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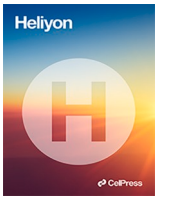

Review article

Rhizopus stolonifer and related control strategies in postharvest fruit: A review

Qianqian Liu [a], Qingmin Chen [b], Hu Liu [b], Yamin Du [a], Wenxiao Jiao [a], Fei Sun [a,**], Maorun Fu [a,*]

[a] College of Food Science and Engineering, Qilu University of Technology (Shandong Academy of Sciences), Jinan, 250353, PR China
[b] College of Food Science and Engineering, Shandong Agriculture and Engineering University, Jinan, 250100, PR China

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ABSTRACT

Rhizopus stolonifer is one of the main pathogens in postharvest storage logistics of more than 100 kinds of fruit, such as strawberries, tomatoes and melons. In this paper, the research on the morphology and detection, pathogenicity and infection mechanism of *Rhizopus stolonifer* was reviewed. The control methods of *Rhizopus stolonifer* in recent years was summarized from three dimensions of physics, chemistry and biology, including the nanomaterials, biological metabolites, light control bacteria, etc. Future direction of postharvest *Rhizopus stolonifer* infection control was analyzed from two aspects of pathogenic mechanism research and new composite technology. The information provided in this review will help researchers and technicians to deepen their understanding of the pathogenicity of *Rhizopus stolonifer*, and develop more effective control methods in the future.

1. Introduction

Globally, 20 %–25 % of fruits and vegetables are lost in the postharvest supply chain due to fungal pathogens every year. *Rhizopus stolonifer*, belongs to *Zygomycetes*, *Mucorales*, *Mucoraceae*, *Rhizopus* and *R. stolonifer*, is one of the most common and fastest-growing species in *zygomycetes* [1]. The spores of *Rhizopus stolonifer* widely exist everywhere, can be spread by airflow and grow rapidly in humid environments, resulting in the decay of many fruits such as *Allium*, *Ananas*, *Cucurbia*, *Fragaria*, *Lycopersicon*, *Solanum* and so on [2]. Among them, strawberry due to fungal invasion, mainly *Rhizopus stolonifer*, its postharvest loss can be as high as 50 % [3]. In addition, tomatoes are also highly susceptible to fungal infection, with retail losses of tomato fruits in the Greater New York market of 9500 tons per year, and in Mexico, one of the world's leading tomato producers, 80 percent of total pre-packaged and bulk tomato fruit losses are caused by *Alternaria* rot and *Rhizopus* rot [[4–6]]. Sweet potato, a vital root crop in various countries and regions worldwide, soft rot caused by *Rhizopus stolonifer* has caused serious losses in the world. In the southeastern United States, soft rot is typically the most serious postharvest disease of sweet potatoes, and in China, annual sweet potato yield loss due to fungal infections is estimated to be approximately 20–40 %, with *Rhizopus stolonifer* being one of the most destructive fungi [7,8]. Therefore, *Rhizopus stolonifer* is considered to be one of the most destructive fungi during storage of various valuable horticultural commodities [9]. However, there were no comprehensive presentations of the pathogenicity of *Rhizopus stolonifer*, as well as the control strategies in postharvest fruit

* Corresponding author
** Corresponding author
E-mail addresses: sunfei31@zju.edu.cn (F. Sun), skyfmr@163.com (M. Fu).

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yet. This article provides a detailed review of the pathogenicity and infection mechanism of *Rhizopus stolonifer* in fruit during post-harvest storage. Most importantly, this article briefly summarized the control methods to alleviate *Rhizopus stolonifer* infection and fruit damage.

2. Pathogenicity of *Rhizopus stolonifer*

2.1. Morphology and detection of Rhizopus stolonifer

As shown in Fig. 1, *Rhizopus stolonifer* is composed of branched, non-septate white hyphae with a length of 900–2700 μm and a diameter of 22–32 μm. The sporangium is spherical, initially white, and then black. There are many spores, most of which are 90–120 μm long. There are thousands of spherical sporangium spores in the sporangia. The sporangium spores are light to dark brown, smooth and simple wall, without septum. Most of the sporangium spores are easily dispersed in the air and fall on decaying fruit to germinate into new mycelium [10].

Scanning electron microscopy (SEM) is a reliable method for the identification of *Rhizopus stolonifer*, which can observe the different shapes and surface ornamentation of fungal spores as well as the mycelial morphology. As shown in Fig. 2, the spores of *Rhizopus stolonifer* are in various forms (spherical, ellipsoidal and angular). The ornamentation on the surface is continuous and obvious ridges along the spores, and uniform and regular long tubes of mycelium with smooth outer surfaces [1,11]. In addition, Sun et al. [12] used the hyperspectral imaging system to obtain the hyperspectral images of *Rhizopus stolonifer* growing on potato dextrose agar (PDA) medium. As shown in Fig. 3A, the growth rate of *Rhizopus stolonifer* was rapid, reaching almost full at 24 h and completely full at 36 h and 48 h. The spectral changes (Fig. 3B) were consistent with the changes of fungal growth. The spectral response values changed rapidly from 12 to 24 h and 24–36 h during the growth stage, and the fungal species were distinguished by principal component analysis (PCA) and partial least squares discrimination analysis (PLS-DA). The method showed a high accuracy rate of 97.5 %, demonstrating the applicability of hyperspectral imaging technology for identifying *Rhizopus stolonifer*. For the commercial evaluation of Rhizopus soft rot, the ideal method for detecting fruit infection should be reliable, affordable and fast. Spore detection is primarily carried out by the process of isolation in PDA medium on a plate. However, Hahn et al. [13] found that the spectral detection method can be used for efficient detection. Through discriminant analysis of spectral data, the conidia of *Rhizopus stolonifer* can be detected. The spectral detection can be completed in a relatively short period of time, which makes up for the lack of conventional laboratory techniques that require one day to detect the conidia of *Rhizopus stolonifer*, and is sensitive and rapid, with a success rate of 78 %. However, the wide application of hyperspectral imaging is limited due to drawbacks such as high cost, time-consuming operation, and complex processing. Zhu et al. [14] used hyperspectral transformation of RGB images to detect *Rhizopus stolonifer* infection in apples, and converted the response of RGB images into pseudo reflectance spectra, which combined with machine learning method to achieve accurate detection of fungal infection. In addition, Liao et al. [15] used Raman spectroscopy and cascade forest to

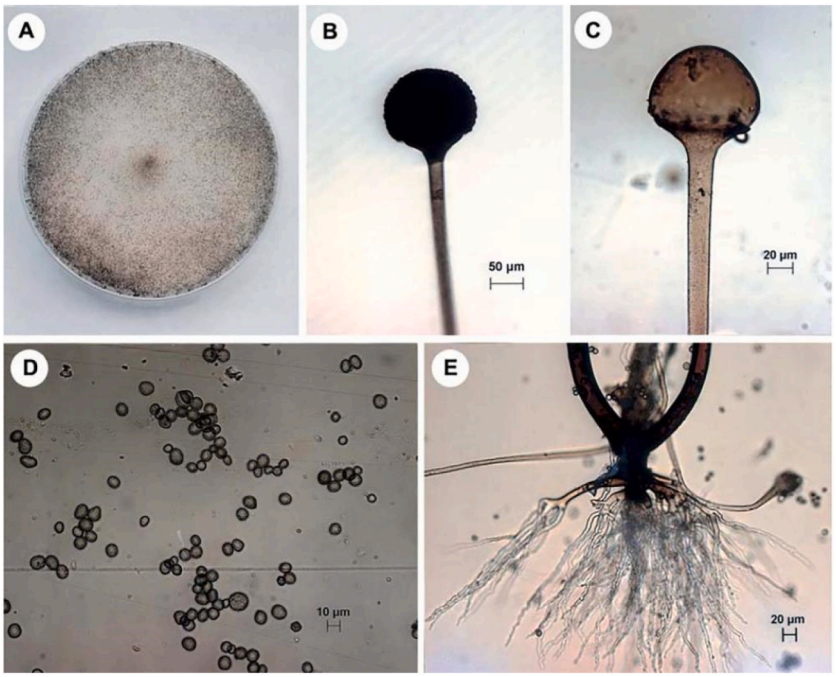

Fig. 1. Morphological characteristics of *Rhizopus stolonifer* (A: Mycelial growth on PDA after 48 h incubation, B: Sporangium and sporangiophore, C: Columella, D: Sporangiospores, E: Rhizoids and stolons) [10].

