephemeral nature, (2) no concern over presence of residual toxicity on produce, (3) low possibility of developing resistance in pathogen, and (4) in addition, most of the EOs components have no definite cellular targets. [145] The wide variety of EOs obtained from various plants such as clove, cinnamon, oregano, lemongrass, thyme, basil, and nutmeg are most widely used as natural fungicide and food preservatives. [146] Many researchers have used various plant-derived EOs in the management of storage pathogens of fruits and vegetables. [147-149] In fungal growth control, thyme and cinnamon EOs significantly reduced the Penicillium spp. driven green and blue mold incidence on harvested citrus fruits and also controlled the occurrence of other



Table 2. Representative lists of microbial antagonists and reported mode of their actions implicated in the biological control of post-harvest *Penicillium* diseases/decay on different fruits.

	Target			
Microbial antagonist(s)	pathogen(s)	Host	Reported mode of action	References
Yeasts/fungal antagonists				
Pichia membranaefaciens	Penicillium expansum	Peach	Release of lytic enzyme and activation of host defense	[122]
Pichia caribbica	P. expansum	Apples	Activation of host resistance via production of defense proteins	[123]
Cryptococcus laurentii	P. expansum	Pear	Release of lytic enzyme	[112]
Cryptococcus laurentii	Penicillium italicum	Jujube	Nutrient and space competition	[124]
Cryptococcus laurentii, Candida sake	Penicillium digitatum	Orange	Nutrient competition	[125]
Rhodotorula glutinis	P. digitatum	Citrus	Nutrient and space competition	[126]
Rhodotorula mucilaginosa	P. digitatum	Oranges	Activation of host resistance via production of defense proteins	[127]
Debaryomyces hansenii	P. digitatum	Citrus	Nutrient and space competition	[128]
Kloeckera apiculata	P. italicum	Citrus	Nutrient and space competition	[129]
Metschnikowia fructicola	P. digitatum	Grapefruit	Induction of pathogen defense related proteins in host	[130]
Rhodosporidium paludigenum	P. digitatum	Citrus	Induction of host resistance and pathogen defense system	[131]
Meyerozyma guilliermondii	P. expansum	Pears	Stimulation of antioxidant enzymes activities and defense protein in hosts	[132]
Aureobasidium pullulans	Blue mold	Grapes	Nutrient competition; Induction of host resistance	[133]
Trichoderma harzianum	P. expansum	Pears	Not reported	[134]
Muscodor albus	P. italicum	Lemon	Antifungal volatile compounds production	[135]
Verticillium lecanii Bacterial antagonists	P. digitatum	Citrus	Induction of resistance	[103]
Bacillus subtilis	Penicillium digitatum	Citrus	Antibiosis production	[95 98]
Bacillus amyloliquefaciens	Penicillium crustosum	Citrus	Antibiotic production	[119]
Bacillus subtilis Agrobacterium radiobacter	P. digitatum	lemon	Production of mycolytic enzymes	[97]
Pseudomonas spp.	P. digitatum	Orange	Nutrient and space competition	[99]
Serratia plymuthica	Penicillium spp.	Citrus	Antibiosis and nutrients competition	[136]
Pantoea agglomerans	Penicillium spp.	Citrus	Not detected	[137]
Pantoea agglomerans	P. digitatum P. digitatum P. italicum	Citrus Mandarin	Triggers H_2O_2 production and enzymatic activities Nutrient competition	[100] [138]
Streptomyces globisporus Enterobacter cloacae	P. italicum P. digitatum	Citrus Citrus	Release of lytic enzyme Production of antifungal volatiles	[101] [139]

fungal rots. In a similar way, treatment of apples with oregano, clove, and cinnamon EOs effectively restricted fungal spoilage of Penicillium spp. The result showed that penicillium infection was absent in 14% of the apples kept in control, on the contrary, 39-42% of the oregano-treated samples lacked fungal infections.^[150] The antifungal profile of EOs can make them a feasible alternative to the synthetic fungicides used in controlling storage pathogens. The mechanism by which EOs' restrain the growth of pathogens is not clearly deciphered, though; suggested assumptions explicate their antifungal activity. These include (i) adverse modification of cellular enzymes and intracellular organelle functions due to OH groups presence and multiple hydrogen bonds formed by EOs, (ii) morphological alteration due to destruction of cellular firmness and integrity, (iii) destabilization



of cellular membrane, and (iv) disruption in the membrane permeability and cytoplasmic granulation.[151-154]

