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REVIEW



Pre- and postharvest measures used to control decay and mycotoxigenic fungi in potato (*Solanum tuberosum* L.) during storage

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ABSTRACT

Potato (*Solanum tuberosum* L.), a worldwide, staple food crop, is susceptible to postharvest rots caused by a variety of fungal pathogens, including *Fusarium* spp., *Alternaria* spp., *Phytophthora infestans*, *Helminthosporium solani*, *Rhizoctonia solani*, and *Colletotrichum coccodes*. Rots resulting from infections by these pathogens cause a significant reduction in potato quality and marketable yield. Importantly, some of these decay fungi also produce mycotoxins that represent a potential risk to human health. In the present review, an overview and discussion are provided on the epidemiology and pathogenesis of decay fungi, especially *Fusarium* spp., that include recent data derived from genomic and phylogenetic analyses. The biosynthesis and functional role of fungitoxic metabolites such as trichothecene mycotoxins and fusaric acid, produced in rotted potatoes are also reviewed. Advances in pre- and postharvest measures for rot management, especially eco-friendly methods including physical control, biological control, the use of natural compounds, and other agricultural management practices are also reviewed. Lastly, novel approaches to control potato dry rot such as the use of mycoviruses and CRISPR technology are highlighted.

KEYWORDS

Decay control; food safety; postharvest rot; potato

Introduction

Potato (*Solanum tuberosum* L.) is the fourth most-important food crop in the world after rice, wheat, and maize. It is the only major non-grain food crop that is considered to play a central role in global food security (Potato Genome Sequencing Consortium 2011). Potato is a main source of antioxidants in the human diet, and also provides basic nutrients such as carbohydrates, dietary fiber, as well as several vitamins and minerals (e.g., potassium, magnesium, iron, zinc) (King and Slavin 2013; Lovat et al. 2016). About 5000 potato varieties have been reported to be grown worldwide (Zaheer and Akhtar 2016). The latest data from FAO showed that the potato-growing area was 1,75,78,672 ha, with production of 368,168,914 tonnes in 2018 (<http://www.fao.org/faostat/en/?#data/QC>). In addition to being widely planted, potato plants are vigorous, high-yielding, and are adaptable to a wide array of environmental conditions (Cui et al. 2018). Potatoes are susceptible, however, to a variety of plant pathogens, including fungi (Gao et al. 2000; Liu et al. 2019), bacteria (Charkowski 2018; Clarke et al. 2019) and viruses (Yellareddygar, Whitworth, and Gudmestad 2018; Zhan et al. 2019) that cause disease at different stages of potato production. In particular, infections by fungi such as *Fusarium* spp., *Alternaria solani*, *Alternaria tenuissima*,

Phytophthora infestans, *Phytophthora erythroseptica*, *Pythium ultimum*, *Helminthosporium solani*, and *Colletotrichum coccodes* result in significant reductions in quality and marketable yield. Tuber losses average 7.5% during postharvest storage, but these losses can be significantly reduced if appropriate and effective storage management practices are utilized. A representative list of reports on postharvest fungal decay of potato is shown in Table 1. Importantly, some species of *Fusarium* produce mycotoxins that represent a potential risk to human health. As regulatory policies on food safety and environmental protection become more restrictive and public concerns over exposure to chemicals in the human diet increases, eco-friendly management methods such as the use of chitosan (Liu et al. 2019), biocontrol agents (Al-Mughrabi, Vikram, et al. 2013; Recep et al. 2009), essential oils (Al-Mughrabi, Coleman, et al. 2013), and organic and inorganic salts (Conway et al. 1992; Yaganza, Tweddell, and Arul 2014) for controlling postharvest decay of potato are being explored. The aim of the current review is to provide an overview of the epidemiology and pathogenesis of decay fungi associated with potato, the functional role of fungitoxic metabolites produced in rotted potatoes, and advances in pre- and postharvest methods of rot management. Novel management technologies for controlling potato dry rot, such as the use of mycoviruses and CRISPR

Table 1. Representative literatures regarding postharvest fungal decay of potato.

