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Article

Pathogenicity, Mycotoxin Production, Control of Potato Dry Rot Causing by *Fusarium* spp.

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Abstract: *Fusarium* dry rot is one of the major postharvest potato diseases of during storage after harvest, which not only results in quality degradation but also brings up huge economic losses. The disease can be elicited by some species of *Fusarium*, the pathogenic fungi of *Fusarium* causing potato dry rot are considerably diverse in various countries and regions. *Fusarium* spp. infection is associated with dry rot produce mycotoxins, which has phytotoxicity and mycotoxicoses on humans and animals. Chemical synthetic fungicide is considered as the main control measure to *Fusarium* dry rot of potato, nevertheless, it is unfortunate that the persistent application inevitably results in the emergency of resistant strain and environmental contamination. A comprehensive disease control strategy includes potato cultivar selection, appropriate cultural practices (crop rotation, cultivate pattern, fertilization, and irrigation), harvesting process and postharvest treatment (harvesting, classification, packaging, wound healing), storage condition (environmental disinfection, temperature, humidity and gas composition) along with the application of fungicide pre-harvest or postharvest. Recently, emerging studies indicated that eco-friendly strategies include physical control, chemical methods (such as the application of generally recognized as safe (GRAS) compounds or chemical (elicitors) and biological control have been introduced to combat Fusarium dry rot of potato.

Keywords: *Fusarium* spp.; Fusarium dry rot of potato; pathogenicity; mycotoxin; control

1. Introduction

Potato (*Solanum tuberosum* L.) ranks fourth as the most important food crop all over the world, only behind rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), and maize (*Zeamays* L.). It is also a major non-cereal food crop, which plays an irreplaceable role in the global food supply. Potato tuber is rich in plenty of macronutrients (such as carbohydrates and dietary fiber) and micronutrients (such as vitamins and minerals), furthermore, it is also an important source of antioxidants in people's diet [1]. It is reported that, in 2020, the total world production of potatoes was 359 million tons (http://www.fao.org/faostat/en/?#data/QC) and China ranked the first with the production of 17.98 million tons [2-3]. More than 85 % of potato needs to be kept for 3-6 months acting as vegetable and industrial material, the losses due to the disease during storage is very huge [4]. Some fungi, bacteria, and viruses all can result in postharvest disease. Among them, infection of potato tuber resulted from *Fusarium* spp. can particularly cause severe dry rot during storage, which not only lead to quality deterioration but also reduce the marketable yield. Tuber losses range from 6.25% to 25% due to dry rot during storage annually, and up to 60% when potato tubers are injured [5], the financial loss is about $ 100–250 million annually in the United States due to the dry rot of potato (https//www.ars.usda.gov). In Gansu province of China, it is estimated the tuber losses due to dry rot was around 88% of the total postharvest losses [6]. Importantly, some *Fusarium* species associated with dry rot produce mycotoxins, which pose an adverse effect on humans and animals due to their mycotoxicoses.

If we grasp the pathogenesis of *Fusarium* associated with potato tuber, the appropriate and effective management measures are carried out, the losses will be effectively reduced. At present, some chemical synthetic fungicides (such as carbendazim, mancozeb, thiabendazole (TBZ)) are employed to prevent and control dry rot of potato. Nevertheless, chemical synthetic fungicides are not a long-term solution due to ecological environment and drug resistance. Currently, some eco-friendly control measures such as the use of some organic acid and salts [7], inorganic salts [8-9], chitosan [10], plant essential oil [11-12] and biological antagonist [13-14] for management postharvest disease of potato tuber are being explored and developed. The present review focus on dry rot occurrence (including the causal pathogens of dry rot, the symptom of the dry rot, and pathogenesis), mycotoxins production (non-trichothecenes and trichothecenes), and the management strategies.

2. Dry rot of Potato Tuber

2.1. The causal agent causing dry rot

Fusarium is a notorious and huge fungal genus within the Ascomycota phylum containing hundreds of species, which are primarily isolated from soil and plant survival [1]. It is well known that *Fusarium* spp. has the ability to cause potato dry rot, which is a devastating postharvest fungal decay, severely impacting potato tubers quality all over the world [1]. *Fusarium* dry rot causes a remarkable reduction in potato yield, as well as leads to enormous economic losses. Currently, there are 17 species, and 5 variants of *Fusarium* recognized globally as causal agents to cause potato dry rot [15]. Because of the differences in potato cultivars and climatic conditions, diverse *Fusarium* species were isolated and identified from *Fusarium* dry rot of potato in various countries and regions. Among them, *F. sambucinum* was considered as the most predominant pathogenic pathogen to lead to Fusarium dry rot of potato in North America and some regions of Europe [16-18], however, some reports suggested that *F. solani var. coeruleum* was regarded as the most prevalent pathogen causing potato dry rot at low temperature storage in the United Kingdom, occasionally, the pathogen of *F. coeruleum* also caused severe potato harvest disease in the United Kingdom [19-21]. *F. graminearum* was the most frequent *Fusarium* species to cause potato dry rot In North Dakota [22]. *F. oxysporum* and *F. solani* were reported as the main pathogen to cause *Fusarium* dry rot in potato In South Africa, [23-24]. *F. sulphureum* and *F. solani* were found to have a higher incidence and aggressiveness in Iran [25]. In Egypt, the *F. sambucinum* was regarded as the most predominant pathogen, except for *F. oxysporum*, *F. incarnatum* and *F. verticillioide* [26].