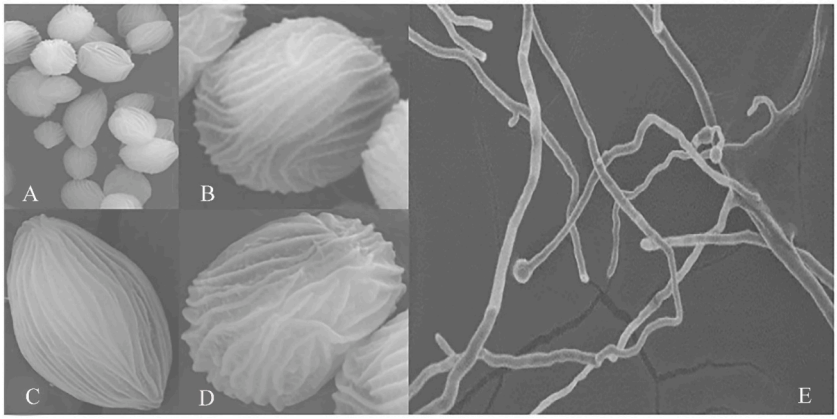

Fig. 2. Morphology of spores and hyphae under SEM (A, B:30 KV 2000x, C:5000x, D:10000x, E:100 μm) [1,11].

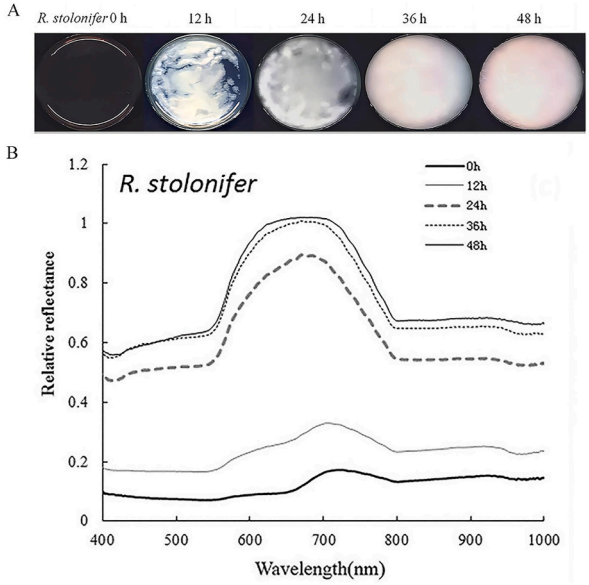

Fig. 3. Spectral characteristics of *Rhizopus stolonifer* (A: Typical hyperspectral RGB images, B: Average original spectra) [12].

determine the damage degree of *Rhizopus stolonifer* on apples and combined different modeling methods with various pretreatment and dimensionality reduction methods to construct models, and the accuracy of the determinations were all over 90 %, which provided a new, rapid and accurate identification method for postharvest fungal hazards of agricultural products.

2.2. Pathogenicity of Rhizopus stolonifer on hosts

Rhizopus stolonifer has high activity, wide range of existence and strong aggressiveness. It can infect a wide variety of hosts, including cherry tomato [16], strawberry [17], grape [18], peach [19], sweet cheery [20], sweet potato [11] and other fruits and vegetables. *Rhizopus stolonifer* is a saprophytic fungus that can survive in a wide range of temperature and humidity, with an optimum temperature of 25 °C [21]. The fruit diseases usually caused by *Rhizopus stolonifer* are known as soft rot, black mold and Rhizopus rot. When the fruit is infected, the infection area is first soaked, and then becomes soft and rotten. The initial symptoms appear approximately one day after infection under appropriate temperature and humidity. Rapidly growing and abundant mycelium are observed on the surface of the fruit and cover the affected part by producing clusters of fibrous gray sporangia. The infected tissue is eventually decomposed into water-like decay, and its longitudinal section becomes very soft and slowly decays. And after about 2–3 days, the infected fruit may release juice with fermented or acidic odor [10]. The hosts of *Rhizopus stolonifer* and main symptoms are summarized in Table 1.

Table 1
Hosts of *Rhizopus stolonifer* and the main symptoms.

Hosts	Pictures	Symptoms	References
Squash (*Cucurbita moschata*)	–	The lesion began with water-soaked, rapidly softened, and then the area gradually expanded	[22]
Papaya (*Carica papaya* L.)	–	The edge of the water-immersed lesion spread irregularly. At the later stage, the lesions increased, white hyphae grew, the color darkened, the fruit collapsed, and sometimes the smell was unpleasant	[23]
Citrus fruit	–	The lesion was water-immersed and rapidly softened	[24]
Sweet potato (*Dioscorea esculenta* (Lour.) Burkill)		Softened and watery decayed of the whole root	[25]
Tomato (*Solanum lycopersicum* L.)		Wound tissue softened, skin broke and fluid was constantly exuded	[26]
Cherry tomato (*Lycopersicon esculentum* var. *cerasiforme* A. Gray)		The infection site was first water-soaked and then softened. The mycelium did not grow out from the infection, and the infected tissue was finally decomposed in a water-decayed manner	[18]
Loquat (*Eriobotrya japonica*)	–	Irregular dark brown water immersion damage	[27]
Pear (*Pyrus serntina*)		The infection site was first water-soaked, and then quickly softened and decayed. White hyphae grew from the infection site and covered the infection site by producing gray sporangia	[10]
Jackfruit (*Artocarpus heterophyllus*)		The fruit was black, rotten, shrunk, and sometimes dried	[28]
Grape (*Vitis vinifera* L.)	–	The juice of the infection site exuded and quickly decayed	[29]
Strawberry (*Fragaria* × *ananassa* Duch.)		Tissue severely decayed; juice released	[30]

2.3. Infection mechanism of *Rhizopus stolonifer*

Infection mechanism of *Rhizopus stolonifer* on fruit is demonstrated in Fig. 4. The spores and mycelia of *Rhizopus stolonifer* typically invade and spread rapidly through the wound of the fruit when the temperature is higher than 5 °C, and the infection symptoms appear after 24 h–48 h. *Rhizopus stolonifer* spores release several amino acids, enzymes and other proteins during germination, and these enzymes include polygalacturonase and pectin methylesterase. *Rhizopus stolonifer* spores use polygalacturonase and pectin methylesterase produced during germination to invade host injured tissues, rapidly digest host cell wall components, cause tissue cell

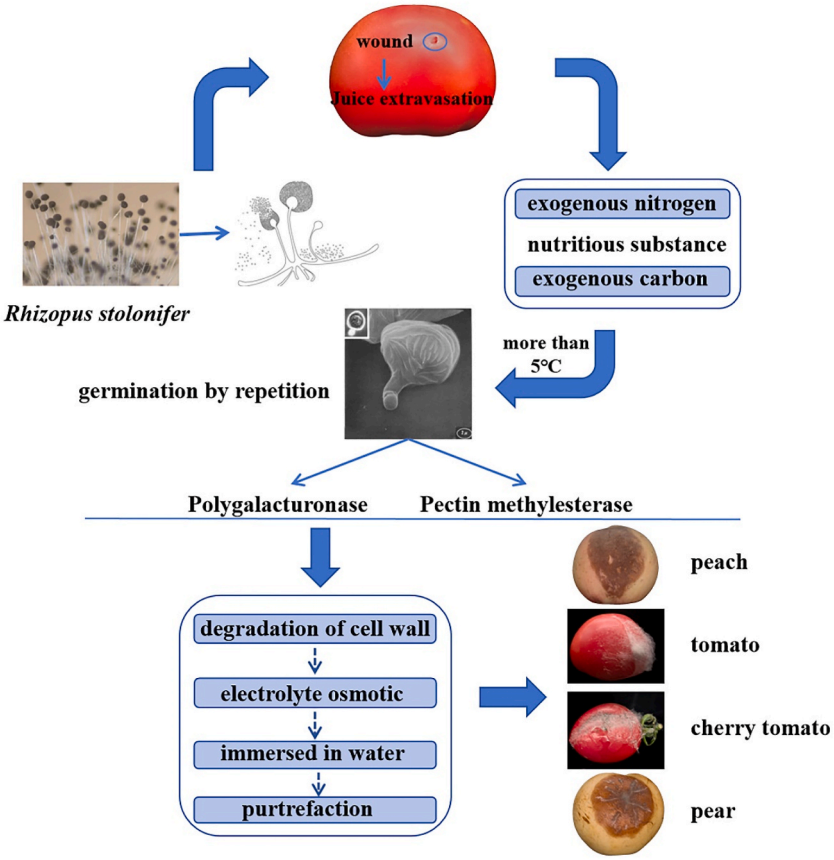

Fig. 4. Probable infection mechanism of *Rhizopus stolonifer* on fruit.

electrolyte extravasation, and decay [31]. The germination of spores requires certain nutrients. *Rhizopus stolonifer* cannot germinate when it lacks certain nutrients in the spore suspension, which may be due to the fact that spores contain insufficient endogenous carbon to germinate. Whereas, when sufficient exogenous carbon and nitrogen are available, the spores will germinate to produce infectious mycelia after 3–5 h. At present, it is generally believed that *Rhizopus stolonifer* can only penetrate the host tissue through fresh wounds, minimally invasive wounds and mechanical damage caused during harvesting and processing. However, it has also been reported that *Rhizopus stolonifer* successfully infected tomato and peach fruits without surface damage. Baggio et al. [32] found that when spores germinate in external nutrient supply, *Rhizopus stolonifer* can directly infect fruits without wounds. The incidence of uninjured fruits inoculated with *Rhizopus stolonifer* in nutrient solution is as high as that of fruits inoculated directly after injury. In addition, researchers have found that adding peach juice to the spore suspension of *Rhizopus stolonifer* could promote pathogen growth and nectarine infection. This indicates that the juice released from the wound can make the spores of *Rhizopus stolonifer* germinate, and then produce pectin esterase to destroy the fruit tissue.