Disease	Casual pathogen	Source
Dry rot	<i>F. solani</i>	Chehri, Ghasempour, and Karimi 2014; El-Hassan et al. 2007; Falert and Akarapisan 2019; Lobato et al. 2011
Dry rot	<i>F. sambucinum</i>	Corcuff et al. 2011; Du et al. 2012; El-Hassan et al. 2007; Gachango et al. 2011; Heltoft et al. 2015; Patil et al. 2017; Sagar et al. 2011
Dry rot	<i>F. oxysporum</i>	Du et al. 2012; El-Hassan et al. 2007; Gachango et al. 2011
Dry rot	<i>F. avenaceum</i>	Du et al. 2012; Heltoft et al. 2015
Dry rot	<i>F. culmorum</i>	Heltoft et al. 2015
Dry rot	<i>F. graminearum</i>	Estrada et al. 2010; Falert and Akarapisan 2019
Dry rot	<i>F. acuminatum</i>	Du et al. 2012
Dry rot	<i>F. coeruleum</i>	Heltoft et al. 2015
Dry rot	<i>F. sulphureum</i>	Yin et al. 2010
Dry rot	<i>F. equiseti</i>	El-Hassan et al. 2007
Alternaria rot	<i>Alternaria solani</i>	Wharton et al. 2012
Alternaria rot	<i>A. tenuissima</i>	Liu et al. 2019
Late blight	<i>Phytophthora infestans</i>	Gachango, Kirk, et al. 2012; Johnson 2008; Lobato et al. 2011
Pink rot	<i>Phytophthora erythroseptica</i>	Gachango, Kirk, et al. 2012; Johnson 2008
Pythium leak	<i>Pythium ultimum</i>	Gachango, Kirk, et al. 2012; Lui and Kushalappa 2003
Silver Scurf	<i>Helminthosporium solani</i>	Errampalli, Saunders, and Holley 2001; Geary et al. 2007; Johnson 2007; Johnson and Cummings 2015; Wood, Miles, and Wharton 2013
Black Scurf	<i>Rhizoctonia solani</i>	Buskila et al. 2011; Chand and Logan 1984; Tsrar 2010
Black dot	<i>Colletotrichum coccodes</i>	Johnson and Cummings 2015; Lee and Hilton 2003; Peters et al. 2016; Wood, Miles, and Wharton 2013

technology, are highlighted. While bacterial pathogens of potato tubers (e.g. *Erwinia carotovora*, *Pectobacterium*, and *Dickeya* species) also represent a significant problem, the focus of the present review is on fungal and mycotoxigenic fungi. The readers are referred to recent review articles on bacterial diseases of potato tubers by Charkowski (2018), Prajapat, Marwal, and Jha (2013), and Umunna and Austin (2016).

Dry rot

The causal pathogens

Dry rot caused by *Fusarium* spp. is a devastating fungal disease that affects potatoes worldwide (Gachango, Hanson, et al. 2012; Lastochkina et al. 2020). Infected tubers rot after they are harvested and infected seed pieces decay after planting. Dry rot losses during storage have been estimated to range from 6% to 25%, and occasionally as high as 60% in extreme cases (Du et al. 2012; Gachango, Hanson, et al. 2012). *Fusarium* dry rot symptoms first appear on tubers at wound sites as shallow, small brown lesions after about one month of storage. The initial infection then enlarges in all directions and eventually the periderm collapses and the growing lesion may appear as concentric rings as the underlying dead tissue desiccates (Bojanowski et al. 2013). Cavities underneath the brown, dry decay area are typically lined with mycelia (Ali, Rivera, and Secor 2005). *Fusarium* is a large fungal genus within the Ascomycota phylum comprising a few hundred species that are mainly distributed in soil and in association with plants (Summerell et al. 2010). Thirteen species of *Fusarium* have been designated globally as causal agents of potato dry rot (Bojanowski et al. 2013; Cullen et al. 2005). The most common casual agents are *F. solani*, *F. sambucinum*, *F. oxysporum*, *F. avenaceum*, and *F.*

culmorum, with *F. solani* and *F. sambucinum* being the most predominant species (Bojanowski et al. 2013; Du et al. 2012). The pathogenicity of these species varies significantly depending on potato cultivar, geographic location, and season (Choiseul, Allen, and Carnegie 2001; Esfahani 2005). For example, *F. sambucinum* is a more aggressive pathogen than other *Fusarium* species in most potato cultivars in Great Britain, while *F. avenaceum* and *F. culmorum* are relatively weaker pathogens (Peters et al. 2008). Similarly, Du et al. (2012) found that the majority of potato cultivars grown in northern China are moderately to highly susceptible to *F. sambucinum*. Esfahani (2005) evaluated the susceptibility of 43 commercially-available potato cultivars to *F. sulphureum*, *F. solani* and *F. oxysporum* under similar conditions over two growing seasons and found that the 43 potato cultivars exhibited varying levels of resistance to the different *Fusarium* species. *F. sulphureum* was found to be more aggressive than the other two species and the resistance to each species was independent of cultivar. Collectively, these reports that susceptibility to dry rot caused by *Fusarium* species may vary in different production areas, and is determined by several factors, including cultivar, climate, and management practices.

Genome sequences and genetic diversity in *fusarium* spp

An ever-increasing amount of genetic and phylogenetic data on *Fusarium* spp. has become available due to advances in DNA sequencing and bioinformatic tools. *F. sambucinum*, a major causal agent of potato dry rot in both field and storage, also produces secondary metabolites that are toxic to humans and animals (Bertero et al. 2018; Desjardins 1995). Patil et al. (2017) published a draft genome sequence of *F. sambucinum* Fckl. (strain F-4), which was estimated to be

Table 2. Representative literatures regarding mycotoxins associated with postharvest dry rot of potato.