There are different climatic conditions in China, different species of *Fusarium* were isolated and characterized in different regions. Potato planting regions are divided into four regions of Northeast, North China, Northwest, and South planting regions in China. In Northwest of potato planting regions, *F. avenaceum*, *F. oxysporum*, *F. sporotrichiodes*, *F. solani*, *F. trichothecioides*, *F. solani var. coeruleum*, *F. sambucinum*, *F. semitectum*, *F. solani*, *F. sambucinum*, *F. culmorum*, *F. gibbosum*, *F. macroceras*, *F. solani var. coeruleum*, *F. acuminatum*, *F. equiseti* and *F. redolens* were identified in Heilongjiang Province and Inner Mongolia Autonomous Region [27]; In North of China, *F. sambucinum* and *F. avenaceum*, *F. solani var. coeruleum*, *F. oxysporum*, *F. acuminatum* were isolated in Shanxi Province [27]. In Northwest of China, *F. sambucinum*, *F. avenaceum*, *F. oxysporum*, *F. equiseti* are identified in Ningxia Hui Autonomous Region; *F. sambucinum*, *F. solani*, *F. sulphureum*, *F. avenaceum*, *F. graminearum* are identified in Gansu Province [7,8,10,12]; F. tricinctum, F. avenaceum, F. oxysporum, *F. solani*, *F. acuminatum*, *F. equiseti* are mainly identified in Qinghai Province [6]. In Zhejiang Province of South of China, *F. solani*, *F. solani var. coeruleum*, *F. moniliforme var. intermedium*, *F. moniliforme var. zhejiangense*, *F. redolens* were mainly identified [6].

Fusarium species to cause potato dry rot is not only influenced by countries and regions, the potato variety, chemical synthetic fungicide application, as well as seed tuber source also play the significant roles. For instance, Xue's research group [28] compared the pathogenicity of *F. sulphureum* for different potato cultivars, and found that the variety of Longshu No. 3 is susceptible, while the variety of Longshu No. 6 is resistant for *F. sulphureum*.

2.2. Pathogen infection and the symptom of potato dry rot

In general, *Fusarium* spp. can infect potato tuber through surface wounds or natural openings on tubers during pre-harvest or post-harvest, and the infection way is shown in Figure 1. Pathogenicity is a crucial factor when understanding the pathogen of *Fusarium* infection potato tuber. And the extracellular enzymes and reactive oxygen species (ROS) play the more important roles for the pathogenicity of *Fusarium*. Pathogen can secrete extracellular enzymes to destroy the cell wall and middle lamellar of the host plant, which makes the pathogen can spread to the surrounding cell and

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successfully infect the host plant. Numerous researches indicated that cell wall degrading enzymes (CWDEs) are important pathogenic factors for *Fusarium* when infecting and spreading [29-30]. Yang et al. [29] suggested that the activities of CWDEs (such as polygalacturonase (PG), carboxymethyl cellulose (Cx), polymethyl-galacturonase (PMG), and so on) were found to increase during *F. sulphureum* infection potato tubers. Cutinase enzymes were also involved in the pathogenicity when *F. solani* infected potato tuber. Moreover, ROS also plays vital role for the pathogenicity of pathogen. As we know, ROS production is early events during host-pathogen interactions, excessive ROS can attack cellular biomolecules, such as lipid, protein, and DNA, then cause lipid peroxidation cell membrane damage of hosts, finally leading to infection. For instance, Bao et al. [31] compared with the difference in pathogenicity between *F. sambucinum* and *F. sulphureum* during pathogens infection potato tubers and found that *F. sulphureum* showed the higher pathogenicity in inoculated tubers association with a higher ROS level, which caused a higher malondialdehyde (MDA) content, and a lower level for cell membrane integrity, ultimately lead to a bigger lesion diameter in inoculated tuber. The contrary result was observed in the tubers inoculated with *F. sambucinum* due to a lower ROS accumulation. Xue et al. [28] also observed that, compared to *F. sambucinum* and *F. solani*, *F. sulphureum* manifested the strongest infection ability and pathogenicity in inoculated with tubers (cv. Longshu No.3) in Gansu province. In addition, the pathogenicity of *Fusarium* was also related to host nonspecific phytotoxin trichothecenes, for instance, fusaric acid produced by *Fusarium* destroyed the cell membrane structure of the host plant, then decreased respiration rate, which is beneficial for *Fusarium* infection potato tuber.

Table 1. The reported *Fusarium* spp. to lead to dry rot of potato in diverse countries and regions.