Usually, when the temperature is higher than 5 °C, *Rhizopus stolonifer* can penetrate the healthy fruit placed next to the diseased fruit through its stolons. Baggio et al. [33] studied the spatiotemporal analyses of Rhizopus rot progress in peach fruit inoculated with *Rhizopus stolonifer*. It was found that the peach fruits inoculated with *Rhizopus stolonifer* spore suspension were infected, and almost all the surrounding uninoculated fruits were gradually infected. Furthermore, the rate of disease infection increased over time, which may be related to the shortening of the incubation period of the disease, which may be the result of the efficiency of pathogen infection and colonization, or may be related to maturity. As the fruit matures, its nutrient contents increase, but it also becomes more susceptible to pathogen infection and colonization. Petrasch et al. [34] investigated the ability of *Rhizopus stolonifer* to infect mature and immature tomatoes, and confirmed that *Rhizopus stolonifer* could not infect immature fruits and required the host tissue to undergo a specific maturation process to cause disease. In addition, the infection ability of *Rhizopus stolonifer* may also be related to the fruit harvest season. It is reported that strawberry harvested in late season is more susceptible to *Rhizopus stolonifer* infection than early season strawberry, indicating that late season fruit may be more susceptible to pathogen infection.

3. Control strategies of *Rhizopus stolonifer*

3.1. Physical control

Physical control methods are commonly as fungistatic compositions used for fungal inhibition in food with low energy consumption, high efficiency and no secondary pollution. Physical control methods include low temperature storage, irradiation treatment, heat treatment, ozone treatment, ultrasonic treatment, microwave treatment, etc. The inhibition effects of some physical control methods on *Rhizopus stolonifer* are summarized in Table 2.

Physical control methods are one-time sterilization, which have strong effect on pathogens and will not produce resistance. During the treatment process, no chemical substances are added, which has no side effect on the environment, and the sterilization conditions are easy to control, the operation is simple, and the influence of the external environment is small. However, the control strength of the physical control methods is limited and does not have universal applicability. It needs to be combined with other technologies to achieve better control effect on *Rhizopus stolonifer*. It has been reported that the use of 0.6 kGy gamma-ray irradiation can reduce the occurrence of sweet potato Rhizopus soft rot, and the effect is significantly enhanced after combined treatment with 10 mg L^{-1} sodium dichlorocyanisourate [25]. However, irradiation has not been used on a large scale in the production process because of its high cost and the fact that many consumers do not accept irradiated products, even though irradiation has the advantages of significant fungicidal effect, no contamination, no residues, etc. In addition, Zhao et al. [40] found that the infection rate of *Rhizopus stolonifer* was 46 % after heat treatment at 38 °C for 24 h and storage for 7 days. However, heat treatment combined with *Pichia guilliermondii* could

Table 2
Inhibitory effect of physical methods to control *Rhizopus stolonifer*.

Physical control method	Treatment	Effect	Feature	References
Low-temperature storage	Stored at-1 °C, 0 °C, 3 °C for 3 weeks	The viability of 'non-dormant' spores decreased rapidly at −1 °C and 0 °C, and decreased significantly at 3 °C	It can inhibit the physiological metabolism of fruit, delay senescence, and reduce disease by inhibiting the growth of pathogenic fungi. It is easy to operate but not enough to control	[35]
	The fruits were stored at 35 °C for 1h and then cooled at 2 ± 0.5 °C and 85 %–95 % relative humidity	The decay rate of fruits was reduced by 15 %, and the severity was reduced by 29 %		[36]
Irradiation treatment	UV irradiation at a wavelength of 360 nm for 6 min	It inhibited mycelial growth, reduced fruit infection rate and maintained fruit quality	It can inhibit its physiological metabolic activities, reduce the production of ethylene, and eliminate pathogenic microorganisms in fruits and vegetables. The sterilization effect is remarkable and the dose can be adjusted	[37]
	UV-C (3.6 kJ $m^{-2)}$ irradiation at a wavelength of 254 nm for 5 min	The treated tomato had resistance to polygalacturonase secreted by *Rhizopus stolonifer*, delayed tomato senescence and reduced the incidence of soft rot		[38]
	LED irradiation at a wavelength of 405 nm, light intensity was 2.68 ± 0.5 mW cm^{-2}	The antifungal effect on *Rhizopus stolonifer* after 12 days of illumination was 3.4 log CFU g^{-1}		[39]
	Gamma irradiation (0.6 kGy) + sodium dichloroisocyanurate (10 mg L^{-1})	It inhibited the spore germination of *Rhizopus stolonifer* and reduced the incidence of Rhizopus soft rot of sweet potato		[25]
Heat treatment	38 °C for 24 h	It significantly inhibited mycelium growth and spore germination of *Rhizopus stolstonifer*, and thus prevented postharvest fungal rot of cherry tomato	It is economical, efficient and convenient to use heat to kill or inhibit pathogenic microorganisms on fruit and vegetables. However, when pathogen contamination occurs after heating, heat treatment has little effect	[40]
	55 °C hot water treatment + ultrasonic (500 W, 10 min)	It inhibited mycelial growth, induced intracellular and protein leakage, changed the ultrastructure and mycelial morphology of *Rhizopus stolonifer*, and reduced the degree of Rhizopus soft rot of sweet potato		[41]
Ozone treatment	The supply rate was 8 mg min^{-1}, the air flow rate was 500 mL min^{-1}	Ozone treatment for 20 min can induce phytoalexins, significantly inhibit fungal decay caused by *Rhizopus stolonifer*, and reduce the microbial community on the berry surface	Ozone can oxidize microbial cells and cause their death. Membrane components are the main targets of ozone, and they will be decomposed into oxygen after use, which is pollution-free	[42]
Ultrasonic treatment	Ultrasound (500 W, 55 °C, 10 min) + acidic electrolyzed water (available chlorine concentration 50 mg L^{-1})	Significantly inhibited spore germination and germ tube elongation of *Rhizopus stolonifer*	This method is simple, safe and efficient to destroy the cell wall, cell membrane and DNA of microorganism	[11]
Microwave treatment	Microwave (0.45 kW, 2 min) + *Cryptococcus laurentii* (1×10^8 CFU mL^{-1})	The growth of *Rhizopus stolonifer* was inhibited, and the fruit decay rate was reduced by 71.3 % compared with the control	It has a certain fungicidal effect by producing heat to reduce the physiological and biochemical effects of the fruit. Its energy consumption is low and the operation is simple	[43]

Table 3
Inhibitory effect of chemical control methods on *Rhizopus stolonifer*.

Chemical control method	Treatment	Effect	Feature	References
Fungicide	Botran 75WP (1.2 g L^{-1}) impregnation 30 s	Compared with the control, the incidence of sweet potato Rhizopus soft rot can be reduced by 43.3 %	It has wide sterilization range, quick effect and cost saving, but it is easy to make pathogenic fungi produce drug resistance	[44]
	Available chlorine atmosphere (20 mg L^{-1})	It can inhibit the growth of *Rhizopus stolonifer* and reduce the incidence of strawberry Rhizopus soft rot		[45]
	Free chlorine (30 mg L^{-1})	Killed the spores of *Rhizopus stolonifer* and reduced the rot rate of tomato by 50 %		[46]
	Boscalid + Pyraclostrobin (9.1, 18.1, 36.3, and 72.5 oz per 100 gal of water, Pristine 38WG)	It can significantly inhibit the Rhizopus soft rot of sweet potato and reduce the rot rate by more than 85 %		[47]
Calcium chloride ($CaCl_2$)	$CaCl_2$ (2 % w/v) + Yeast antagonists (*Candida guilliermondii*, *Pichia membranefaciens*, 5×10^8 CFU mL^{-1})	The spore germination rate and germ tube length were reduced, the growth of *Rhizopus stolonifer* was completely inhibited, and the incidence of peach Rhizopus soft rot was reduced	Inhibition of fungal pathogens by direct inhibition of spore germination and growth is non-toxic, harmless, safe and long-lasting	[48]
	$CaCl_2$ (20 g L^{-1}) + lemongrass oil (1.5 mL L^{-1})	The growth of *Rhizopus stolonifer* was inhibited, and the incidence and severity of fruit were reduced by 80 % and 82 %, respectively		[49]
	$CaCl_2$ (2 %)	The colony diameter was 8.5, and the inhibition rate was 90.44 %		[50]
Salicylic acid (SA)	SA (100 μg mL^{-1}) + *Rhodotorula glutinis* (1×10^8 CFU mL^{-1})	It significantly inhibited the incidence and lesion diameter of strawberry Rhizopus soft rot, inhibited spore germination and induced host defense enzymes	As a signal transduction molecule, can activate defense mechanisms when attacked by pathogens, which is economical and efficient	[51]
	SA (MIC: 0.33 g L^{-1}) + thymol (MIC: 0.17 g L^{-1})	It destroyed the cell membrane of *Rhizopus stolonifer*, released nucleic acid and protein, caused mitochondrial dysfunction, and increased the activity of tomato defense enzymes		[52]
	SA (2 mM) + chitosan (0.5 %) + methyl jasmonate (0.01 mM)	The mycelial growth and spore germination of *Rhizopus stolonifer* were completely inhibited, and the morphology of mycelia and spores was destroyed		[53]
Peroxyacetic acid (PAA)	PAA (250 mg L^{-1})	The incidence of soft rot of sweet cherries, apricots, peaches and nectarines caused by *Rhizopus stolonifer* was reduced, and the treatment effect was related to the soaking time	Its decomposition products are acetic acid, water and oxygen, which are harmless to the environment	[54]
Nanomaterial	CuO nanomaterial (50 mg L^{-1})	Reduced the severity of sweet potato Rhizopus soft rot and plaque diameter	It is a non-antibiotic fungicide with high thermal stability, biodegradability and non-toxicity	[55]
	ZnO nanoparticles (300 mg L^{-1})	It showed antifungal activity against *Rhizopus stolonifer* and inhibited the occurrence of Rhizopus soft rot of sweet potato		[56]

reduce the infection rate to 8 %. Most physical control methods require complex equipment, high investment and footprint, and some methods can negatively affect the sensory quality of the fruit, which severely limits their promotion and application in the industry.