Decay fungus	Mycotoxin	Source
<i>F. sambucinum</i>	diacetoxyscirpenol	Ellner 2002
<i>F. sambucinum</i>	sambutoxin	Kim and Lee 1994; Kim, Lee, and Yu 1995
<i>F. sambucinum</i>	trichothecene	El-Hassan et al. 2007; Ismail, McCormick, and Hijri 2011, 2013; Xue et al. 2014
<i>F. oxysporum</i>	trichothecene	El-Hassan et al. 2007
<i>F. oxysporum</i>	moniliformin	Kim and Lee 1994
<i>F. graminearum</i>	trichothecene	Delgado et al. 2010; Pasquali et al. 2016; Stefańczyk et al. 2016
<i>F. graminearum</i>	zearalenone	Stefańczyk et al. 2016
<i>F. solani</i>	trichothecene	El-Hassan et al. 2007; Xue et al. 2014
<i>F. sulphureum</i>	trichothecene	Xue et al. 2014
<i>F. culmorum</i>	trichothecene	Pasquali et al. 2016;
<i>F. culmorum</i>	zearalenone	Stefańczyk et al. 2016
<i>F. equiseti</i>	trichothecene	El-Hassan et al. 2007

around 42 Mb. The draft assembly contains 12,845 protein coding genes comprising greater than 35,900 exons and possessing a gene density of 3.13 genes per 10 Kb. *F. sambucinum* is evolutionary most closely-related to *F. graminearum* within the *Fusarium* species complex. This genome assembly provides a valuable resource for understanding pathogenicity and virulence factors, and their evolution within the complex and highly plastic *Fusarium* genus. A genome sequence and assembly of *F. graminearum* was also published by King et al. (2015) and represented the first complete genome assembly for a species within the Sordariomycetes. A total of 741 *F. graminearum* species-specific genes were identified in that assembly.

Pathogenicity and virulence of *Fusarium* spp

Isfahani, Alizadeh, and Ramazani (2014) investigated differences in the pathogenicity of *F. sulphureum*, *F. solani*, and *F. oxysporum* in 43 potato genotypes using similar-sized tubers in their evaluation. More specifically, 10 tubers of each of each genotype were separately inoculated with each species of *Fusarium*, and placed in storage in plastic boxes for eight weeks at 10 °C. Results indicated that *F. sulphureum* exhibited the greatest pathogenicity, followed by *F. solani*, and then by *F. oxysporum*. Notably, differences between genotypes were also readily apparent. Heltoft et al. (2015) evaluated the resistance of ten potato cultivars commonly grown in Norway to *F. coeruleum*, *F. avenaceum*, and *F. sambucinum*, and found that *F. sambucinum* was the most aggressive species, while *F. avenaceum* and *F. culmorum* only caused minor dry rot symptoms in the tubers. Furthermore, Heltoft et al. (2016) investigated the prevalence of *Fusarium* dry rot in potatoes produced in Norway, and found that the most commonly isolated species was *F. coeruleum*, followed by *F. avenaceum*, *F. sambucinum*, and *F. culmorum*. In that study, a quantitative PCR assay was developed that was specific to *F. coeruleum*, and could be used to successfully identify Norwegian isolates of this species. Du et al. (2012) conducted phylogenetic analysis of *Fusarium* isolates responsible for potato dry rot in China using a 700bp DNA fragment of the *translation elongation factor-1 alpha* gene as a molecular marker. A set of primers of a single gene, however, does not appear to be sufficient for identifying and separating the *Fusarium* species-complex responsible for potato dry rot. Stefańczyk et al. (2016)

evaluated the genetic diversity of *Fusarium* spp. associated with potato dry rot in Poland, and identified their putative fungal isolates as *Fusarium* species using partial nucleotide sequences of the internal transcribed spacer, *translation elongation factor 1-α* and *β-tubulin* genes. Raja et al. (2017) has recommended that both morphological and molecular data should be used whenever possible for fungal identification. Such an approach may provide a more reliable identification and phylogenetic analysis of the *Fusarium* spp. responsible for causing potato dry rot.

Mycotoxins associated with dry rot

Contamination of food and feedstuff with mycotoxins is a serious issue throughout the world, especially given the increase in global trade. Mycotoxins are secondary metabolites produced by filamentous fungi, such as *Fusarium*, in response to specific environmental conditions (Bertero et al. 2018). Infections of potato tubers by specific species of *Fusarium* is typically accompanied by the production of mycotoxins, thus representing a potential risk to human health and food safety. Ingestion of low to moderate amounts of *Fusarium* mycotoxins is common and generally does not result in obvious intoxication. These low amounts, however, may impair intestinal health and immune function in humans and animals (Antonissen et al. 2014). The representative studies on mycotoxin production by *Fusarium* spp. are listed in Table 2.