The plant-derived secondary metabolites encompass a broad array of antimicrobial compounds including alkaloids, EOs, flavonoids, phenols, quinones, saponins, sterols, and tannins. [141] Among them, compounds that exhibit promising antimicrobial activities are acetaldehyde, allicin, benzaldehyde, glucosinolates, isothiocyanates, hexanal and hexanol, methyl salicylate, benzyl alcohol, ethyl formate, jasmonates, and lipoxygenases, etc. [155,156] Generally, phenolic substances, the main group of secondary metabolites, contain more than 8,000 phenolic structures and are found in many genera of a different plant family. [146] The proposed actions that are responsible for their fungicidal properties includes (i) disruption and dysfunctioning of cellular membrane, (ii) inhibition of cellular enzymatic activities, spore germination, germ tube extension and mycelia development, (iii) interference with ATP production and dissipation of electrical potential and pH gradient, and (iv) enhanced production of ROS that causing conformational changes in the membrane proteins. [157,158] The capability of different phenolic compounds in inhibiting rot causing fungi in multiple foodstuffs has been documented. For example, phenolic compounds of herbaceous plants origin effectively managed the growth and development of P. digitatum, Monilinia laxa, and Botrytis cinerea, all of which are responsible for postproduction spoilages on oranges, nectarines, apricots, and table grapes, respectively. Additionally, these compounds lowered the incidence of green mold on oranges by about 92%, when observed after the 25th day of post-treatment storage. [159] Likewise, the report of Sanzani et al. [160] showed the effectiveness of several phenolic compounds (such as ferulic acid, esculetin, quercetin, scopoletin, resveratrol, scoparone, and umbelliferone) in controlling the blue mold infection of P. expansum on "Golden Delicious" and "Granny Smith" apples. However, quercetin and umbelliferone were found the most effectual, preventing Penicillium decay by about 86-92%. In addition tophenolics, certain other plant originated antimicrobial metabolites such as acetaldehyde, benzaldehyde, cinnamaldehyde, ethanol, benzyl alcohol, nonanone, and nerolidol, citral were also effective in protecting citrus fruit from the spoilage of pathogen P. digitatum. [155-161] Citral is an active compound found in the citrus fruit peel that hampers pathogen (P. digitatum) growth and spore germination, [161] and initiates host defense against this pathogen. [162] The role of different isothiocyanate in reducing the incidence of apple spoilage pathogens (P. expansum and B. cinerea) by up to 85% has been demonstrated. [163]

The extensive screening on novel plant extracts of potent fungicidal nature has been done and constantly being performed worldwide. The antifungal properties of both aqueous and organic solvent-based plant extracts against several pathogens of harvested citrus, apples, pear, and other fruits have been reported. [164-168] In general, method/ solvent employed for plant extracts extraction influences its antifungal activity, probably due to the polarity of solvent used for extraction. For example, methanol, a polar solvent, can remove many plants antimicrobial compounds such as phenolic compounds, alkaloids, tannins, triterpene glycosides, and sesquiterpene lactones. [141] Their antimicrobial action is due to the presence of a large number of bioactive ingredients. [145] Some extract, for example, methanol extracts of Withania somnifera and Acacia seyal control the green mold infection via induction of host defenses.^[165–169] The antimicrobial activities of crude plant extracts are documented; however, an in-depth assessment of their biological

activity, phytotoxicity, dispersal in fruit tissues, and formulation development requires scientific attention for their use as botanical pesticides on the economic scale. [170]

In regards to their delivery,, they can be applied by incorporating into coatings of fruits or dipping fruits in the concentrated solution of botanicals containing EOs, plant extracts or secondary metabolites.^[148–171] Their use by incorporating it into fruit coating is more popular, as, it allows closer and longer interaction with the pathogen on the fruit surface, hence, resulting in the successful control of decay pathogens. [171] In order to develop an effective antimicrobial plant compound into botanical fungicide, they must be: (a) effective at lower concentrations, even at short duration treatments, (b) should not have adverse effects on, aroma, flavor, and acidity of produce, and (c) the lowest appropriate dose for practical application. [140-170] The partial list of some plant-derived antifungal botanicals against different species of post-harvest decay-causing Penicillium have been given in Table 3.

Sanitation as effective means for microbial decontamination and managing Penicillium rotting of fruits

To a certain extent, indirect control of food spoilage is achieved through sanitation and hygiene of keeping rooms, processing equipments, produce surfaces, and washing water. The sanitation of fresh produce, occasionally followed by fungicidal treatment, is crucial in reducing up to 50% or more decay losses. [181] They are extensively used for lowering surface contamination, especially of pathogens concerned with human health. [182] In contrast to fungicide use, sanitation causes fast mortality of pathogens without depositing any residue on fruit surfaces. The most common sanitizers that have been employed for reducing the inoculums of post-harvest fruit associated pathogenic Penicillium species are described in the following sections.