3.2. Chemical control

Chemical control methods have wide range of effects and obvious effects, which are commonly used fruit postharvest management strategy. Chemical control methods include fungicides, calcium chloride, salicylic acid, peracetic acid, nanomaterials, etc. The inhibition effects of some chemical control methods on *Rhizopus stolonifer* are listed in Table 3.

Chemical control methods are effective, low-cost, and easy to implement, which has led to their widespread use in postharvest preservation of fruits and vegetables. But the use of chemicals such as fungicides has been controversial [57]. The use of chemical control methods may lead to the residue of some chemical substances, which poses a certain threat to human health and the environment. Meanwhile, excessive use of chemical fungicides may make pathogens resistant, which is one of the reasons why consumers are difficult to accept [58]. Several chemical control methods require coating. Certain fruit and vegetables with rough surfaces hinder the formation of a consistent and durable film by some reagents, thus hastening the spoilage process. Therefore, it is necessary to find a safer and more effective alternative method to control the infection of *Rhizopus stolonifer* in postharvest fruits.

Table 4
Inhibitory effect of plant volatile compounds on *Rhizopus stolonifer*.

Name	Concentration	Main chemical components	Effect	References
Clove essential oil (*Syzygium aromaticum* (L.) Merr. & Perr.)	200 μL mL^{-1}, complete suppression	Eugenol (79.4 %), Eugenylacetate (9.2 %), Isocaryophyllene (7 %)	Significantly inhibited the mycelial growth and spore germination of *Rhizopus stolonifer* in a dose-dependent manner	[69]
Origanum vulgare L. essential oil	MIC:10 μL mL^{-1}	Carvacrol (66.01 %), Linalool (5.17 %), Thymol (3.51 %), o-cymene (3.03 %), γ-terpinen (2.54 %), Borneol (2.53 %)	It inhibited spore germination, caused morphological changes of spores and mycelium, and significantly reduced the infection rate of fruit	[18]
Mentha spicata L. essential oil	MIC:5 μL mL^{-1} MFC: 10 μL mL^{-1}	Carvone (61.71 %), Limonene (20.22 %), 1,8-cineole (5 %), Sabinene (2.28 %), *Cis*-dihydrocarvone (1.63 %), α-thujene (1.4 %)	95 % of spore germination was inhibited and effectively reduced the severity and incidence of *Rhizopus stolonifer* infection	[70]
Fennel essential oil (*Foeniculum vulgare Mill.*)	800 μL mL^{-1}, complete suppression	Anethole (75.15 %), Fenchone (9.37 %)	The growth and spore germination of *Rhizopus stolonifer* were inhibited in a dose-dependent manner	[71]
Eucalyptus staigeriana F. Muell. ex Bailey essential oil	1.5 μL mL^{-1}	Limonene (14.93 %), α-thujene (11.22 %), Geraniol (8.34 %)	It acted on the cell wall and cell membrane, changing the structure of mycelium, causing the mycelium to dehydration and rupture	[72]
Citrus sinensis (lima orange) essential oil	100 μL mL^{-1}	Limonene (95.2 %)	Inhibition of mycelial growth of *Rhizopus stolonifer* in a dose-dependent manner	[73]
Satureja richingeri essential oil	500 μL L^{-1}	Carvacrol (87.0 %), G-terpinene (4.7 %), P-cymene (1.7 %), Linalool (1.4 %), Limonene (1.2 %), B-bisabolene (1.2 %), Terpinen-4-ol (1.0 %)	It had a significant inhibitory effect on spore germination and mycelial growth of *Rhizopus stolonifer*, and mycelium was more sensitive than spores	[74]
Cymbopogon citratus (Dc. Ex Nees) essential oil	MIC: 5 μL mL^{-1}	Monoterpenes geranial (β-citral isomer) (29.2 %), Neral (α-citral isomer) (27.0 %)	It inhibited spore germination and mycelial growth by affecting the integrity of the spore plasma membrane	[75]
Rosmarinus officinalis L. essential oil	1000 μL L^{-1}	Camphor (15.1 %), Verbenone (14.3 %), α-pinene (13.6 %), 1,8-cineole (11.8 %)	It showed 100 % antifungal activity against *Rhizopus stolonifer* and reduced fruit decay rate	[76]
Sweet basil essential oil	30 μL 400 mL^{-1} air space	Linalool (55.78 %), Eugenol (12.15 %), 1,8-Cineol (10.26 %), Methyl eugenol (3.79 %)	It showed antifungal activity against *Rhizopus stolonifer*	[77]
Geranium essential oil	0.12 % (v/w)	D-limonene (45.10 %), β-pinene (20.50 %), γ-terpinene (10.59 %)	It inhibited the growth of *Rhizopus stolonifer* and reduced the incidence of papaya decay by 40 %	[78]

3.3. Biological control

3.3.1. Natural extracts

Attention is increasingly focused on the use of natural extracts to control postharvest decay in fruits and vegetables. Chitosan and Tea polyphenols have been reported more frequently.

Chitosan is a deacetylated derivative of chitin with positive charge, which gives it unique physiological and biological properties for fighting against fungi, bacteria and viruses [59]. Different molecular weights of chitosan have different effects on *Rhizopus stolonifer*. Low molecular weight chitosan had a certain inhibitory effect on mycelial growth, medium molecular weight chitosan had a major effect on the release of protein, which increased, while high molecular weight chitosan had an effect on spore morphology and germination [60,61]. In addition, studies have found that chitosan can affect the membrane permeability of *Rhizopus stolonifer*, resulting in an increase in extracellular pH and inhibition of H^+-ATPase activity [62,63]. Chitosan, however, has limitations such as poor solubility in water, solubility in acetic acid, as well as inadequate stability and mechanical properties, which restrict its commercial applications [64,65].

Tea polyphenols are a complex of phenolic compounds in tea, which have antioxidant, fungicidal and antiviral effects, and are widely used in food and pharmaceutical industries. Yang and Jiang [66] found that tea polyphenols can interfere with the synthesis of the cell wall of *Rhizopus stolonifer*, destroy the plasma membrane, cause the lysis of mycelia and spores, inhibit the growth of mycelia and the germination of spores in a dose-dependent manner, and control the soft rot of nectarine fruit by inducing antifungal activity and defense enzyme activity.

3.3.2. Plant volatile compounds (VOCs)

Plant essential oil are natural and volatile aromatic compounds, which is a secondary metabolite obtained from different plant organs. Due to their biological properties, especially antifungal properties, there is potential to preserve products as an alternative to many traditional antifungal agents. Oliveira et al. [67] used several essential oils combined with hydroxymethyl cellulose to control *Rhizopus stolonifer* in strawberry. Among them, 125 μL L^{-1} *Lippia sidoides* essential oil can completely inhibit the mycelial growth of *Rhizopus stolonifer*, resulting in morphological degradation, severe damage to plasma membrane and intracellular components, manifested as blurred intracellular organelles and loss of cytoskeleton, indicating that it has high antifungal activity in a dose-dependent manner. Phyo et al. [68] found that thymol and cinnamaldehyde have a synergistic effect. 2MIC (minimum inhibitory

Table 5
Inhibitory effects of microorganisms and their secondary secretions on *Rhizopus stolonifer*.