Fusarium graminearum and *F. culmorum* are the main cause of trichothecene type B contamination. Pasquali et al. (2016) established a database containing information on the production of different trichothecene compounds by different genotypes of *F. graminearum* and *F. culmorum*. Among the examined isolates of *F. graminearum*, the predominant genotype (82.9% of the tested isolates) produced 15-acetyldeoxynivalenol (15-ADON), followed by a genotype (13.6% of the tested isolates) that produced 3-acetyldeoxynivalenol (3-ADON), and finally a genotype (3.5% of the tested isolates) that produced nivalenol (NIV). The predominant genotype (59.9%) among isolates of *F. culmorum* produced 3-ADON, while the other isolates (40.1%) were characterized as a genotype producing NIV. The geographical patterns of the distribution of trichothecene genotypes were also identified. For example, the study found that there was a limited spread of 15-ADON trichothecene genotypes into the

Northern latitudes. An earlier study of 14 *F. graminearum* isolates found that 12 isolates were classified as a deoxynivalenol (DON) genotype and 2 as a NIV genotype, with trichothecenes only being detected in rotting tissues (Delgado et al. 2010). Notably, Song et al. (2014) reported that in addition to trehalose biosynthesis, trehalose 6-phosphate phosphatase was also required for development, virulence and mycotoxin biosynthesis in *F. graminearum*. Since the publishing of the genome sequence of *F. graminearum* (Cuomo et al. 2007; King et al. 2015), significant progress has been made in understanding the DON biosynthesis and its regulation. Details on this topic can be found in the review by Chen, Kistler, and Ma (2019). The toxicology involved in the effect of these mycotoxins on human health also needs to be further investigated.

Other major rots

In addition to dry rot caused by *Fusarium* spp., other fungal rots of potato are also economically-important (Table 1). *Alternaria solani* causes early blight in potato plants, characterized on leaves by dark brown to black lesions with concentric rings (Yellareddygaru et al. 2019). Zheng and Wu (2013) reported on the occurrence of *Alternaria* blight of potato in China caused by *A. tenuissima*, and Zheng et al. (2015) later reported that *A. tenuissima* was the most prevalent species within the population structure of *Alternaria* species associated with potato foliar diseases. Both of these species, however, are also responsible for causing considerable levels of tuber rot during postharvest storage (Liu et al. 2019; Wharton et al. 2012). Potato late blight, caused by *Phytophthora infestans*, is among the most severely damaging diseases of potato leaves and tubers worldwide (Mohammadi et al. 2020). While *P. infestans* can spread rapidly in the field, a substantial amount of tuber-to-tuber spread of *P. infestans* can also occur during the mechanical harvesting and transfer of potato tubers to processing and storage facilities. Tuber-to-tuber spread is facilitated when injury to the tuber or even just the tuber skin occurs during the harvesting and transfer process. Tuber loss due to *P. infestans* of injured potatoes is well recognized and can result in tuber losses during storage that are much higher than would be predicted based on pathogen levels in the field. Johnson (2008) reported that severity of late blight on locally-grown potato tubers (cv. Shepody) in Northern Maine, was over 95% after 30 days of a storage at 13 °C and >95% relative humidity without the application of any control measures. The severity of pink rot of potato tubers, caused by *Phytophthora erythroseptica* could also be $\geq 95\%$ under the same storage conditions. However, the application of phosphorous acid compounds was found to have the ability to control postharvest late blight and pink rot of potato tubers.

Pythium leak of potato tubers, also known as water rot, caused by *Pythium ultimum*, is characterized by spongy, wet, internal rot of tubers. The pathogen is a soil-borne fungus that can survive in soils for a long period of time and infect a wide range of host plants. Sporangia enter potato

tubers through lenticels and wounds, so injuries to tubers that occur during cultural management and harvesting operations increase the probability of infection. Once infected, lesions continue to expand and develop during storage if environmental conditions are favorable. Lui and Kushalappa (2003) developed a predictive model for the potential infection of tubers by *P. ultimum* based on the duration of wetness and temperature and the model can be used to help manage water rot. Errampalli, Saunders, and Holley (2001) indicated in their review that during the 1990s, silver scurf, caused by *Helminthosporium solani*, emerged as an economically-important disease of table-stock and processing potatoes. The disease cycle of silver scurf comprises two phases: field and storage. Primary infection occurs in the field and in storage, while conidia produced in stored potatoes serve as inoculum for secondary infection cycles. Increases in this disease have been attributed to *H. solani* isolates that are resistant to the postharvest fungicide, thiabendazole (TBZ). Geary et al. (2007) reported that silver scurf incidence varied by geographic location, and first demonstrated the existence of TBZ and thiophanate-methyl resistant isolates of *H. solani* in the potato production area of Columbia Basin (Oregon and Washington States, USA). In addition to silver scurf, black scurf, caused by *Rhizoctonia solani*, of potato tubers can also result in significant economic losses (Tsrur 2010). Storage temperatures of 5, 10, or 15 °C at either low or high relative humidity can increase the incidence of black scurf. The number of sclerotia per tuber were lowest when tubers were stored at 5 °C under low relative humidity (Chand and Logan 1984). Lee and Hilton (2003) reported that black dot, caused by *Colletotrichum coccodes*, can also be an economically-important disease problem in potato and can represent both a pre- and postharvest disease. Infections are characterized by silvery lesions on the tuber surface that result in a deterioration in skin quality. Peters et al. (2016) reported that soil inoculum levels and crop duration (days from 50% emergence to harvest) collectively provide a reasonable ability to predict potential black dot severity at harvest and after 20 weeks of storage. The collective, postharvest rot diseases discussed in this review are responsible for both significant economic losses for the potato industry, but can also have a direct impact on food safety. Fortunately, a number of management practices exist that can ameliorate the health concerns and economic losses represented by these fungal diseases.