Chlorine compounds and ozone

The dissolved solution of chlorine (Cl₂) or hypochlorite (OCl) is the most widely used aqueous sanitizer for decontamination purpose in the purification of drinking water and food industry on a commercial scale. [183] Their ability of rapidly killing pathogen propagules is valuable in preventing the pathogens spread from infected fruits to healthy. The chlorine-containing compounds have found effective against Penicillium mold associated with fruit decay. For example, the free solution of chlorine (200 mg L⁻¹) inactivated about 95% conidia of the citrus green mold pathogen, P. digitatum. The time (in seconds) required for conidial inactivation was 13.2, 19.1, 29.4, and 88.4 sec at pH 7, 8, 9, or 10, respectively. [184] The efficacy of chlorine dioxide (ClO₂) gas in preventing harmful fungal and bacterial growth on fresh produce has been demonstrated. [185,186] In most of studies, control efficacy of these compounds had been shownd on the human pathogens. The successful use of both Cl2 and ClO2 at almost similar concentrations killed conidial growth of numerous pathogens such as P. expansum and Mucor piriformis [187], and P. expansum, Botrytis cinerea, Cryptosporiopsis perennans, and M. piriformis, occurring in the storage and packinghouses of apple and pear fruits. [188] The tolerance level of fungi to chlorine compounds is often high than for bacteria and viruses. During commodities storage, chlorine gases are applied experimentally either for a short period or incessantly to

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Source (s)	[150]	[172 173]	[47]	[174]	[175]	[176]	[177]	[159]	[178]	[179]	[180]
Treatments/ results/remarks	Treatments of fruits with the essential oils of oregano, clove, and cinnamon successfully retarded fungal growth	The antifungal activity of thyme and cinnamon EOs considerably controlled fungal green [172 173] and blue rotting mold on harvested apples	Treatment of fruits with the phenolic compounds of olive-mill wastewater (4mg mL-1 and 8 mq mL-1) minimized the fungal decay incidence by 30% and 15%, respectively	The methanolic extracts of Clove, Dodonaea, Garlic, showed antifungal activity against blue rot pathogen	20 different plants leaf extracts and 3 essential oils were screened for their antifungal potential. Among them, dip treatment of infected fruits with the leaf extract of neem (Azadirachta indica) significantly reduced Penicillium rot.	Antifungal assay of water and ethanolic extracts of A. <i>indica</i> leaves and Aframomum melegueta seeds revealed that the plant extracts of A. <i>indica</i> was more fungicidal than A. <i>melegueta</i> and prevented post-harvest cassava spoilage caused by pathogenic fungi	Among the aquous extracts of <i>Aloe vera</i> , Eucalyptus and Ocimum botanicals, extract of <i>A. vera</i> was found to most effective in the controlling blue and green mold pathogen of fruits under in vitro conditions.	Plant extract obtained from the herb (Sanguisorba minor and Plantago lanceolata) significantly inhibited the pathogen spore germination and germ tube elongation. Further, phenolic compounds impeded the growth of pathogen by about 92%, after 25th day storage.	soy protein fractions (@50-3,000 mgL-1]) of soybean four extracts significantly inhibited pathogen <i>in vitro</i> and full germination inhibition was noticed when it was used at a concentration of 2000 mgL-1]	Antifungal botanicals of Eugenia caryophyllata considerably reduced green mold pathogen growth	Thymus derived antimicrobial compounds was found effective in checking the proliferation of pathogen growth
Antifungal constituents	Essential oils	Essential oils	Phenolic compounds	Solvent extracts	Crude extracts and essential oils	Solvent and aqueous extracts	Aqueous extracts	Extract containing caffeic acid derivatives and flavonoids	Extract of soyaben flour containing β-conglycinin and glycinin	Essential oil, β-caryophyllene and eugenol	Essential oil, thymol, <i>p</i> -cymene, carvacrol, and <i>6</i> -terpinene
Host	Apple	Citrus	Pomegranate	Apple	Apple	Cassava	Kinnow mandarin	•			
Disease/decay	<i>Penicillium</i> decay	Green and blue mold	<i>Penicillium</i> decay	Blue mold	Blue mold	Penicillium and other fungal rot	Green and blue mold	Green and blue mold	Penicillium decay pathogens	Green mold	Green mold
Target pathogen(s)	spp.	Penicillium digitatum, Penicillium italicum	Penicillium adametzioides	P. expansum	P. expansum	Penicillium oxalicum Penicillium and Cassava and other decay other fungal fungi	P. digitatum, P. italicum	P. digitatum, P. italicum	P. digitatum P. glabrum	P. digitatum	P. digitatum

products for preventing microbial spoilage. In Israel, the commercial MegAir1 technology, being used for the continuous on-site production of both Cl₂ and ClO₂, is deployed for the safe storage of freshly harvested fruits. [189] The presence of ClO₂ residues is found negligible and comparatively non-persistent in treated fruit. [186-190] For example, numerous fruits such as apples, tomatoes, strawberries, oranges, and cantaloupe treated with chlorine compounds (@ 0.1-5.0 mg L⁻¹ for 10-30 min) were devoid of any residue, and if present, it was reduced noticeably after 14 days.