***Fusarium* species**	**region**	**reference**
F. sambucinum	North Amercian and some regions of Europe	[16, 17, 18]
F. coeruleum	United Kingdom and Great Britain	[19,20,21]
F. graminearum	North Dakota	[22]
F. solani and *F. oxysporum*	South Africa Michigan	[23-24]
F. sulphureum *and F. solani*	Iran	[25]
F. sambucinum *F. oxysporum* *F. verticillioides* *F. incarnatum*	Egypt	[26]
F. avenaceum, *F. oxysporum*, *F.sporotrichiodes* *F. solani*, *F. trichothecioides*, *F. solani var. coeruleum* *F. sambucinum* *F. semitectum*, *F. solani* *F. sambucinum* *F. culmorum*,	Heilongjiang Province and Inner Mongolia Autonomous Region	[27]

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F. gibbosum, *F. macroceras*, *F. solani var. coeruleum*, *F. acuminatum*, *F. equiseti* and *F. redolens*		
F. sambucinem *F. avenaceum* *F. solani var. coeruleum*, *F. oxysporum*, *F. acuminatum*	North of China Shanxi Province	[27]
F. sambucinem *F. avenaceum* *F. graminearum* *F. solani* *F. sulphureum*	Northwest of China, Gansu Province, Ningxia Hui Autonomous Region	[7,8,10, 11,12,27]
F. tricinctum, *F. avenaceum*, *F. oxysporum*, *F. solani*, *F. acuminatum*, *F. equiseti*	Northwest of China, Qinghai Province	[6]
F. solani, *F. moniliform*, *F. redolens*	South of China Zhejiang Province	[6]

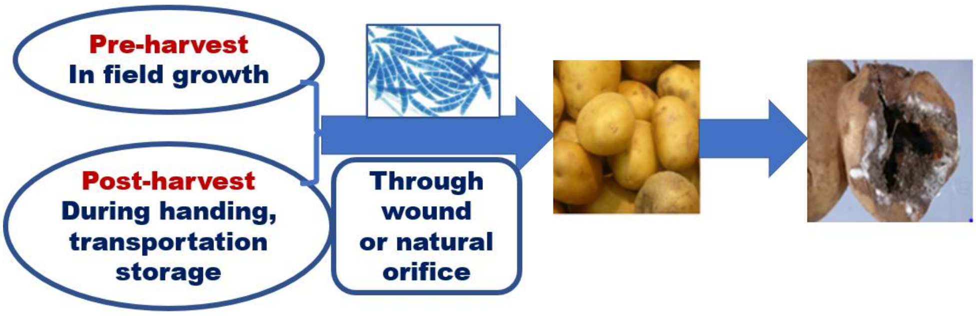

Figure 1. *Fusarium* species infect potato tuber through surface wound or natural openings of tuber.

The typical symptom of the skin of the infected potato tuber by *Fusarium* spp. mainly manifests wrinkled brown, and sunken tissue with a dry and leathery appearance. The initial symptoms is observed as shallow, small brown spots at tuber wound sites after approximately 30 days of storage. Subsequently, the infected tissue begins to enlarge in every direction, and the periderm of tuber gradually subsidences and collapses. Ultimatelly, concentric rings is observed on the enlarging lesions, and the dead tissue begins to desiccate [1, 32]. The cottony white, or purple, or yellow, or pink, or brick spore and mycelia of *Fusarium* spp. are observed in the cavity under the rotted lesion [33]. As the disease progresses, the whole tubers with the symptom of severe decay always manifests a shriveled and dehydrated appearance. In severe cases, the affected potatoes may completely decay, resulting in a mushy texture and foul odor. Therefore, it is important to identify and manage potato dry rot to prevent further spread and minimize economic losses.

2.3. Mycotoxin accumulation associated with Fusarium dry rot

Potato dry rot resulting from *Fusarium* is associated with mycotoxins accumulation. Mycotoxins are a type of secondary metabolites produced by toxigenic fungi under suitable temperature and humidity conditions, which can lead to a potential health threat to human and animal [34, 35]. The mycotoxin metabolized by *Fusarium* is classified into two types of non-trichothecene and trichothecenes. The main non-trichothecene metabolized by *Fusarium* spp. are shown in Table 2. BEA and ENN are cyclic hexadepsipeptides with antimicrobial, insecticidal, phytotoxic, and cytotoxic properties, which were detected in the potato tuber infected with *F. oxysporum* [36]. ZEA and FUS were detected in the tubers infected with *F. sambucinum*, *F. solani*, *F. oxysporum*, with estrogenic syndromes in swine and other experimental animals [37-40]. FUM is linked to leukoencephalomalacia in brain lesions of horses and rabbits with hepatotoxic and carcinogenic influences, also associated with esophageal carcinoma in human with phytotoxic effect, which was detected potato contaminated with *F. equiseti*, *F. sambucinum*, and *F. oxysporum* [41]. El-Hassan and Kim [42-44] observed SAM in potato dry rot infected by *F. sambucinum*, *F. semitectum*, *F. solani* and *F. oxysporum* that resulted in hemorrhage for stomach and intestines, bodyweight loss, apastia, and death for rats. Sonja et al. [45] found the FA production in *F. oxysporum* infected potato tuber, Venter group [46] and El-Hassan group [41] indicated that FA content was positively correlated to the incidence of dry rot. Pre- and postharvest strategies was carried to control FA accumulation in dry rot of potato tuber [1].

Table 2. Non-trichothecenes generated by *Fusarium* spp. in potato dry rot.

***Fusarium* species**	**non-trichothecenes**	**reference**
F. oxysporum	BEA, ENN	[36]
F. sambucinum *F. solani* *F. oxysporum* *F. crookwellense*	ZEA, FUS	[37,38, 39, 40]
F. equiseti *F. oxysporum* *F. sambucinum*	FUM	[41]
F. semitectum *F. oxysporum* *F. solan* *F. sambucinum*	SAM	[41, 42, 43, 44]
F. oxysporum	FA	[1, 41, 45, 46]

Note: BEA: beauvericin, ENNs: enniatins, FA: fusaric acid, FUM: fumonisin, FUS: fusarin C, SAM: sambutoxin.