Eco-friendly management strategies

Although the current management of postharvest decay in harvested crops, including potato tubers, primarily relies on the use of synthetic chemical fungicides, increasing consumer demands for reducing exposure to commonly-used agricultural chemicals, stricter regulation by government agencies on the use of synthetic pesticides, and general concerns about the environment, have created a strong interest in developing alternative strategies that address major concerns about the use of synthetic chemicals in agriculture (Alamar et al. 2017). A discussion of the various alternative approaches, including natural compounds, growth regulators, biological control,

physical management strategies, and genetic enhancement, are the subject of the present review.

Natural compounds

The use of natural compounds including essential oils, biopolymers, salts, and growth regulators have been explored for their potential to control postharvest decay and preserve produce quality.

Essential oils – Plant-derived essential oils are produced by glandular trichomes and other secretory structures, and are often secreted onto the surface of plant organs, particularly flowers and leaves. In other cases, they are secondary metabolites that are generally produced in plant cells or in specific organs such as seeds. These essential oils have been historically used by humans as flavor food (spices), pharmaceuticals, and perfumes. In some cases, their role in plant ecology has been documented, however, in other cases their benefits to plant fitness remains ambiguous. Some essential oils can function as plant defense compounds against invading pathogens and herbivores either directly in the plant producing the compound(s), or after they are extracted and applied to plants in general (Sharifi-Rad et al. 2017). Some oils, as volatile natural compounds that possess antimicrobial or fungicidal properties, play a key role in food safety without affecting the quality (Bhavaniramy et al. 2019). Since essential oils are naturally produced and are biodegradable, their use is considered to be environmentally friendly. The use of essential oils has been explored as an alternative approach for controlling potato storage diseases and inhibiting sprouting (Alamar et al. 2017; Jia et al. 2019; Wei et al. 2020). S-carvone, L-menthone, peppermint, and spearmint oils have been evaluated in vitro by Al-Mughrabi, Coleman, et al. (2013) against *F. coeruleum*, *F. sambucinum*, *F. avenaceum*, *F. oxysporum*, *A. solani*, *R. solani*, *H. solani*, *Phytophthora infestans*, *Phytophthora erythroseptica*, *Pythium ultimum*, and *Phoma exigua*, all of which are causal agents of major potato storage diseases. All four essential oils exhibited significant inhibitory effects on the tested pathogens testes, however, peppermint oil was the least effective. In that study, aluminum starch octenylsuccinate was demonstrated to enhance the inhibitory effect of L-menthol or peppermint oil on *F. sambucinum* and *R. solani*. Elsherbiny, Amin, and Baka (2016) reported that application of a methanol extract of pomegranate peels significantly reduced dry rot development in potato tubers inoculated with *F. sambucinum*. The extract was shown to have both preventative and curative (inhibition of pre-established infections) activity. Notably, chlorogenic acid (42.401 mg/g) was the predominate phenolic compound present in the methanol extract and was suggested to play a major role in the inhibitory activity. Morphological modification of *F. sambucinum* hyphae, including curling, twisting and collapse, as well as inhibition of spore germination was observed after exposure of the fungus to the methanol extract. Similar results were reported for the essential oil of *Zanthoxylum bungeanum*, which decreased cell membrane integrity and inhibited spore germination of *F. sulphureum*. Ultrastructural alterations

were also observed, including cells devoid of cytoplasm and the generation of osmiophilic granules (Xing-Dong and Hua-Li 2014). Correspondingly, the essential oil effectively controlled dry rot of potato inoculated with *F. sulphureum*. Although essential oils have shown a great potential of managing postharvest decay of potatoes, the complexity of active components in these oils limits the deeper investigation of mode of action, and thus confines large-scale application. The identification and extraction of active components in the essential oils in further studies may accurate and enhance the control efficacy. Although many essential oils are commercially available, large-scale application of essential-oil-based fungicides would require significantly high levels of production of the specified oils from a large amount of plant material. In addition, the chemical profile of a plant species can vary depending on the location where it is grown, its genotype, as well as climatic and seasonal factors. Therefore, pesticide manufacturers would need to develop quality and efficacy testing standards that could be costly and time-consuming to ensure that their products perform consistently (Koul, Walia, and Dhaliwal 2008). Importantly, the safety of certain chemical compounds present in essential oils to human health would need to be scientifically validated, as is currently required for synthetic pesticides (Gurjar et al. 2012). Such safety testing and approval by regulatory agencies would require a significant monet-ary investment.