Ozone (O₃) is another most potent biocidal compound. Historically, it has been utilized for decontamination of wastewater, bottled drinking water, aquaculture, and swimming pool. [191] Its germicidal property is reliant on the concentration used, temperature, exposure time, humidity, and the residing substrate. However, short half-life, poor diffusion, partial water solubility, rapid decomposition, and high operating costs make ozone use often challenging. [191,192] Many literature reviews related to ozone application on fresh produce of fruit and vegetables have been published. [193-195] In post-harvest Penicillium decay control, ozone gas is effective at both lower and higher concentrations. At low concentrations, it hampers the pathogens hyphal growth, though, infrequently can activate conidial production. [196] The periodic exposure of UV-generated ozone to the conidia of P. digitatum, P. expansum, P. italicum, Alternaria alternate, Aspergillus flavus, and Aspergillus niger in a humid atmosphere (during storage of 100 days at 2°C of air or 0.15 mL L⁻¹ ozone) caused 95% conidial mortality after 2-3 months of storage. [197] Indirectly, ozone gas confers some benefits to host fruits through the; (1) retardation of fruit senescence driven by reduction in ethylene, (2) minimizing the air-borne inoculums via conidial suppression, and (3) elicitation of host resistance against pathogen. [198,199] Also, it prolongs shelf life of various fruits such as grapes, raspberries, and other berries without any injury. [18] At higher concentrations, ozone gas effectively inactivates pathogens conidia. The exposure of pathogens such as P. italicum, P. digitatum, and B. cinerea to different ozone concentrations (at 25°C and 95% RH) for 1 h reduced conidial germination by almost 99%. [200] However, the toxic effect of ozone on conidial growth was reduced significantly with the decrease in RH.

Ethyl alcohol and hydrogen peroxide

Ethyl alcohol, two carbon-containing alcohols, is mostly used for microbial decontamination in the medicinal field. [201] It deactivates microbial metabolism through inducing cellular membrane damages and protein denaturation. The negative effect of ethanol on fungi includes temperature-dependent inhibition of conidial germination. [202] The first study on the potential ethanol use for surface disinfestation of freshly harvested lemon fruit was done for the control of green mold disease, inflicted by P. digitatum; however, high temperature (44°C) was needed for complete prevention of fungal rot using higher (20% or 40%) concentrations of ethanol. [203] Likewise, ethanol vapors also suppressed fungal growth during storage of fruits, where it successfully impeded green and blue mold decay of orange fruits caused by P. digitatum and P. italicum. Apart from this, these compounds were also effective in managing other fungal decay on harvested fruits during post-harvest handling and storage phase. [204] Hydrogen peroxide (H₂O₂), recognized as a GRAS compound, is toxic to microbial cells due to strong oxidizing power, generation of ROS, and OH radicals, which inactivate cellular respiratory enzymes, damages nucleic acid

and triggers several physiological, biochemical, and molecular response within cells. [205,206] Certain in vivo and in vitro experiments have proved its antifungal activity against Penicillium spoilage of various horticultural produce. For example, sequential application of NaOCl and H2O2 in combination with cupric salt suppressed mycelia growth and conidia germination of P. expansum and P. digitatum infecting apple and lemons. [207] This treatment caused disorganization in the fungal conidia and rigorous cellular damage. In another study, Cerioni et al. [208] reported that mycelium of P. digitatum was more susceptible than its conidia to the H₂O₂ treatment when applied relatively at higher concentrations. Furthermore, the proteomic studies revealed severe oxidative damages to the mitochondria membrane proteins and cellular respiratory system due to H₂O₂ treatment. The pH and exposure time-dependent conidial inhibition were reported in P. digitatum, whereby, inhibition was high when exposed to low pH and more time of H₂O₂ treatment. [209] Hydrogen peroxide when combined with other food-grade compounds also controlled Penicillium spoilage incidence. Its combined application with as sodium bicarbonate, potassium sorbate, or potassium phosphate effectively managed the blue mold decay of lemons. [210] Though H₂O₂ is effective for *Penicillium* decay control, sometimes, it may become phytotoxic and can incite color bleaching on fresh tissue, as same reported in table grapes (green to yellow discoloration) and lemons (red to bronze discoloration). [18]

Organic acids

The biocidal property of some food-grade organic acids (acetic, citric, oxalic, malic, propionic, and tartaric acid) projects their use successful in post-harvest control of *Penicillium* and other rot-inducing fungi. In food matrices, they can perform the role of antimicrobial compounds as well as antioxidants that help in preventing color, flavor, and textural changes. Besides these, some plant-based organic acids such as salicylic acid and jasmonic acid stimulate host defense systems against *Penicillium* and other rotting fungi. The acetic acid (4–6%) containing vinegar vapors retarded conidial germination of pathogen *P. expansum*, *M. fructicola*, and *B. cinerea* causing spoilage in apples, stone fruit, and strawberries, respectively. Among the various combination of treatment, apple fruits when treated with hot acetic acid solutions (1%, 2%, and 3% for 1, 2 and 3 min, respectively) at 50°C significantly reduced fungal decay, more particularly, 3% acetic acid treatment for 2 min and 2% acetic acid treatment for 3 min was the most efficient combination. Funitation using acetic acid or its combine application with heat treatment for 3 significantly reduces the incidence of *Penicillium* decay on table grapes and mandarin fruits.