Name	Source	Concentration	Effect	References
Pichia guilliermondii	China Center of Industrial Culture Collection (CICC No. 32333)	1×10^8 CFU mL^{-1}	The incidence of peach can be reduced by more than 50 % by activating the activities of defense-related enzymes, destroying the formation of cell wall structure, increasing energy supply, activating energy metabolism and improving disease resistance	[19]
Debaryomyce hansenii	China Typical Culture Collection (CCTCC M 2021610 Y3)	$1x10^8$ cells mL^{-1}	The spore germination rate and germ tube length of *Rhizopus stolonifer* were reduced, and the activity of related defense enzymes in fruits was induced	[82]
Cryptococcus laurentii	Pear	1×10^8 CFU mL^{-1}	The spore germination was inhibited, and the natural decay rate was reduced by 70 %	[83]
Bacillus cereus AR156	College of Plant Protection, Nanjing Agricultural University, China	1×10^8 CFU mL^{-1}	It can reduce the incidence and lesion diameter by 38.6 % and 21.0 % respectively after two days of inoculation, and enhance the antioxidant activity of peach by initiating defense response	[84]
Bacillomycin D	*Bacillus subtilis* fmbj, (CGMCC No.0943)	50 mg L^{-1}	It inhibited mycelial growth and spore germination, destroyed spore plasma membrane structure and enhanced fruit resistance	[16]
Fengycin	*Bacillus subtilis* fmbj, (CGMCC No.0943)	50 μg mL^{-1}	Inhibition of mycelial growth and spore germination, resulting in protein and nucleic acid leakage, and low concentration induced apoptosis, high concentration induced cell necrosis	[85]
Iturin A	*Bacillus amyloliquefaciens* LZ-5	512 μg mL^{-1}	It inhibited mycelial growth and spore germination, destroyed cell integrity, improved fruit resistance, and reduced the incidence of soft rot	[86]
Bacteriocin LF-1	*Lactobacillus plantarum*	20 %	The spore germination of *Rhizopus stolonifer* was significantly inhibited. Compared with the control, the spore germination rate was reduced by 64.7 %, and the decay rate of strawberry was reduced	[87]

concentration) thymol-cinnamaldehyde can completely inhibit the germination of *Rhizopus stolonifer* spores, change the cell membrane permeability, destroy the cell structure, inhibit the growth of mycelium, and thus play an antifungal role. The inhibitory effects of other plant volatiles on *Rhizopus stolonifer* are shown in Table 4.

Plant essential oils have the advantages of green, pollution-free and high safety, but the process of extraction is complicated, and some of them are expensive and difficult to be applied in large quantities. In addition, the antifungal components of some plant essential oils are unknown, most of which are still in the laboratory research stage and cannot be applied in practice.

3.3.3. Microorganisms and their secondary secretions

Microbial control methods refer to that microorganisms inhibit or kill pathogenic fungi by producing some active substances or competing with pathogenic fungi for nutrients. This kind of method has the advantages of not polluting the environment and not producing drug resistance, and has become a research hotspot in recent years. Zhang et al. [79] found that the volatile organic compounds produced by *Bacillus siamensis* G-3 had a significant control effect of 89.4 % on the postharvest diseases of raspberries caused by *Rhizopus stolonifer*. *Pichia Caribbica* can compete with *Rhizopus stolonifer* for space and nutrition, and induce the activities of defense-related enzymes such as peroxidase (POD), catalase (CAT) and phenylalanine ammonia lyase (PAL) in peach to enhance resistance [80]. In addition, Bonaterra et al. [81] found that *Pantoea agglomerans* EPS125 significantly reduced the incidence and lesion diameter of soft rot in peach, nectarine, apricot and other fruits by direct interaction with *Rhizopus stolonifer* cells. At the medium concentration, the strain EPS125 was highly effective in controlling *Rhizopus stolonifer*, and the control efficiency of soft rot caused by *Rhizopus stolonifer* was between 49 % and 61 %. The inhibitory effects of other microorganisms and their secondary secretions on *Rhizopus stolonifer* are shown in Table 5.

Microbial control, while promising, is not without its limitations in practical applications. The antifungal effect of microorganisms is contingent upon their growth state, leading to variability in efficacy. Furthermore, there exist challenges related to biosafety concerns and the requirement for commercial registration. These factors collectively hinder the large-scale utilization of microbial control methods in real-world production settings.

4. Conclusion and prospect

Fungal diseases caused by *Rhizopus stolonifer* have posed a serious threat to the postharvest storage of fruit worldwide. For fungal diseases, most of them still rely on chemical fungicides. However, chemical fungicides can cause environmental pollution, chemical residues, and drug resistance of pathogens, they pose a serious threat to humans and the environment. Therefore, people have gradually shifted their attention to safe and pollution-free biological control. Although there are many studies on essential oils and microbial antagonists used to control *Rhizopus stolonifer*, most of them are difficult to put into practical application due to insufficient control effect, high cost and immature technology.

In the future, the research on *Rhizopus stolonifer* and its prevention and control technology also needs to pay attention to the following aspects: (1) Multidimensional research on enzymatic, metabolic and infection mechanisms of *Rhizopus stolonifer* to provide a theoretical basis for further exploration and instructions for prevention and control strategies; (2) On the basis of effective *in vivo* and *in vitro* experiments, new natural antifungal products that can be used for commercial are developed; (3) Explore the mechanism of action of various control strategies on *Rhizopus stolonifer*, and provide guidance for its future application as a safe control technology; (4) In view of the different stages of *Rhizopus stolonifer* infection, natural antifungal agents were combined with other technologies to develop antifungal methods that can be applied to actual production and achieve commercial scale.

Data availability statement

No data was used for the research described in the article.

Ethics statement

Review and/or approval by an ethics committee was not needed for this study because [This work is a review of the literature and does not address the ethical considerations of animal and human experimentation.].

CRediT authorship contribution statement

Qianqian Liu: Writing – original draft, Methodology, Formal analysis, Conceptualization. **Qingmin Chen:** Methodology, Funding acquisition, Data curation. **Hu Liu:** Formal analysis. **Yamin Du:** Writing – review & editing. **Wenxiao Jiao:** Writing – review & editing. **Fei Sun:** Writing – review & editing, Supervision, Methodology. **Maorun Fu:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