Biopolymers – Biopolymers, including polysaccharides, proteins, and lipids, used alone or in combination, have been evaluated as edible coatings for use on fresh produce as a replacement for synthetic waxes and postharvest fungicides. The compounds used in the edible coatings are readily available and low cost and the coatings have been shown to have antifungal activity, elicit defense responses, regulate gaseous exchange and water loss, and the ability to serve as a medium to carry other additives that contribute to the maintenance of produce quality (Saber and Golding 2018). Edible films have been generated from sodium alginate (NaAlg), high molecular weight (HMW) chitosan, and low molecular weight (LMW) chitosan. In vitro studies demonstrated that the addition of 1% fludioxonil was added to a formulation of NaAlg or chitosan-LMW films, antifungal activity of the coating against *F. solani* was significantly greater than the edible film alone. In vivo studies demonstrated that Chitosan-LMW-1% fludioxonil films reduced the incidence of *F. solani* in potato tubers kept at 25 °C for 2 weeks (Bilbao-Sainz et al. 2016). Chitosan with about 90% deacetylation was also reported to significantly inhibit the in vitro growth of *A. tenuissima* (Liu et al. 2019) and *F. sulphureum* (Sun et al. 2008), and acted as a natural elicitor of host defense response in potato tuber tissues. Collectively, the reported studies indicate that biopolymers have the potential control postharvest diseases and also maintain potato tuber quality, thus contributing to the extension of shelf life (Saha, Gupta, and Tyagi 2014). A greater emphasis on the safety aspects of antimicrobial agents and edible-coating components may be needed in the development of

biopolymer technology and its application (Cha and Chinnan 2004; Nor and Ding 2020).

Salts - Some organic and inorganic salts and their corresponding acids or bases, used typically for food preservation, have been shown to have antimicrobial properties and the potential to control postharvest diseases. Calcium deficiency results in several physiological disorders in harvested crops, including potato, that degrade product quality and reduce their economic value. Due to the inhibitory effects of calcium ions against postharvest fungal pathogens (Wisniewski et al. 1995), calcium dips was one of the methods that were explored as an alternative method of controlling postharvest diseases of produce. Conway et al. (1992) furthered this technology and demonstrated that postharvest vacuum infiltration of potato tubers with calcium nitrate reduced bacterial soft rot caused by *Erwinia carotovora* subsp. *astroseptica*. Calcium also played a role in minimizing the incidence and severity soft rot of potato tubers in storage caused by the bacterial *Pectobacterium* and *Dickeya* species (Mantsebo et al. 2014). Further research has been conducted of the ability of salt derivatives to prevent fungal decay. Sodium silicate strongly inhibited spore germination and mycelial growth of *F. sulphureum* in vitro, and effectively controlled dry rot of tubers in vivo (Li et al. 2009). Bicarbonate and carbonate salts, aluminum salts, potassium sorbate, calcium propionate, and sodium metabisulfite have all been shown to control potato tuber silver scurf (*Helminthosporium solani*) (Olivier et al. 1998; Olivier, MacNeil, and Loria 1999; Hervieux et al. 2002). A variety of aluminum-containing salts have also been shown to provide effective control of dry rot (*F. sambucinum*) at a minimal inhibitory concentration of 1–10 mM by spray, with 2 mL of solution per tuber. Aluminum chloride and aluminum sulfate were generally the most effective, followed by aluminum sulfate (Kolaei et al. 2013). Some sulfur-containing salts including ammonium sulfate, magnesium sulfate, potassium sulfate and sodium sulfate at the concentrations of 50–200 mM by spray, with 2 mL of solution per tuber (biosafe treatment dosage) have also been shown to significantly reduce potato dry rot severity (Kolaei, Tweddell, and Avis 2012). While these findings indicate that aluminum-containing/sulfur-containing salts represent an alternative to synthetic fungicides to control dry rot, and are generally recognized as safe, their use is not eco-friendly as these compounds are not readily biodegradable and can build up to toxic levels over time. In fact, the buildup of heavy metals in agricultural soils is a significant problem and is high-regulated by government agencies.

Growth regulators

Plant growth regulators are widely used in horticultural production in the field but also have applications related to postharvest disease resistance and quality (Asghari and Aghdam 2010; Lurie 2010; Pétriacq, López, and Luna 2018). β -aminobutyric acid (BABA), a non-protein amino acid, is naturally present in plants (Thevenet et al. 2017). BABA has been shown to induce resistance against fungal pathogens in a variety of crops. Yin et al. (2010) reported that postharvest