Another organic acid, oxalic acid, when applied during pre-harvest stage improved ascorbic acid content, decreased fruit firmness and further, reduced blue mold incidence and lesion diameter of *P. expansum* on kiwi fruits. Proteomic analysis of jujube fruits, following application of oxalic acid, revealed augmented fruit resistance against blue mold pathogen, *P. expansum* and also adversely affected ethylene metabolism that delayed senescence. Cinnamic acid obtained from cinnamon bark exhibited biocidal action against *P. expansum* and other decay pathogens such as *B. cinerea* and *A. niger*. The disintegration of plasma membrane integrity and generation of toxic ROS was the principal modes by which cinnamic acid hampered the fungal growth. [219] In a similar



way, propionic, sorbic, decanoic, benzoic, and citric when used at different concentrations were successful in the averting growth of Penicillium commune induced decay on litchi fruits and against other pathogenic fungi including P. digitatum, P. italicum, and Geotrichum candidum.[220]

Electrolyzed water

More recently, the use of electrolyzed water (EW) as sanitizer has become more popular in the food supply chain. [221] Their main applications are disinfection of processing utensils, meat and products, cutting boards, and in livestock management, and in latest times, sanitation of water chiefly used for fresh fruit and vegetable washing. [222,223] The use of EW for managing food-borne diseases and the growth of spoilage microbes in processed vegetables were also reported. [224] The harmful effect of EW in combination sodium bicarbonate (1.25%) on inhibition of *Penicillium* spp. growth has been documented by Fallanaj et al. [223] Authors demonstrated that population of *Penicillium* spp. was reduced by 93% in citrus wash water after 1 hr of the beginning of the electrolysis process. The same results were obtained only after 7 hr when electrolyzed tap water without sodium bicarbonate was used. Further, the electrolyzed sodium bicarbonate solution completely stopped the growth of *Penicillium* spp., and hence, no decay development was noticed. The fungicidal actions of EW are not entirely known,thoughsome proposed mechanisms for its antimicrobial action include; (1) cellular oxidative damage by the oxidants produced^[225] (2) up-regulation and activation of host defense genes coding phenylalanine ammonia-lyase, chitinase, and peroxidase etc. [226], (3) antimicrobial action is also due to the joint action of oxidative radicals, pH, free chlorine, and other unknown active compounds of EW. [227] Examples of different GRAS chemicals and disinfecting agents used for management of Penicillium induced infection in different fruits are given in Table 4.

Modern physical approaches for managing Penicillium and related fungal infections in the harvested produce

Cold storage and its impacts on fruit spoiling pathogens

Cold storage is the most commonly used physical method for minimizing the negative impacts of biotic and abiotic stresses on freshly harvested produce. The low-temperature storage is effective in prolonging shelf life along with retention of nutritional and sensory attributes of fruits and vegetables. [237] It not only controls these stresses but also ensures safety and quality fresh produce. [238] Low temperature brings down the metabolism rate, especially respiration of commodities and enhances their shelf life. Low temperature, like sanitizers, does not have direct biocidal action but contributes significantly in slowing the growth of microbes through freezing their enzymatic activities. Further, cold storage also maintains the host resistance to storage pathogen via reduced host metabolism and therefore minimize the activities of spoilage-causing pathogens. With the exception of psychrophile, the growth of other microbes, commonly occurring at surfaces and epidermal areas of fruits are generally stopped at a low-temperature range (4-11°C). The lowest sustained temperatures for growth and development of several fungi are in the region of 0° C, although certain rotting fungi are capable to grow even at freezing temperature. The

Table 4. Examples of food-grade chemicals, and disinfecting agents used for management of Penicillium induced infection in different fruits.