[1] S. Bautista-Baños, M.G. Velaquez-Del Valle, A.N. Hernandez-Lauzardoa, E.A. Barka, The *Rhizopus Stolonifer*-Tomato Interaction, Plant-Microbe Interactions, 2008, pp. 269–289.
[2] S. Bautista-Baños, E. Bosquez-Molina, L.L. Barrera-Necha, Chapter 1 - *Rhizopus stolonifer* (soft rot), in: S. Bautista-Baños (Ed.), Postharvest Decay, 2014, pp. 1–44, https://doi.org/10.1016/B978-0-12-411552-1.00001-6.
[3] R.I. Ventura-Aguilar, E.P. Díaz-Galindo, S. Bautista-Baños, S. Mendoza-Acevedo, J.E. Munguía-Cervantes, Z.N. Correa-Pacheco, E. Bosquez-Molina, Monitoring the infection process of *Rhizopus stolonifer* on strawberry fruit during storage using films based on chitosan/polyvinyl alcohol/polyvinylpyrrolidone and plant extracts, Int. J. Biol. Macromol. 182 (2021) 583–594, https://doi.org/10.1016/j.ijbiomac.2021.03.187.
[4] M.J. Ceponis, J.E. Butterfield, Losses in fresh tomatoes at the retail and consumer levels in the greater new york area, J. Am. Soc. Hortic. Sci. 104 (1979) 751–754, https://doi.org/10.21273/JASHS.104.6.751.
[5] L. Alfaro-Sifuentes, M. Juan, D.E. Meca, M.A. Elorrieta, J.L. Valenzuela, Effectiveness of chemical and thermal treatments on control *Rhizopus Stolonifer* fruit infection comparing tomato cultivars with different sensitivities to cracking, Int. J. Environ. Res. Publ. Health 16 (2019) 2754, https://doi.org/10.3390/ijerph16152754.
[6] F. Hahn, *Rhizopus stolonifer* detection by sensing the tomato peduncle scar, Biosyst. Eng. 95 (2006) 171–179, https://doi.org/10.1016/j.biosystemseng.2006.06.010.
[7] R.R. Stange, S.L. Midland, G.J. Holmes, J.J. Sims, R.T. Mayer, Constituents from the periderm and outer cortex of *Ipomoea batatas* with antifungal activity against *Rhizopus stolonifer*, Postharvest Biol. Technol. 23 (2001) 85–92, https://doi.org/10.1016/S0925-5214(01)00105-3.
[8] L. Li, H. Sun, M. Zhang, T. Mu, Exploring the potential in postharvest preservation of sweet potato: 2-Methylbutanoic acid, isobutyric acid, perillaldehyde and salicylaldehyde, to control *Rhizopus stolonifer*, Postharvest Biol. Technol. 210 (2024) 112785, https://doi.org/10.1016/j.postharvbio.2024.112785.
[9] H. Du, X. Sun, X. Bian, W. Zhang, J. Xie, Z. Zhu, Y. Wen, pH and amylase dual stimuli-responsive electrospinning membrane for smart releasing thymol to control melon *Rhizopus stolonifer*, Chem. Eng. J. 471 (2023) 144473, https://doi.org/10.1016/j.cej.2023.144473.
[10] J. Kwon, C. Lee, Rhizopus soft rot on pear (*Pyrus serotina*) caused by *Rhizopus stolonifer* in korea, MYCOBIOLOGY 34 (2006) 151–153, https://doi.org/10.4489/MYCO.2006.34.3.151.
[11] L. Li, T. Mu, M. Zhang, Contribution of ultrasound and slightly acid electrolytic water combination on inactivating *Rhizopus stolonifer* in sweet potato, Ultrason. Sonochem. 73 (2021) 105528, https://doi.org/10.1016/j.ultsonch.2021.105528.
[12] Y. Sun, X. Gu, Z. Wang, Y. Huang, Y. Wei, M. Zhang, K. Tu, L. Pan, Growth simulation and discrimination of *Botrytis cinerea, Rhizopus stolonifer* and *Colletotrichum acutatum* using hyperspectral reflectance imaging, PLoS One 10 (2015) e143400, https://doi.org/10.1371/journal.pone.0143400.
[13] F. Hahn, I. Lopez, G. Hernandez, Spectral detection and neural network discrimination of *Rhizopus Stolonifer* spores on red tomatoes, Biosyst. Eng. 89 (2004) 93–99, https://doi.org/10.1016/j.biosystemseng.2004.02.012.
[14] G. Zhu, S. Zheng, Q. Xu, M. Qiu, H. Wang, S. Weng, Detection of fungal infection in apple using hyperspectral transformation of RGB images with kernel regression, Postharvest Biol. Technol. 206 (2023) 112570, https://doi.org/10.1016/j.postharvbio.2023.112570.
[15] S. Liao, Y. Wu, X. Hu, S. Weng, Y. Hu, L. Zheng, Y. Lei, L. Tang, J. Wang, H. Wang, M. Qiu, Detection of apple fruit damages through Raman spectroscopy with cascade forest, Spectrochi, Acta Part A Mol. Biomol. Spectrosc. 296 (2023) 122668, https://doi.org/10.1016/j.saa.2023.122668.
[16] F. Lin, Y. Xue, Z. Huang, M. Jiang, F. Lu, X. Bie, S. Miao, Z. Lu, Bacillomycin D inhibits growth of *Rhizopus stolonifer* and induces defense-related mechanism in cherry tomato, Appl. Microbiol. Biotechnol. 103 (2019) 7663–7674, https://doi.org/10.1007/s00253-019-09991-w.
[17] V. Ghate, I. Yew, W. Zhou, H. Yuk, Influence of temperature and relative humidity on the antifungal effect of 405 nm LEDs against *Botrytis cinerea* and *Rhizopus stolonifer* and their inactivation on strawberries and tomatoes, Int. J. Food Microbiol. 359 (2021) 109427, https://doi.org/10.1016/j.ijfoodmicro.2021.109427.
[18] N.S.T. Dos Santos, A.J.A. Athayde Aguiar, C.E.V. de Oliveira, C. Veríssimo De Sales, S. de Melo E Silva, R. Sousa Da Silva, T.C.M. Stamford, E. L de Souza, Efficacy of the application of a coating composed of chitosan and *Origanum vulgare* L. essential oil to control *Rhizopus stolonifer* and *Aspergillus niger* in grapes (*Vitis labrusca* L.), Food Microbiol. 32 (2012) 345–353, https://doi.org/10.1016/j.fm.2012.07.014.
[19] C. Li, K. Wang, Y. Zou, C. Lei, Z. Chen, Y. Zheng, Extracellular self-DNA induced a PTI-related local defence against Rhizopus rot in postharvest peach fruit, Postharvest Biol. Technol. 200 (2023) 112306, https://doi.org/10.1016/j.postharvbio.2023.112306.
[20] G. Qin, S. Tian, Y. Xu, Biocontrol of postharvest diseases on sweet cherries by four antagonistic yeasts in different storage conditions, Postharvest Biol. Technol. 31 (2004) 51–58, https://doi.org/10.1016/S0925-5214(03)00130-3.
[21] J. Kwon, S. Kang, J. Kim, C. Park, Rhizopus soft rot on cherry tomato caused by *Rhizopus stolonifer* in Korea, MYCOBIOLOGY 29 (2001) 176–178, https://doi.org/10.1080/12298093.2001.12015783.
[22] J.H. Kwon, S.W. Kang, C.S. Park, Occurrence of rhizopus soft rot on squash (*Cucurbita moschata*) caused by *Rhizopus stolonifer* in korea, Plant Pathol. J. 16 (2000) 321–324.
[23] P. Singh, A.K. Mishra, N. Tripathi, Assessment of mycoflora associated with postharvest losses of papaya fruits, Int. J. Agric. Technol. 8 (2012) 961–968.
[24] J.H. Kwon, C. Park, Rhizopus soft rot on citrus fruit caused by *Rhizopus stolonifer* in Korea, Korean J. Mycol. 30 (2002) 166–169, https://doi.org/10.4489/KJM.2002.30.2.166.
[25] J. Jeong, M. Yoon, K. Lee, K. Jung, H. Kim, H. Park, R. Jeong, Effect of the combined treatment with gamma irradiation and sodium dichloroisocyanurate on postharvest Rhizopus soft rot of sweet potato, J. Plant Dis. Prot. 121 (2014) 243–249, https://doi.org/10.1007/BF03356519.
[26] C. Zambrano, G. Moreno, L. Sequeda-Castañeda, A. García-Caicedo, D. Albarracín, L. Barreto-Charry, Determining the effectiveness of *Candida guilliermondii* in the biological control of *Rhizopus stolonifer* in postharvest tomatoes, Univ. Sci. 19 (2014) 51–62, https://doi.org/10.11144/Javeriana.SC19-1.debc.
[27] N.A. Abbasi, M.N. Aslam, G. Irshad, F.N. And, Morpho-molecular identification of *Rhizopus stolonifer* causing postharvest soft rot of Loquat (*Eriobotrya japonica*), Mycopathologia 16 (2020) 117–121.
[28] R. Ghosh, S. Barman, A. Mukhopadhyay, N.C. Mandal, Biological control of fruit-rot of jackfruit by rhizobacteria and food grade lactic acid bacteria, Biol. Control 83 (2015) 29–36, https://doi.org/10.1016/j.biocontrol.2014.12.020.
[29] J.H. Kwon, C. Shim, Y. Chae, C. Park, Rhizopus soft rot on grape caused by *Rhizopus stolonifer* in Korea, Radiat. Protect. Dosim. 13 (2007) 57–60, https://doi.org/10.5423/RPD.2007.13.1.057.
[30] R.I. Ventura-Aguilar, E.P. Díaz-Galindo, S. Bautista-Baños, S. Mendoza-Acevedo, J.E. Munguía-Cervantes, Z.N. Correa-Pacheco, E. Bosquez-Molina, Monitoring the infection process of *Rhizopus stolonifer* on strawberry fruit during storage using films based on chitosan/polyvinyl alcohol/polyvinylpyrrolidone and plant extracts, Int. J. Biol. Macromol. 182 (2021) 583–594, https://doi.org/10.1016/j.ijbiomac.2021.03.187.
[31] K.M. Priya Sethu, T.N. Prabha, R.N. Tharanathan, Post-harvest biochemical changes associated with the softening phenomenon in *Capsicum annuum* fruits, Phytochemistry 42 (1996) 961–966, https://doi.org/10.1016/0031-9422(96)00057-X.
[32] J.S. Baggio, F.P. Gonçalves, S.A. Lourenço, F.A.O. Tanaka, S.F. Pascholati, L. Amorim, Direct penetration of *Rhizopus stolonifer* into stone fruits causing Rhizopus rot, Plant Pathol. 65 (2016) 633–642, https://doi.org/10.1111/ppa.12434.
[33] J.S. Baggio, B. Hau, L. Amorim, Spatiotemporal analyses of Rhizopus rot progress in peach fruit inoculated with *Rhizopus stolonifer*, Plant Pathol. 66 (2017) 1452–1462, https://doi.org/10.1111/ppa.12691.

[34] S. Petrasch, C.J. Silva, S.D. Mesquida-Pesci, K. Gallegos, C. van den Abeele, V. Papin, F.J. Fernández Acero, S.J. Knapp, B. Blanco Ulate, Infection strategies deployed by *Botrytis cinerea, Fusarium acuminatum*, and *Rhizopus stolonifer* as a function of tomato fruit ripening stage, Front. Plant Sci. 10 (2019), https://doi.org/10.3389/fpls.2019.00223.

[35] C. Dennis, J.M. Blijham, Effect of temperature on viability of sporangiospores of *Rhizopus* and *Mucor species*, Trans. Br. Mycol. Soc. 74 (1980) 89–94, https://doi.org/10.1016/S0007-1536(80)80012-X.

[36] M.C. Do Nascimento Nunes, A.M.M.B. Morais, J. Brecht, S. Sargent, J. Bartz, Prompt cooling reduces incidence and severity of decay caused by *Botrytis cinerea* and *Rhizopus stolonifer* in strawberry, HortTechnology 15 (2005), https://doi.org/10.21273/HORTTECH.15.1.0153.

[37] A.M. Alawami, I.A. El-Samra, S.M. Shama, A.M. Hussein, Effect of ultraviolet (UV) on mycelial growth and postharvest infection of peach fruits by *Botrytis cinerea* and *Rhizopus stolonifer*, Acta Hortic. 877 (2010) 1637–1642, https://doi.org/10.17660/ActaHortic.2010.877.225.