treatment of potato tubers with BABA induced resistance against dry rot caused by *F. sulphureum*. Dryocrassin ABBA, a novel flavonoid, natural product derived from *Dryopteris crassirhizoma*, has been reported to have antiviral (Ou et al. 2015), and antibacterial activities (Zhang et al. 2016). Regarding its antifungal activity, Wang et al. (2017) reported that dryocrassin ABBA strongly inhibited mycelial growth and spore germination of *F. solani* in vitro at concentrations of 2.0, 0.5 and 0.1 mg/mL. Dryocrassin ABBA induced morphological changes in hyphae of *F. solani*, including the formation of abnormal, tightly-twisted hyphae. Dryocrassin ABBA treatment of potato tubers at 2 mg/ml was also shown to effectively control dry rot in potato tubers inoculated with *F. solani*. The control was partially attributed to the induction of antioxidant enzyme activity and the increased expression of genes encoding lipid-transfer proteins (LTPs). More recently, the use of an endophytic strain of *Bacillus subtilis* as a biocontrol agent, combined with salicylic acid, on the development of postharvest diseases caused by *Phytophthora infestans* and *F. oxysporum* in stored potato tubers was evaluated by Lastochkina et al. (2020). Salicylic acid was found to enhance the biocontrol efficacy of *B. subtilis* by promoting the ability of *B. subtilis* to colonize internal potato tuber tissues, increase the level of ascorbic acid, and decrease pathogen-induced proline accumulation and lipid peroxidation in tubers. Jasmonate and its derivatives are lipid-based hormones that regulate a wide range of processes in plants. Allah et al. (2018) reported that 0.01 mM/L jasmonic acid decreased weight loss, decay, and sprouting in potato tubers during long-term storage (140 days) at $10 \pm 1^\circ\text{C}$ and $85 \pm 5\%$ relative humidity. Other growth regulators/signaling molecules, such as melatonin (Xu, Chen, and Kang 2019), brassinosteroids (Zhu et al. 2010), and nitric oxide (Hu et al. 2014) have also been reported to induce disease resistance in different horticultural crops. It would be worthwhile to investigate if these agents have similar positive effect on controlling postharvest decay in stored potato tubers. The mechanism by which these compounds induce resistance in potato tubers also remains to be elucidated. Plant hormones are part of complex networks that respond to developmental and environmental cues and thus a careful studies need to be conducted to balance their impact on the normal physiology and defense response of plants (Denancé et al. 2013). Additionally, in some cases, there are health concerns about exposure to hormones and the impact they may have on human health. Therefore, any expanded use of these substances would require strict and comprehensive analyses of their safety.

Biocontrol agents

A considerable amount of research effort has focused on the use of antagonistic microorganisms for the management of postharvest diseases. In addition to many fruit crops, biological control of postharvest rots of potato tubers using bacteria, fungi, and mycoviruses has been reported to be effective under experimental conditions. *Bacillus cepacia* was

demonstrated to have antifungal activity in vitro and in vivo (on potato tubers) against *F. sambucinum*, *F. oxysporum*, and *F. culmorum*, all of which are causal agents of dry rot disease in potato (Recep et al. 2009). The bacterial species, *Pseudomonas fluorescens* strain S22:T:04 (1×10^8 CFU/mL), has also been reported to be effective against dry rot (*F. sambucinum*) of potato tubers under commercial storage conditions (Schisler et al. 2000).

Despite their ability to inhibit postharvest diseases, the use of an antagonist alone has not proven to be sufficient to achieve consistent and reliable control under commercial conditions. Therefore, the use of a combination of different antagonists or other control methods has been explored to address this problem (Wisniewski et al. 2016). Preharvest field applications of *Bacillus licheniformis* and *Bacillus cereus* were also reported to control dry rot disease on seed tubers caused by *F. roseum* (Sadfi et al. 2002). The biocontrol agents also increased yield parameters, and decreased dry rot incidence in cold storage. Two bacterial biocontrol agents of *Bacillus* species (*Bacillus subtilis* and *B. pumilus*) were evaluated in two storage trials over two years for their ability to suppress infection of tubers by *Phytophthora infestans*, *Phytophthora erythroseptica*, *Pythium ultimum*, and *F. sambucinum* (Gachango, Kirk, et al. 2012). Results indicated that the biocontrol agents were as effective as conventional treatments with phosphorous acid, azoxystrobin, or hydrogen peroxide. Al-Mughrabi, Vikram, et al. (2013) reported that the application of the biopesticides, Bio-Save® 10LP (Jet Harvest Solutions, Longwood, FL, USA, based on *Pseudomonas syringae* strain ESC-10) and Bio-Save® 11LP (Longwood, FL, USA, based on *P. syringae* strain ESC-11) at the concentration of 9×10^{10} CFU/g, was effective against silver scurf (*H. solani*) and dry rot (*Fusarium* spp.) diseases of potato, and proposed that *P. syringae* may be a viable option as a postharvest treatment against some potato storage diseases. Antibiosis is one of the common and important mechanisms of action by bacterial antagonists to control postharvest fungal diseases (Carmona-Hernandez et al. 2019; Jamalizadeh et al. 2011). Therefore, concerns about the potential impact of using antibiotic-producing organisms on the development of antibiotic-resistant pathogens, especially human pathogens, is an aspect that needs to be addressed and further investigated.

Fungi have also been evaluated as biocontrol agents for the management of potato postharvest rots. *Trichoderma* is one of the most studied fungal genera and is well recognized for its ability to inhibit many different fungal pathogens and control both preharvest and postharvest diseases (Adnan et al. 2019). *Trichoderma harzianum* and *Trichoderma viride* were evaluated for their antagonistic activity against *F. oxysporum*, *F. solani*, *F. graminearum*, and *F. sambucinum*, causal agents of potato dry rot in Tunisia (Daami-Remadi et al. 2006). In this study, individual potato tubers, cv. Spunta, were inoculated with 100 μ L of a spore suspension of *Trichoderma* spp. (10^8 spores/mL) in artificially administered wounds. The biocontrol agent was administered 24 h prior to inoculating the tubers with *Fusarium* species. Results indicated a significant reduction in dry rot