	() () () ()			(s)
	Blue and green mold	Citrus	Potassium sorbate	[528]
P. digitatum, P. Italicum	Green and blue mold	Citrus	Sodium ethyl paraben	[529]
P. digitatum	Green mold	Citrus	Sodium bicarbonate	[230]
P. digitatum, P. italicum Ozone treatment	Green and blue mold	Lemon	Potassium sorbate	[231]
	Naturally occurring decay	Tangerine	Tangerine Showed fungicidal property against pathogen	[232]
P. digitatum, P. expansum, P. italicum, P.	Penicillium and other		Ozone treatment at 2°C of air with or 0.15 mL L-1 in humid storage resulted in 95% conidial	[197]
	fungus induced decay			500
P. Italicum, P. digitatum, and B. cinerea, P. f	<i>Penicillium</i> and other fungus induced decay		Different concentrations of ozone (at 25°C and 95% RH) for 1 h reduced conidial germination by almost 99%	[700]
Hydrogen peroxide				
P. expansum	Blue mold	Apple	Suppressed mycelia growth and conidia germination	[233]
P. digitatum G	Green mold	Lemon	Suppressed mycelia growth and conidia germination	[508]
P. expansum	Blue mold		stem	[234]
P. italicum B	Blue mold	Lemon	Chronologically treatment of NaOCI (200 mg L—1 for 2 min), followed by H ₂ O ₂ (20 g L—1for a second), in the presence of cupric sulfate reduced 50% incidence of green mold disease	[235]
Electrolyzed water				
Penicillium spp.	Penicillium decay	Citrus	EW when used in combination sodium bicarbonate (1.25%) inhibited pathogen growth by 93%	[223]
<i>P. digitatum</i> Organic acids	Green mold	Tangerine	The EW has detrimental impacts on the decay pathogen	[336]
	Blue mold	Apple	4–6% concentration of acetic acid effectively retarded pathogens conidial germination	[213]
P. expansum B	Blue mold	Kiwifruit	Preharvest use of oxalic acid, improved ascorbic acid content, decreased fruit firmness, blue mold incidence and disease lecion diameter on fruits	[216]
P. expansum, B. cinerea, A. niger	decay pathogens		ng antimicrobial activity against decay pathogens	[218]



lowest recorded temperatures for the sustenance of certain fungal species are -4°C for Cladosporium herbarum, -3°C for P. expansum and A. alternate, and -2°C for B. cinerea. Though effective in microbial growth retardation, certain fruits and vegetables held in cold storage may experience chilling injuries, which are further dependent on their genetic makeup and background, crop and cultivar, crop location, physiological status during harvesting, and exposure time. [5]

Controlled and modified atmosphere storage

Controlled atmosphere (CA) storage has exact control of CO₂ and O₂ level and ethylene produced during storage, while, modified atmosphere (MA) storage implies any kind of synthetic atmosphere, without control of its constituent gases, especially oxygen and carbon dioxide^[239,240] The altered storage gas compositions have a significant impact on the physiology and metabolism of harvested commodities and keeping quality of produce.^[241] During CA storage, it has favorable effects on the stored produce and adverse impacts on the fungal pathogen affecting commodities. Also, it delays the process of ripening and senescence and postpones the time at which fruits may become susceptible to the fungal attack and decay development. Simultaneously, it reduces the growth, metabolism, and pathogenesis-related activities of decay inflicting fungal pathogens. However, the lower concentration of O₂ (less than 1%) is often essential to cause a considerable inhibition of spore germination, pathogens growth, and sporulation.

In regards to post-harvest disease control, the importance of CA in the effective reduction of P. expansum, an etiological agent of blue mold decay in apple fruits has been shown. Considerably, apples artificially inoculated with the pathogen, P. expansum and subsequently, held at 0°C under CA conditions of 3% O2 and 2% CO2 were with less incidence of blue rotting, as compared to normal cold-stored fruits. [242] The results of a study by Conway et al. [243] demonstrated the combined action of microbial antagonist and sodium bicarbonate on the P. expansum, blue mold pathogen of apple stored under the controlled storage (containing 1.4 kPa O₂ and 3 kPa CO₂) for a period of 16 weeks at 1°C. This treatment effectively improved the viable population of antagonists that resulted in the successful elimination of fungus-induced decay under CA storage atmosphere. MA is usually achieved by sealing definite commodities in a polymer containing semipermeable packaging film. This process increases CO₂ level and decreases O₂ level in the packed film and reduces the respiration rate from the stored commodities, [244,245,] which further augment the post-harvest life of produce. [5] The increased level of CO2 is fungistatic and reduces the development of decay pathogen in sealed packaging materials.

Hot water and hot air treatments

Hot water treatment (HWT) is a non-traditional, energy-efficient, safer and low-cost technique for post-harvest decay management. [246,247,] It is more effective due to great efficient heat transfer-mediated impacts on pathogen and surface microorganisms. HWT, in particular, is mostly used in managing pests of tropical and subtropical fruit crops, which have phytosanitary and quarantine regulatory importance. HWTs is generally applied either as hot water dips, brushing, or/and rinsing. In post-harvest disease control, fruits are successfully treated using HWT typically involving hot water with temperature