The trichothecenes are categorized as another main type of mycotoxins found in Fusarium dry rot of potato that is a type of structurally related sesquiterpenes compound. Up to the present, there are more than 190 known trichothecenes are found.

The trichothecenes are classified into four different types: A, B, C, and D based on the chemical structural difference, the chemical structures are listed in Figure 2. Types A and B of trichothecenes are found in cereal crops and their contaminated products. Additionally, trichothecenes were found in potato dry rot [35], *Fusarium* dry rot in muskmelon [47], and core rot in apple [48]. As we know, Trichothecenes can pose a serious health threat to human and animal due to phytotoxicity and mycotoxicoses [28]. For instance, in some severe cases, trichothecene has the potential carcinogenic, teratogenic, and mutagenic effect [49]. Trichothecenes were reported in *Fusarium* dry rot of potato tuber (Table 3). Type A and B of trichothecenes are often mainly found in the lesion tissue of the rotted potato tuber. Xue et al. [4] found trichothecene of 3-ADON, T-2, FUS, and DAS not only in the lesion

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part but in the adjacent asymptomatic part of potato dry rot contaminated by *F. sulphureum*, *F. solani*, and *F. sambucinum*; it was interested that the concentration of trichothecens were negatively correlated the distance from the infected point. Similarly, Ellner et al. [50] suggested that both DAS and 4,15-DAS were detected in rotten tissue, as well as in adjacent asymptomatic tissue in tubers contaminated by *F. sambucinum*, and the similar changing trend to Xue's report was observed. Delgado et al. [57] suggested that DON, NIV, FX, 3-ADON, 15-ADON were detected in potato inoculated with *F. graminearum*, almost a similar trend to Xue's and Ellner's reports were found.

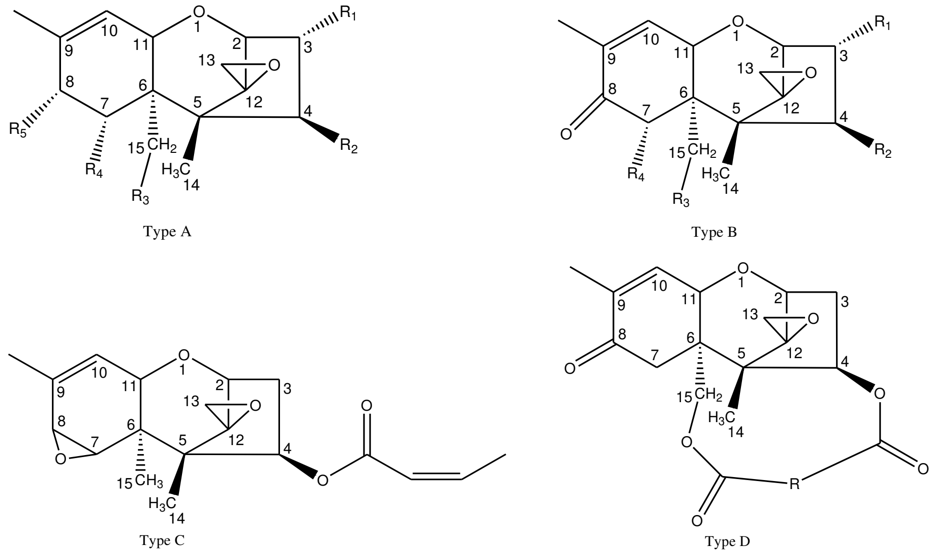

Figure 2. basic chemical structure of trichothecenes.

Table 3. Trichothecenes generated by *Fusarium* spp. in potato dry rot.

***Fusarium* species**	**trichothecenes**	**reference**
F. sambucinum	*trichothecene*	[37, 38, 39]
F. solani		
F. oxysporum		
F. sulphureum,	3-ADON, T-2, FUS, DAS	[4]
F. solani		
F. sambucinum		
F. sambucinum	4,15-DAS, DAS	[50]
	DAS, MAS, NEO, T-2, HT-2	[51]
	4,15-DAS, 15-MAS, 4-MASc	[52]
	DON, NIV, HT-2	[53]
	T-2	[41]
F. sambucinum	MAS, DAS	[54]
F. solani		
F. crookwellense	NIV, FX	[38]
	NIV, DAS	[55]
	FX	[56]
F. graminearum	DON, NIV, FX, 3-ADON, 15-ADON	[57]
	DON, NIV, FX	[40]
	NIV, T-2, 3,15-ADON, 15-SCRP	[59]

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	NIV, FX, DON, 3-ADON, 15-ADON	[56]
	DON, 3-ADON, 15-ADON	[59]
	NIV, FX, DON, 3-ADON	[56]
	NIV, FX, 4,15-MAS, DAS, SCR	
F. culmorum	DON, 3-ADON	[60]
	NIV, FX, DON, 3-ADON	[56]
F. equiseti	NIV, FX, 4,15-MAS, DAS, SCR	[56]
	T-2	[41]
F. oxysporum	T-2	[41]

Note: DAS: diacetoxyscirpenol, 4,15-DAS: 4,15-diacetoxyscirpenol, DON: deoxynivalenol, 3-ADON: 3-acetyldeoxynivalenol, 15-ADON: 15-acetyldeoxynivalenol, HT-2: HT-2 toxin, MAS: monoacetoxyscirpenol, 4-MAS: 4-acetyl-monoacetoxyscirpenol, NIV: nivalenol, FX: fusarenone X, NEO: neosolaniol, SCR: scirpentriol, 15-MAS: 15-acetyl-monoacetoxyscirpenol, T-2: T-2 toxin,15-SCRP: 15-acetylscripenol.