[38] C. Stevens, J. Liu, V.A. Khan, J.Y. Lu, M.K. Kabwe, C.L. Wilson, E.C.K. Igwegbe, E. Chalutz, S. Droby, The effects of low-dose ultraviolet light-C treatment on polygalacturonase activity, delay ripening and Rhizopus soft rot development of tomatoes, Crop Protect. 23 (2004) 551–554, https://doi.org/10.1016/j.cropro.2003.10.007.

[39] L. Chong, V. Ghate, W. Zhou, H. Yuk, Developing an LED preservation technology to minimize strawberry quality deterioration during distribution, Food Chem. 366 (2022) 130566, https://doi.org/10.1016/j.foodchem.2021.130566.

[40] Y. Zhao, K. Tu, S. Tu, M. Liu, J. Su, Y. Hou, A combination of heat treatment and *Pichia guilliermondii* prevents cherry tomato spoilage by fungi, Int. J. Food Microbiol. 137 (2010) 106–110, https://doi.org/10.1016/j.ijfoodmicro.2009.11.002.

[41] L. Li, M. Zhang, H. Sun, T. Mu, Contribution of ultrasound and conventional hot water to the inactivation of *Rhizopus stolonifer* in sweet potato, Lebensm. Wiss. Technol. 148 (2021) 111797, https://doi.org/10.1016/j.lwt.2021.111797.

[42] P. Sarig, T. Zahavi, Y. Zutkhi, S. Yannai, N. Lisker, R. Ben-Arie, Ozone for control of post-harvest decay of table grapes caused by *Rhizopus stolonifera*, Physiol. Mol. Plant Pathol. 48 (1996) 403–415, https://doi.org/10.1006/pmpp.1996.0032.

[43] H. Zhang, C. Fu, X. Zheng, Y. Xi, W. Jiang, Y. Wang, Control of postharvest Rhizopus rot of peach by microwave treatment and yeast antagonist, Eur. Food Res. Technol. 218 (2004) 568–572, https://doi.org/10.1007/s00217-004-0902-9.

[44] A. Scruggs, L. Quesada-Ocampo, Cultural, chemical, and alternative control strategies for Rhizopus soft rot of sweetpotato, Plant Dis. 100 (2016) 1532–1540, https://doi.org/10.1094/PDIS-01-16-0051-RE.

[45] T.J. Avis, C. Martinez, R.J. Tweddell, Effect of chlorine atmospheres on the development of Rhizopus rot [*Rhizopus stolonifer*] and gray mold [*Botrytis cinerea*] on stored strawberry fruits, J. Indian Dent. Assoc. 28 (2006) 526–532, https://doi.org/10.1080/07060660609507330.

[46] J.A. Bartz, C.G. Eayre, M.J. Mahovic, D.E. Concelmo, J.K. Brecht, S.A. Sargent, Chlorine concentration and the inoculation of tomato fruit in packinghouse dump tanks, Plant Dis. 85 (2001) 885–889, https://doi.org/10.1094/PDIS.2001.85.8.885.

[47] B. Edmunds, G. Holmes, Evaluation of alternative decay control products for control of postharvest Rhizopus soft rot of sweetpotatoes, Plant Health Prog. 10 (2009), https://doi.org/10.1094/PHP-2009-0206-01-RS.

[48] S.P. Tian, Q. Fan, Y. Xu, A.L. Jiang, Effects of calcium on biocontrol activity of yeast antagonists against the postharvest fungal pathogen *Rhizopus stolonifer*, Plant Pathol. 51 (2002) 352–358, https://doi.org/10.1046/j.1365-3059.2002.00711.x.

[49] E.A. Salem, K. Youssef, S.M. Sanzani, Evaluation of alternative means to control postharvest Rhizopus rot of peaches, Sci. Hortic. 198 (2016) 86–90, https://doi.org/10.1016/j.scienta.2015.11.013.

[50] J.B. Bhalerao, R.A. Chavan, B.B. Dharbale, C.S. Swami, P.B. Kardile, A.H. Kendre, Studies on in-vitro efficacy of chemicals against major fungi associated with post-harvest rot of tomato, J. Pharmacogn. Phytochem. 8 (2019) 1159–1163.

[51] H. Zhang, L. Ma, M. Turner, H. Xu, X. Zheng, Y. Dong, S. Jiang, Salicylic acid enhances biocontrol efficacy of *Rhodotorula glutinis* against postharvest Rhizopus rot of strawberries and the possible mechanisms involved, Food Chem. 122 (2010) 577–583, https://doi.org/10.1016/j.foodchem.2010.03.013.

[52] J. Kong, Y. Zhang, J. Ju, Y. Xie, Y. Guo, Y. Cheng, H. Qian, S.Y. Quek, W. Yao, Antifungal effects of thymol and salicylic acid on cell membrane and mitochondria of *Rhizopus stolonifer* and their application in postharvest preservation of tomatoes, Food Chem. 285 (2019) 380–388, https://doi.org/10.1016/j.foodchem.2019.01.099.

[53] A. Ramos-Guerrero, R.R. González-Estrada, G. Hanako-Rosas, S. Bautista-Baños, G. Acevedo-Hernández, M.E. Tiznado-Hernández, P. Gutiérrez-Martínez, Use of inductors in the control of *Colletotrichum gloeosporioides* and *Rhizopus stolonifer* isolated from soursop fruits: in vitro tests, Food Sci. Biotechnol. 27 (2018) 755–763, https://doi.org/10.1007/s10068-018-0305-5.

[54] M. Mari, R. Gregori, I. Donati, Postharvest control of *Monilinia laxa* and *Rhizopus stolonifer* in stone fruit by peracetic acid, Postharvest Biol. Technol. 33 (2004) 319–325, https://doi.org/10.1016/j.postharvbio.2004.02.011.

[55] L. Pang, M. Adeel, N. Shakoor, K. Guo, D. Ma, M.A. Ahmad, G. Lu, M. Zhao, S. Li, Y. Rui, Engineered nanomaterials suppress the soft rot disease (*Rhizopus stolonifer*) and slow down the loss of nutrient in sweet potato, Nanomaterials 11 (2021) 2572, https://doi.org/10.3390/nano11102572.

[56] N.A. Nafady, S. Alamri, E.A. Hassan, M. Hashem, Y.S. Mostafa, K.A.M. Abo-Elyousr, Application of ZnO-nanoparticles to manage Rhizopus soft rot of sweet potato and prolong shelf-life, Folia Horti 31 (2019) 319–329, https://doi.org/10.2478/fhort-2019-0025.

[57] U.L. Opara, J. Atukuri, O.A. Fawole, Application of physical and chemical postharvest treatments to enhance storage and shelf life of pomegranate fruit—a review, Sci. Hortic. 197 (2015) 41–49, https://doi.org/10.1016/j.scienta.2015.10.046.

[58] D. Ma, D. Ji, J. Liu, Y. Xu, T. Chen, S. Tian, Efficacy of methyl thujate in inhibiting *Penicillium expansum* growth and possible mechanism involved, Postharvest Biol. Technol. 161 (2020) 111070, https://doi.org/10.1016/j.postharvbio.2019.111070.

[59] J. Palma Guerrero, H.B. Jansson, J. Salinas, L.V. Lopez Llorca, Effect of chitosan on hyphal growth and spore germination of plant pathogenic and biocontrol fungi, J. Appl. Microbiol. 104 (2008) 541–553, https://doi.org/10.1111/j.1365-2672.2007.03567.x.

[60] M.G. Guerra-Sánchez, J. Vega-Pérez, M.G. Velázquez-del Valle, A.N. Hernández-Lauzardo, Antifungal activity and release of compounds on *Rhizopus stolonifer* (Ehrenb.:Fr.) Vuill. by effect of chitosan with different molecular weights, Pestic. Biochem. Physiol. 93 (2009) 18–22, https://doi.org/10.1016/j.pestbp.2008.09.001.

[61] A.N. Hernández-Lauzardo, S. Bautista-Baños, M.G. Velázquez-del Valle, M.G. Méndez-Montealvo, M.M. Sánchez-Rivera, L.A. Bello-Pérez, Antifungal effects of chitosan with different molecular weights on in vitro development of *Rhizopus stolonifer* (Ehrenb.:Fr.) Vuill, Carbohydr. Polym. 73 (2008) 541–547, https://doi.org/10.1016/j.carbpol.2007.12.020.

[62] J. García-Rincón, J. Vega-Pérez, M.G. Guerra-Sánchez, A.N. Hernández-Lauzardo, A. Peña-Díaz, M.G. Velázquez-Del Valle, Effect of chitosan on growth and plasma membrane properties of *Rhizopus stolonifer* (Ehrenb.:Fr.) Vuill, Pestic. Biochem. Physiol. 97 (2010) 275–278, https://doi.org/10.1016/j.pestbp.2010.03.008.

[63] A. Hernández-Lauzardo, J. Vega-Pérez, M. Valle, N. Sánchez, A. Peña, G. Guerra-Sanchez, Changes in the functionality of plasma membrane of *Rhizopus stolonifer* by addition of chitosan, J. Phytopathol. 159 (2011) 563–568, https://doi.org/10.1111/j.1439-0434.2011.01802.x.