ranging in between 45°C and 60°C and time-varying from few seconds to 20 min. [242] For some post-harvest pathogens, the duration of exposure has a direct influence on the success of treatment. For example, HWT was unable to manage infection of P. expansum or P. digitatum, when fruits were treated after 2 h of pathogen inoculation, contrary; HWT of fruits after 24 h of pathogens inoculation was effective in reducing the incidence of blue or green mold incidence. [248,249] Most studies have demonstrated the effectiveness of HWT as curative measures of post-harvest disease prevention, but, its use as preventive control measures has been less studied. Some latest reports illustrated that this treatment, when applied 1 or 4 h before pathogen inoculation, resulted in 30% decline of apple blue mold incidence, probably by stimulating defense responses in fruit. [250] HWT as a preventive measure is also effective in reducing disease development and improving skin color, as observed in mango. The mango transcriptomic analysis of hot water treated mango fruit and its peel samples revealed a differential level of gene expression and host phenotypic response. [251] The genes involved in the abiotic stress responses, host resistance to the pathogen, and carbohydrates and flavonoid metabolism were highly upregulated while genes linked with the chlorophyll degradation and photosynthesis, were down-regulated. The effective use of other HWT methods such as hot water dipping and hot water rinse brushing is also demonstrated in the successful management of post-harvest penicillium spoilage occurring in the pear, orange, lemons, grapefruits, and tangerine. [252-254] Usually, improperly hot water treated fresh commodities can experience internal and external injuries including symptoms of as skin browning, pitting, colored spots, and browning. [255]

Hot air treatment employs longer exposure (several hours or days) of fruits in a heated air atmosphere having temperature and RH of more than 30°C and 90%, respectively. The time and temperature of treatment depend on the incidence and severity of pathogen damage. This method has a less success rate as compared to other methods. Its effectiveness in decay control can be enhanced by its integrative use with antagonistic microbes, food-grade chemicals, modified atmosphere, or combination of these. Hot air treatment in the successful control of Penicillium decay incidence on several harvested fruits has been reported. For example, a long hot air treatment at 33°C for 65 h successfully managed both blue and green mold disease, inflicted by P. italicum and P. digitatum and, respectively, on lemon and orange fruits. [242] As reported by other researchers, the similar level of Penicillium and other fungus-induced spoilage control in various fruits and their different varieties by hot air treatments have been achieved. [256]

Cold plasma technology in preventing post-harvest fungal spoilage

Plasma is a partly neutral ionized gas and considered as the fourth state of matter, following solids, liquids, and gases. Cold plasma (CP) is produced by passing an electric current to a gaseous mixture and it usually contains nitrogen, helium, argon, air or oxygen. [17] In general, the key components of CP include a mix of atoms, charged particles, excited molecules, and reactive species of oxygen and nitrogen (RONS) such as superoxide, ozone, hydroxyl, hydroperoxyl, nitric oxide, nitrogen dioxide, dinitrogen pentoxide, and UV photons. [257] These reactive ions are generally lethal to the pathogen growth and metabolism and do not have any concerns of harmful residues or by-products generation in the environment.

CP is portrayed as a method for the successful decontamination of pathogenic microbes in a chemical and residue-free way. The effective use of CP for bacterial decontamination of various agro-horticultural commodities such as fresh fruit and vegetables, nuts, seeds and spices, etc. has been reported. [258-262] Although, most of the studies on the use of CP is concerned with surface bacterial decontamination, however, report of some latest studies has demonstrated its strong fungicidal actions against many fungal pathogens, hence, signifying its potential use in managing decay. The surface washing, from the fruits of red grapes, strawberries, and cherries, stored in pack-house, when disinfected with CP for 7.5 min, successfully reduced viable spore's count of several fungal pathogens including P. italicum, Aspergillus niger, and A. alternate. [263] Won et al. [264] demonstrated that effective surface decontamination of Satsuma mandarins' fruits with CP for 10 min reduced pathogen spores and further caused 84% reduction in the incidence of blue mold disease, inflicted by pathogen P. italicum. In another study, cold plasma treatment was effective in reducing the inoculums of post-harvest green mold pathogen infecting lemon fruits. Authors observed that fruit treated with 10 min of CP were free of disease symptoms and nearly 100% inactivation of pathogens spore was noticed. [265]

The precise antimicrobial mode of CP is vague, though prevention of pathogen growth and stimulation ofdefense systems in host tissue is believed as the main reasons for its antifungal activity. Many cellular components of pathogens such as cell wall, cell membrane, DNA, protein, enzymes, and fatty acids are functionally inactivated by the actions of cold plasma treatments, which results in the decontamination of harmful microbes from the foodstuffs. In general, some reported damaging effects of CP treatments on pathogens included: (1) alteration in cell membrane/cell wall permeability, (2) destruction and deformation in cell membrane, (3) protoplasmic leakage of cytoplasmic contents, and (4) serious damage to cellular proteins, and DNA molecule through generation of RONS and possibly by UV photons. [266,267] With microscopic analysis, Ye et al. [268] (2012) found that CP treatment of blue mold pathogen, P. expansum, distorted the protoplasmic membrane, reduced cytoplasmic volume, vacuolar expansion, and completely disrupted cellular fluids. They also observed invagination and lysis of cell membrane, followed by external leakage of the protoplasmic contents. The proposed mechanisms of cold plasma actions implicated in functional deactivation of microbial cell are schematically represented (Fig. 2)