2.4. Dry rot of control

Given the severity of potato dry rot, how to control the disease of dry rot has become an urgent question. Currently, the chemical synthetic fungicides such as thiabendazole, benzimidazole, 2-aminobutane, imazalil, flusilazole, difenoconazole is the main strategy to control the disease. However, as we all know, a series of problems such as the resistance to fungicide, environmental contamination, and pesticide residues have come up, which ask scientists to develop integrated disease management to combat the problems. An integrated disease control strategy includes potato cultivar selection, appropriate cultural practices, harvesting process and postharvest treatment, storage condition along with the application of fungicide pre-harvest or postharvest.

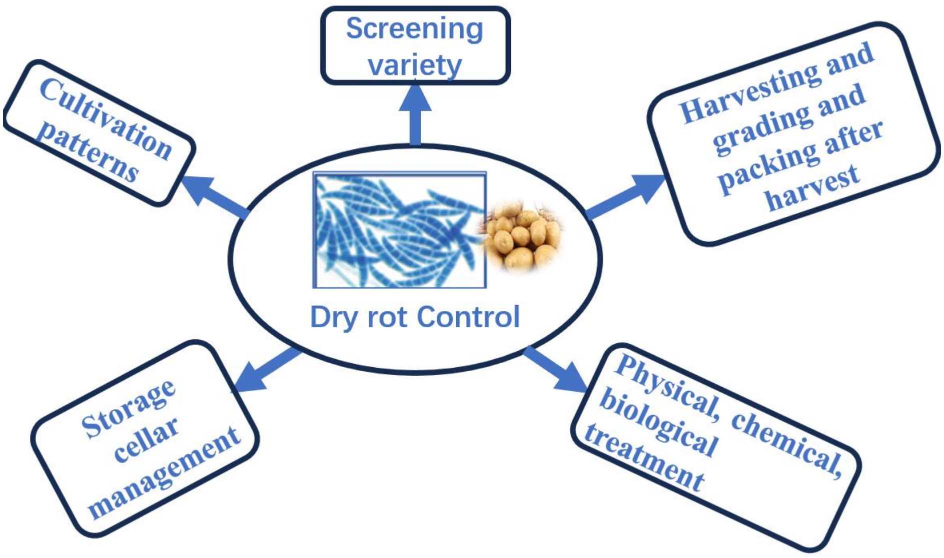

Figure 3. The strategy of controlling potato dry rot.

2.4.1. Varieties Screening

Resistant varieties screening plays a crucial role in controlling postharvest disease. More than 5000 potato varieties were reported to be planted all over the world [61-62]. Most of the varieties are sensitive to *Fusarium*. Du's research group investigated 21 potato varieties and 46 breeding lines against *F. sambucinum*, and found that 67 kinds of potato clones were sensitive to *Fusarium* in China

[27] Xue' group [28] investigated the varieties of Longshu No.6 and Longshu No.3 against *F. sulphureum* and found that the variety of Longshu No.3 showed more susceptibility to *F. sulphureum* and had more serious disease and higher levels of FUS, DAS, 3ADON and T-2 toxin in potato tubers contaminated by *F. sulphureum* comparing with the variety of Longshu No. 6. In Tunisia, Trabelsi et al [63] indicated that the varieties of Mondial, Spunta, and Liseta were less sensitive to *F. sambucinum*, *F. oxysporum*, and *F. graminearum*. In Iran, Esfahani et al. [64] screened 43 potato varieties to *F. solani*, *F. sulphureum*, and *F. oxysporum* were found only the variety of Saturna was resistant against the three fungi. In Canada, Yilma et al. indicated that the variety of Owyhee Russet showed a significant higher resistance than Russet Burbank to dry rot. In fact, the resistance to every *Fusarium* spp. is mainly independent and genetically distinct to some extent. The resistance to a species of *Fusarium* is transmitted to progeny but appears to be associated with recessive alleles [66-67]. Even though numerous potato cultivars and clones were tested for sensitivity, none of variety is resistant to all the Fusarium complex. At the same time, varieties may be sensitive to one species of Fusarium, nevertheless, the resistance is to another species of *Fusarium*. Similarly, a certain strain of *Fusarium* maybe pathogenic to one cultivar, but non-pathogenicity is shown to another cultivar. Because the susceptibility-resistance outcome varies depending on the strains, the varieties, and the prevailing culture and environmental conditions in different regions of the world. Some researches pointed the role of storage temperature for cultivar's susceptibility against *Fusarium* species. Mejdoub-Trabelsi et al. [68] found cultivars at temperature 30 °C were less susceptible, while the cultivars at temperature 15 °C were highly susceptible. Therefore, it is indispensable to study the populations of *Fusarium* in field and the pathogenicity to optimize the varieties to grow in each field. At present, breeding resistant cultivars against dry rot are very efficient because of laborious phenotyping [69]. Genome-editing technique by using Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/Cas9 system to target genome modifications has become a potential and powerful tool to genetic engineering in potato [70]. CRISPR/Cas9 system can provide an alternative strategy to conventional genetic engineering [71], and is expected to produce disease-resistant cultivars by designing and constructing gene-specific single guide RNA (sgRNA) vectors.