[64] M. Ma, M. Gu, S. Zhang, Y. Yuan, Effect of tea polyphenols on chitosan packaging for food preservation: physicochemical properties, bioactivity, and nutrition, Int. J. Biol. Macromol. 259 (2024) 129267, https://doi.org/10.1016/j.ijbiomac.2024.129267.

[65] R. Saberi Riseh, M. Vatankhah, M. Hassanisaadi, J.F. Kennedy, Chitosan-based nanocomposites as coatings and packaging materials for the postharvest improvement of agricultural product: a review, Carbohydr. Polym. 309 (2023) 120666, https://doi.org/10.1016/j.carbpol.2023.120666.

[66] X. Yang, X. Jiang, Antifungal activity and mechanism of tea polyphenols against *Rhizopus stolonifer*, Biotechnol. Lett. 37 (2015) 1463–1472, https://doi.org/10.1007/s10529-015-1820-6.

[67] J. Oliveira, M.C.M. Parisi, J.S. Baggio, P.P.M. Silva, B. Paviani, M.H.F. Spoto, E.M. Gloria, Control of *Rhizopus stolonifer* in strawberries by the combination of essential oil with carboxymethylcellulose, Int. J. Food Microbiol. 292 (2019) 150–158, https://doi.org/10.1016/j.ijfoodmicro.2018.12.014.

[68] H.M. Phyo, J. Ju, Q.A. Al-Maqtari, W. Yao, Evaluation of the synergistic antifungal effects of thymol and cinnamaldehyde combination and its mechanism of action against *Rhizopus stolonifer* in vitro and in vivo, Biocatal. Agric. Biotechnol. 49 (2023) 102658, https://doi.org/10.1016/j.bcab.2023.102658.

[69] M.L. Sameza, L.C. Nguemnang Mabou, S.N. Tchameni, M.A. Boat Bedine, F. Tchoumbougnang, P.M. Jazet Dongmo, F. Boyom Fekam, Evaluation of clove essential oil as a mycobiocide against *Rhizopus stolonifer* and *Fusarium solani*, tuber rot causing fungi in yam (*Dioscorea rotundata* poir.), J. Phytopathol. 164 (2016) 433–440, https://doi.org/10.1111/jph.12468.
[70] J. Oliveira Filho, G. Silva, M. Egea, H. Azeredo, M. Ferreira, Essential oils as natural fungicides to control *Rhizopus stolonifer*-induced spoiled of strawberries, Biointerface Res. Appl. Chem. 11 (2021) 13244–13251, https://doi.org/10.33263/BRIAC115.1324413251.
[71] S. Mohammadi, H. Aroiee, M.H. Aminifard, A. Tehranifar, V. Jahanbakhsh, Effect of fungicidal essential oils against *Botrytis cinerea* and *Rhizopus stolonifer* rot fungus in vitro conditions, Arch. Phytopathol. Plant Protect. 47 (2014) 1603–1610, https://doi.org/10.1080/03235408.2013.853456.
[72] P.P.M. Da Silva, J. de Oliveira, A.D.M. Biazotto, M.M. Parisi, E.M. Da Glória, M.H.F. Spoto, Essential oils from *Eucalyptus staigeriana* F. Muell. ex Bailey and *Eucalyptus urograndis* W. Hill ex Maiden associated to carboxymethylcellulose coating for the control of *Botrytis cinerea* Pers. Fr. and *Rhizopus stolonifer* (Ehrenb.: Fr.) Vuill. in strawberries, Ind. Crops Prod. 156 (2020) 112884, https://doi.org/10.1016/j.indcrop.2020.112884.
[73] J.L. Rezende, C.C. Fernandes, A. Costa, L.S. Santos, F. Vicente Neto, E.M. Sperandio, E.L. Souchie, A.C. Colli, A.E. Crotti, M.L. Miranda, Antifungal potential of essential oils from two varieties of citrus sinensis (lima orange and bahia navel orange) in postharvest control of *Rhizopus stolonifer* (ehrenb.: fr.) vuill, Food Sci. Technol. 40 (2020) 405–409, https://doi.org/10.1590/fst.30519.
[74] M. Safari, A. Kamaly, J. Hadian, M. Farzaneh, Inhibition of spore development and mycelial growth of *Rhizopus stolonifer* by essential oil of *Satureja richingeri* from Iran, J. Essent. Oil Res. 23 (2011) 5–10, https://doi.org/10.1080/10412905.2011.9712274.
[75] A.J.A.A. Athayde, P.D.L. de Oliveira, I.C.D. Guerra, M.L. Da Conceição, M.A.B. de Lima, N.M.O. Arcanjo, M.S. Madruga, L.R.R. Berger, E.L. de Souza, A coating composed of chitosan and *Cymbopogon citratus* (Dc. Ex Nees) essential oil to control Rhizopus soft rot and quality in tomato fruit stored at room temperature, J. Hortic. Sci. Biotechnol. 91 (2016) 582–591, https://doi.org/10.1080/14620316.2016.1193428.
[76] Y. Naserzadeh, N. Mahmoudi, E. Pakina, Antipathogenic effects of emulsion and nanoemulsion of cinnamon essential oil against rhizopus rot and grey mold on strawberry fruits, Foods Raw Mater 7 (2019) 210–216, https://doi.org/10.21603/2308-4057-2019-1-210-216.
[77] A. Edris, E. Farrag, Antifungal activity of Peppermint and Sweet Basil essential oils and their major aroma constituents on some plant pathogenic fungi from the vapor phase, Nahrung 47 (2003) 117–121, https://doi.org/10.1002/food.200390021.
[78] E. Bosquez-Molina, E.R. Jesús, S. Bautista-Baños, J.R. Verde-Calvo, J. Morales-López, Inhibitory effect of essential oils against *Colletotrichum gloeosporioides* and *Rhizopus stolonifer* in stored papaya fruit and their possible application in coatings, Postharvest Biol. Technol. 57 (2010) 132–137, https://doi.org/10.1016/j.postharvbio.2010.03.008.
[79] X. Zhang, Z. Gao, X. Zhang, W. Bai, L. Zhang, H. Pei, Y. Zhang, Control effects of *Bacillus siamensis* G-3 volatile compounds on raspberry postharvest diseases caused by *Botrytis cinerea* and *Rhizopus stolonifer*, Biol. Control 141 (2020) 104135, https://doi.org/10.1016/j.biocontrol.2019.104135.
[80] B. Xu, H. Zhang, K. Chen, Q. Xu, Y. Yao, H. Gao, Biocontrol of postharvest Rhizopus decay of peaches with *Pichia caribbica*, Curr. Microbiol. 67 (2013) 255–261, https://doi.org/10.1007/s00284-013-0359-9.
[81] A. Bonaterra, M. Mari, L. Casalini, E. Montesinos, Biological control of *Monilinia laxa* and *Rhizopus stolonifer* in postharvest of stone fruit by *Pantoea agglomerans* EPS125 and putative mechanisms of antagonism, Int. J. Food Microbiol. 84 (2003) 93–104, https://doi.org/10.1016/S0168-1605(02)00403-8.
[82] L. Zhao, C. Lan, X. Tang, B. Li, X. Zhang, X. Gu, H. Zhang, Efficacy of *Debaryomyce hansenii* in the biocontrol for postharvest soft rot of strawberry and investigation of the physiological mechanisms involved, Biol. Control 174 (2022) 105011, https://doi.org/10.1016/j.biocontrol.2022.105011.
[83] H. Zhang, L. Wang, X. Zheng, Y. Dong, Effect of yeast antagonist in combination with heat treatment on postharvest blue mold decay and Rhizopus decay of peaches, Int. J. Food Microbiol. 115 (2007) 53–58, https://doi.org/10.1016/j.ijfoodmicro.2006.10.002.
[84] X. Wang, F. Xu, J. Wang, P. Jin, Y. Zheng, *Bacillus cereus* AR156 induces resistance against Rhizopus rot through priming of defense responses in peach fruit, Food Chem. 136 (2013) 400–406, https://doi.org/10.1016/j.foodchem.2012.09.032.
[85] Q. Tang, X. Bie, Z. Lu, F. Lv, Y. Tao, X. Qu, Effects of fengycin from *Bacillus subtilis* fmbJ on apoptosis and necrosis in *Rhizopus stolonifer*, J. Microbiol. 52 (2014) 675–680, https://doi.org/10.1007/s12275-014-3605-3.
[86] M. Jiang, X. Pang, H. Liu, F. Lin, F. Lu, X. Bie, Z. Lu, Y. Lu, Iturin A induces resistance and improves the quality and safety of harvested cherry tomato, Molecules 26 (2021) 6905, https://doi.org/10.3390/molecules26226905.
[87] N. Jia, Y.H. Xie, H.X. Zhang, H. Liu, J.J. Feng, L.D. Zhu, X.B. Zhou, Effect of bacteriocin treatment on storage and quality of postharvest strawberry fruit, Adv. Mater. Res. 554–556 (2012) 1547–1552, https://doi.org/10.4028/www.scientific.net/amr.554-556.1547.