Pulsed light technology

Pulsed light (PL) processing is nonthermal technology primarily being employed for microbial decontamination of various foodstuffs such as fresh fruits and vegetables, fruit juices, and meat products. PL processing, an alternative technology to UV light, utilizes high-intensity light pulse treatment for a small duration of time. [271] The lights used in PL processing have a wide wavelength range (200-1100 nm), comprising ultraviolet range (200-400 nm), visible range (400-700 nm), and near-infrared range covering 700-1100 nm. [272] The potential applications of PL technology in food processing are for rapid microbial disinfection of various commodities such as fresh fruits and vegetables, meat slices or hard cheeses, etc., where surface contamination with harmful microbes is a major concern. The effectiveness of PL treatments in microbial deactivation depends upon microbial light absorption and matrix properties.

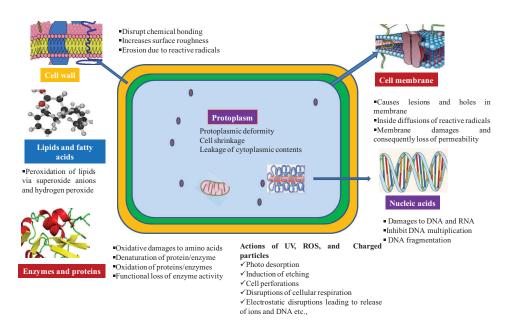


Figure 2. A schematic diagram demonstrating typical mechanisms of cold plasma actions implicated in functional inactivation of microbial cell, thereby resulting in the decontamination of harmful microbes from the foodstuffs. This figure is adopted in modified form from Misra and Jo^[269] and Schluter and Frohling. [270]

PL treatments principally use ultraviolet (UV) rich light region for the killing and effective inactivation of harmful microorganisms from solid and liquid foods. Furthermore, the combined actions of both visible and infrared regions of PL also contribute to the destructive and damaging effects on the harmful microbes. [272] Its antimicrobial activities are mainly due to structural changes in the DNA and proteins caused by absorption UV radiation in the conjugated carbon-carbon double bonds in nucleic acids and proteins. [273–275]

With regards to spoilage fungi control, the PL treatment has detrimental effects on the growth and development of pathogenic *Penicillium* species. The application of PL was effective in reducing the spore count of *Penicillium frequentans* on the surface of apples, pears, and fruits. Similarly, this treatment also caused reduction in the CFU count of dry spores of *P. digitatum*, from 10^6 – 10^4 , on the "Valencia" variety of oranges. In case of liquids, PL treatment of apple juice at a depth of 6 to 10 mm drastically inactivated *P. expansum* and significantly reduced colony-forming units (CFU)/ml⁻¹ from 3.21 to 1.58 log. Inactivating effect was greatly depended on the microbial load that is 1.30 and 3.2 log reduction for 3×10^5 and 2.3×10^4 CFU ml⁻¹, respectively. This technology is capable of reducing risk from foodborne human pathogens, extending shelf life of the product and improved economics during the food supply chain. However, current literature on PL application for disinfestations of fruits and vegetables is scarce; hence more additional scientific data are indispensable to appraise the appropriateness of this technology in controlling lethal microbes and fungal pathogens of harvested commodities.



Conclusions

Post-production wastage of fresh produce due to harmful fungi, more particularly by Penicillium spp., can be huge, hence, requires global attention for reducing losses caused by them. The occurrence of *Penicillium* spp., in certain foods, is often harmful, as, besides food wastage, they are also involved in the production of mycotoxins, alkaloids, and allergens, all of which have negative impacts on human health. The detrimental environmental impacts and regulatory constraints associated with the synthetic chemicals mediated disease suppression have allowed the shift from an era of chemistry to an era of biology. [279,280] Among the proposed and emerging alternatives, use of biocontrol organism, plant-derived natural products; GRAS categorized chemicals and latest emerging physical approaches are gaining impetus in managing key mold pathogens. The simplicity of genome sequencing and information obtained from the genomics, transcriptomics, proteomics, and metabolomics studies have demonstrated huge perspective for the formulation and development of novel "biological" based commercial technologies. In regards to postharvest disease control, we have shifted from simpler to the complex alternative for managing decay in an economically and dependable way. Here, one thing is to note that a single methodological intervention is often not sufficient; henceforth, multiple interventions, at different points of the disease development process, are required to achieve almost a complete control of the post-harvest disease. The non-fungicide-based promising and eco-friendly approaches, when used individually or in combination can affect a successful control of *Penicillium* and other decay pathogens and will ensure safety, quality, and shelf life of produce during post-harvest handling, storage, shipment, and distribution.

Conflict of interest

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