2.4.2. Cultivation patterns

Good cultivation patterns play a crucial role that influence the incidence and severity of storage disease after harvest. Generally, cultivation patterns include crop rotation, cultural methods, fertilization, and irrigation. Crop rotation is usually advised cultural practice in controlling soil-borne disease, however, crop rotation is not very suitable in the management of potato dry rot [72-73]. Because the fungus has a broad host range and can survive in the soil for 5-6 years, which make it very difficult to control infection by crop rotation. Potato crop rotation with barley, red clover did not achieve a significant effect for disease incidence and severity in 2-3 years [74].

Cultural method plays a key role in the management of potato dry rot. Dry rot is not only a soil disease but also a tuber-borne disease. Therefore, the seed tuber is usually considered the main source of inoculum [75]. Planting healthy seed tuber in the field is necessary, if planting the infected seed tuber, which will result in soil infestation around the progeny tuber [76]. The contaminated soil adhering on the tubers' surface will eventually contaminate tubers through wounds or natural orifices during storage after harvest. Reasonable sowing time is also an important factor for potatoes, which make the whole growth period of potato is a relatively suitable temperature and humidity, avoid the high temperature when potato tuber developing and expanding. Finally, reasonable fertilization and irrigation should be considered during the different growth periods.

2.4.3. Harvesting and grading and packing after harvest

Harvesting and processing treatment after harvest have a significant influence on controlling disease and reducing incidence. Because of the fungus of *Fusarium* spp. attacking potato tuber only through the wounds, considerable efforts should be focused on avoiding tuber bruising and injuring when harvesting [15]. In addition, the temperature of 10-18 °C for tuber pulp is best option for harvesting tuber [77]. The maturity level plays an important role when harvesting, the tubers with low maturity have a higher content of sucrose and a poorer skin set, however, the higher level of sucrose that provides nutrition for fungus growth, and the poorer skin is prone to bruise and generate wounds, these properties lead to the low maturity are more vulnerable to the fungus [18]. In general, it is appropriate for potato tubers to harvest after 7-14 days of killing potato vine, which will have sufficient time to wound healing and decrease the chances of fungus attack [15]. It takes 1-2 weeks for the tuber to heal the wound when the environmental humidity is between 95 and 99%, and the tuber pulp temperature is ranged from 13 to 16 °C, which is a favor to rapidly heal the wound after harvest. Taking some steps to accelerate wound healing not only save wound healing time but also decrease labor cost. Our research group previous results suggested that sodium silicate or brassinosteroid treatment accelerated the wound healing process of tuber by activating of phenylpropanoid metabolism [78-79]. Subsequently, Jiang adopted transcriptomics analysis how benzo-(1, 2, 3)-thiadiazole-7-carbothioic acid s-methyl ester (BTH) to induce genes involved in suberin accumulation to accelerate potato wound healing process [80]. Moreover, a careful examination of tuber, grading, and packing should be paid attention to. As mentioned above, the disease of dry rot can easily contaminate through the wounds, when one tuber is decay, the rotten tuber will contaminate the tubers around it, which will ultimately result in a disastrous disease during storage. Therefore, the tubers with wounds (including pests and disease appearance) must be carried out a thorough examination and rejected before storage, actually, the examination process is attributed to proper grading before storage [81]. Finally, packing not only can reduce the disease incidence, but also increase the beauty and value of potatoes.

2.4.4. Storage cellar management

Storage cellar management is a crucial factor to manage dry rot of potato, which includes storage cellar disinfection, temperature, humidity, and gas components. During storage, proper disinfection treatment for storage facilities is mandatory, the common chemical disinfectants include sulfur, potassium permanganate-formaldehyde, peracetic acid, chlorine dioxide, 2-4% formalin solution. Most of these chemical disinfectants are employed for fumigation processing. Storage temperature is the determining factor for the storage quality of potato tuber. The storage temperature should decrease to an appropriate level after wound healing at 15-20 °C. In general, the storage temperature is 2-3 °C for seed potatoes and 4-5 °C for commercial potatoes. During storage, the appropriate humidity is 80-93%, higher humidity will lead to tuber rot and sprout earlier. In addition, proper cool air circulation is also essentially, because the stored potato tubers produce excessive carbon dioxide (CO_2) and heat, which will facilitate the development of adhering *Fusarium* spores [82].

2.4.5. Physical, chemical, and biological treatment

2.4.5.1. Physical treatment

As we know, a minimal environmental impact and no residues in the treated product, the development of a physical application to management postharvest plant diseases has been widely carried out. Among all kinds of physical treatments, the extensive application of ultraviolet-C light (UV-C, 190–280 nm) showed a significant effect, whose mechanism is that, on the one hand, UV-C treatment can directly suppress pathogen growth; on the other hand, UV-C application can induce defense response in host tissues and increase the resistance against disease [83]. The application of UV-C has been shown to control dry rot by inducing the generation of antifungal substances in potato that contributes to disease control [84]. Ranganna et al. [85] also suggested UV-C irradiation completely prevents the development of dry rot caused by *F. solani* in potatoes storage at 8 °C for 3 months. Yu et al. [86] indicated that 35 $kJ \cdot m^{-2}$ UV-C treatment significantly inhibited dry rot of potato by increasing the activities of CAT, POD, and PAL. Another report by Jakubowski and Krolczyk [87], who suggested that UV-C radiation effectively controlled the disease of dry rot in stored potato tubers.

2.4.5.2. Chemical treatment

The most effective strategy to control potato dry rot is the combination of pre-and post-harvest treatment. Firstly, it is necessary to disinfect the seed tuber before planting, chemical treatments to the harvested tubers also play an important role before storage. Thiabendazole is currently considered as the most widely used chemical fungicide to manage *Fusarium* dry rot of potato [88]. Thiophanate-methyl (benzimidazole group) was reported that is extensively applied to manage seed tuber piece disease in Canada. Nevertheless, the employment of thiabendazole has resulted in the occurrence of the drug-resistant strains against the pathogen of *F. sambucinum*, it is fortunate that the rest of the *Fusarium* species viz. *F. solani*, *F. culmorum*, *F. equiseti*, *F. acuminatum* and *F. avenaceum* are still sensitive to the fungicide of thiabendazole [72, 89]. Some alternative fungicides with high-efficiency and low-toxicity (such as fludioxonil) also have incomparable effects to manage dry rot. For instance, fludioxonil was used to effectively control tuber seed disease and sprout rot [90]. The application of azoxystrobin and fludioxonil effectively managed dry rot, the disease incidence decreased to 50% comparing with the control after 21 days of storage [15]. However, with the extensive application of synthesis chemical fungicide, the inevitable problems of drug-resistance, environmental pollution, as well as food safety are becoming more and more prominent. Therefore, it is urgent to develop more safer and efficient fungicides to control Fusarium dry rot of potato.

Accordingly, the generally recognized as safe (GRAS) substances, such as inorganic acid, organic acid, inorganic salts, organic salts, essential oils and phytohormones, all display excellent effects in sustainably controlling the dry rot of potato. Raigond et al. [91] indicated that chitosan application significantly managed dry rot in potato, and he also found that chitosan coating significantly reduced the *Fusarium* incidence by inhibiting *Fusarium* growth. Xue et al. [7] suggested chitosan, sodium silicate and β-aminobutyric acid treatments markedly inhibited the expansion of lesion diameter in tuber infected with *F. sulphureum*, interestedly, trichothecenes concentration was also decreased, the involved action mechanism was attributed to the up-regulation of enzyme activities involved in defense reaction, and down-regulated genes related with trichothecenes biosynthesis pathway. Afterwards, Xue research group found an interesting result that T-2 toxin, as a kind of trichothecenes A, suppressed the expansion of dry rot of potato at a low concentration [92]. Later, Han found the treatments of sodium silicate and brassinosteroid promoted wound healing of potato and accelerating suberin deposit, ultimately enhanced the resistance against dry rot of potato [78-79]. Jiang adopted BTH to treat potato and also observed the similar control effect on potato dry rot by accelerating wound healing [80]. Ma et al. [93] found the gene of *StCDPK23* played an important role on wound healing of potato and suberin deposition, and constructed *StCDPK23*-overexpressing plants to conformed *StCDPK23* participated in the tuber wound healing and contributed the resistance against dry rot of potato.

In addition, essential oils and extracts from plants displayed an excellent effect in suppressing the development of *Fusarium* dry rot by soaking or fumigation treatment [94]. Essential oil from *Zanthoxylum bungeanum* was found to be efficient in inhibiting the expansion of dry rot disease resulted from *F. sulphureum* [11]. The cinnamaldehyde, a major component of cinnamon essential oil, displayed a better control effect on potato dry rot resulted from *F. sambucinum*, the underlying mechanism revealed that cinnamaldehyde suppressed spore germination by impacting the biosynthetic pathway of ergosterol, improving ROS accumulation, ultimately resulting in a breakdown of cell membrane integrity [12]. Similarly, the essential oils from peppermint and fennel also remarkedly suppressed the *F. oxysporum* growing and reduced the Fusarium dry rot developing when treated with a protective emulsifiable concentrate [95]. It is interesting that some essential oils directly influenced mycotoxin metabolism by impacting the biosynthetic pathway of mycotoxins, for instance, the essential oils from palmarose and clove reduced DON and ZEA accumulation by down-regulating the expression of genes involved in mycotoxin the biosynthetic pathway of DON and ZEA [96]. Essential oils from plant, as a sustainable alternative to chemical synthetic fungicides, needs to be studied in-depth in the future [1, 97]. The extract from plant also displays excellent effect on plant disease [98]. The extract from black spruce revealed antifungal and suppressive potential to prevent the development of potato dry rot [99]. The extract from cinnamon also significantly inhibited *F. sambucinum* spore growth *in vitro* and reduced dry rot development *in vivo* [100]. Chlorogenic acid, as a kind of polyphenols with antioxidative activity, is mainly from the methanol extract, and also displayed a better inhibitory activity on the development of *Fusarium* dry rot of potato. The possible action mechanism is attributed to chlorogenic acid application modified morphological structure of *F. sambucinum*, the phenomenon of curling, twisting and collapse was observed after exposure of chlorogenic acid [1].

Additionally, chlorine dioxide and ozone, as the two strong oxidants, also perform an important and crucial role in controlling the *Fusarium* dry rot. Chlorine dioxide (ClO_2) acts as a water-soluble strong oxidant, whose oxidation ability is 2.5 times higher than that of chlorine. ClO_2 can be applied in both gaseous and aqueous solution form to control the postharvest disease on fruits and

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vegetables. For instance, Li et al [101] suggested that 0.75 ug/mL ClO_2 solution application significantly reduced the incidence of *Fusarium* dry rot of potato and suppressed the expansion of the lesion diameter by damaging the morphology and ultrastructure of *F. sulphureun* hyphae. Ozone, as another high efficiency and non-toxic, strong oxidant, also display an important role to control potato dry rot, on the one hand, ozone inhibited the growth of *F. sulphureum* spore, destroyed the structure of *F. sulphureum* [102], on the other hand, ozone treatment activated ROS metabolism of the potato tuber, and induced the resistance against dry rot [103].

2.4.5.3. Biological treatment

Biocontrol is regarded as a greener and safer strategy for the food safety and human health, comparing with the traditional chemical synthetic fungicides. Presently, scientists have been focusing on the research on antagonistic microorganisms to manage plant diseases. Antagonistic microorganism is currently regarded as the most potential alternative option to manage postharvest diseases. For instance, antagonistic microorganisms effectively controlled *Fusarium* dry rot during the potato wounds healing process when the tubers are at their most vulnerable. Schisler's group firstly reported the strains of *Pseudomonas Migula* spp., *Enterobacter Hormaeche* & *Edwards* spp., and *Pantoea Gavini*. spp. remarkedly decreased the incidence of potato dry rot resulted from *F. sambucinum* [104]. Later, the group found the mixtures of various antagonist strains had more efficient to control potato dry rot than that of single strain [105]. Gözdenur and Elif [106] screened 12 bacterial and fungal isolates and found that *Pantoea agglomerans* manifested the most efficacy to suppress the growth of *F. oxysporum* and control the occurrence of potato dry rot.

Trichoderma harzianum and *Bacillus subtilis*, as the two most important biological control agents, were registered to manage potato disease. The two agents were the most studied mycoparasitic species for their antagonistic function against a broad spectrum of pathogenic fungus, as well as recognized as a most promising strategy to inhibit different kinds of pathogenic fungi growth and control both preharvest and postharvest plant diseases occurrence. Daami-Remadi et al. [107] suggested *T. harzianum* and *T. viride* manifested a greater antagonistic activity against Fusarium dry rot in potato in Tunisia. El-Kot [108] compared four strains of fungal, bacterial and bioagents actinomycetes, and suggested that *T. harzianum* displayed the most efficient to inhibit the radial development of *F. sambucinum* and controlling the occurrence of dry rot under green house. Paul et al. [109] also observed *T. harzianum* strains CMML20-26 and CMML20-27 significantly decreased the postharvest disease in sweet potato. *B. subtilis* also plays a vital role to reduce potato disease. Wharton and Kirk [110] used the bioagent of *B. subtilis* in combination with excellent management practices to significantly reduce seed piece decay by 94.3% in 2007. Hussain et al [111] compared the biosurfactant extract, culture filtrate and bacterial cell suspension from *B. subtilis HussainT-AMU* and found bacterial cell suspension (49%) and biosurfactant extract (70%) had the most control effects on the net house and field, respectively.

In recent years, *Trichothecium roseum* was also reported to act as an elicitor to induce resistance against dry rot in potato tuber infected by *F. sulphureum*. During the defense responses induced by elicitor, the genes involved in resistant-reaction were up-regulated, accordingly, the enzymes activities and antifungal compounds contents were also significantly decreased after *T. roseum* application [112]. The possible mode of action for bioagent include mycoparasitism, competition for nutrients, and the production of extracellular enzymes and/or secondary metabolites [113]. For instance, Xue et al. research group [92] indicated that T-2 toxin (secondary metabolites from *F. sulphureum*) at the concentration of 1μg/mL could be act as an elicitor to induce resistance against dry rot by activating ROS metabolism and phenylpropane metabolism in potato.

3. Conclusions

Fusarium dry rot of is regarded as a major disastrous potato decay that damage tubers quality and cause economic losses and mycotoxin contamination. There are 17 species, and 5 variants of *Fusarium* causing potato dry rot all over the world, and the genetic diversity changes relying on the geographical location. The frequency of occurrence and aggressiveness of *Fusarium* dry rot also differ relying on the prevalent variety and ambient condition in a location-specific manner. Because the susceptibility or resistance of a particular cultivar is related to *Fusarium* species and storage

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temperature, a breeding project is in urgent need to design adapting to different cultivars against *Fusarium* species.

To efficiently control *Fusarium* dry rot of potato, an integrated disease controlling strategy is recommended that includes excellent harvesting conditions to avoiding tuber injury, suitable storage conditions (optimum temperature, humidity, CO_2 concentration), as well as planting the seed tubers free visible disease, and registered chemical synthetic fungicides and/or postharvest GRAS treatment. Fusarium dry rot controlling strategies eventually integrate the application of alternative like GRAS and microbial antagonists. The efficient strategy to manage *Fusarium* dry rot mainly depend on further research such as the combination of gene editing and molecular breeding and development efforts between scientists and industry to implement a integrated management measure towards the high-efficient controlling of Fusarium dry rot of potato.

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