development relative to the untreated control tubers, after 21 days of storage at room temperature. Mycoparasitism, competition for nutrients, and the production of extracellular enzymes and/or secondary metabolites have been proposed to be the major modes of action of *Trichoderma*. Yu et al. (2016) reported that another biocontrol fungus, *Trichothecium roseum*, functioning as an elicitor could significantly enhance defense responses in potato tubers against dry rot (*F. sulphureum*). The defense responses included the up-regulation of resistance-related genes as well as an increase in the activity of resistance-related enzymes and level of antifungal compounds. Wharton and Kirk (2014) applied treatments of, T-22 Planter Box® (*T. harzianum* Rifai strain KRL-AG2; Bioworks Inc., Victor, NY, USA) or Serenade Max® (AgraQuest Inc., CA, USA, based on *B. subtilis* strain QST 713) at 250 g per 100 kg potato seed, to potato seed pieces exhibited good control efficacy of decay caused by *F. sambucinum*. Antagonistic yeasts have also been extensively studied and used in the control of postharvest diseases of fruits and vegetables (Liu et al. 2013; Wisniewski et al. 2016). The antagonistic yeast *Wickerhamiella versatilis* has been reported to be effective against soft rot disease of potato caused by the bacterial pathogen, *Pectobacterium carotovorum* subsp. *carotovorum* (Hassan, Bagy, and Bashandy 2019). Hadwiger, McDonel, and Glawe (2015) reported that wild yeast strains, *Metschnikowia pulcherrima*, *Curibasidium pallidicorallinum*, and *Candida saitoana*, applied to potato leaves prior to inoculation with *P. infestans* reduced symptoms in a manner suggestive of induced immunity. However, the use of yeasts as biocontrol agents against postharvest fungal rots of potato has not yet been extensively explored. Biological control utilizing fungal antagonists to detoxify *Fusarium* mycotoxins has also been explored. Ismail, McCormick, and Hijri (2011, 2013) reported that an arbuscular mycorrhizal fungus, *Glomus irregulare*, could modulate mycotoxin gene expression in *F. sambucinum*, inhibit its growth, and significantly reduce the production of DAS. Tian et al. (2016) reported that antagonistic *Trichoderma* strains were able to detoxify DON, produced by *F. graminearum*, via glycosylation. The evaluation of mycoparasites as biocontrol agents that can prevent plant diseases and detoxify/degrade mycotoxins is an ongoing topic of research (Kim and Vujanovic 2016).

Mycoviruses are widespread throughout the major taxonomic groups of fungi (Kotta-Loizou and Coutts 2017; Yu et al. 2013). Most mycoviruses have RNA genomes, either double-stranded RNA (dsRNA) or single-stranded RNA (ssRNA), although a few mycoviruses are composed of single-stranded circular DNA (Li et al. 2020; Yu et al. 2010). Although most mycoviruses do not have a significant impact on their hosts, some may cause hypovirulence diminishing the ability of the pathogenic fungus to cause disease (Marzano et al. 2016; Xie and Jiang 2014). Hypovirulence-based biocontrol has already been employed to control chestnut blight, caused by *Cryphonectria parasitica*, in chestnut trees in Europe. This has persuaded mycologists and plant pathologists to explore hypovirulent factors in fungi globally. Mycovirus-associated hypovirulence has been

reported in several *Fusarium* species that infect different crops in several countries around the world. The genomes of most of the reported mycoviruses contain double-stranded RNA in the form of isometric particles (Sharma et al. 2018). Most *Fusarium* mycoviruses do not cause any morphological changes in their hosts, however, *Fusarium graminearum* virus 1 (FgV1) does cause hypovirulence. Genomic data for seven of the dsRNA mycoviruses infecting *Fusarium* species indicate that these mycoviruses exist as complexes of one to five dsRNAs. Phylogenetic analysis indicates that the *Fusarium* mycoviruses identified to date belong to four families: *Chrysoviridae*, *Hypoviridae*, *Partitiviridae*, and *Totiviridae* (Cho et al. 2013). A dsRNA mycovirus (FgV-ch9) has been reported to cause hypovirulence in *F. graminearum* which infects wheat and maize (Darissa, Adam, and Schäfer 2012). More recently, Li, Bian, et al. (2019) have identified a novel hypovirulence-inducing ssRNA mycovirus infecting an *A. alternata* f. sp. *mali* strain isolated from an apple orchard in China. Ma et al. (2019) have isolated a new dsRNA virus named *Alternaria alternata* botybirnavirus 1 (AaBRV1) from *A. alternata* strain SD-BZF-19, which is a phytopathogenic fungus infecting watermelons in China. In this study, a complete genome sequence was assembled and a phylogenetic analysis of the RNA dependent RNA polymerase domain of the polyprotein revealed that AaBRV1 clusters together with members of the genus *Botybirnavirus*. As the amount of genomic information on mycoviruses increases, it is expected that a greater understanding will be forthcoming on the mechanisms mycoviruses use to infect their hosts and that more mycoviruses with biocontrol potential will be identified. Moreover, warranting the biosafety and overcoming the difficulties in formulation, the shortness of shelf life, and inconsistency in performance will be the key elements for large-scale development and application of biocontrol products based on microorganisms.

Physical management strategies

The development of physical treatments to control postharvest diseases in fruits and vegetables has been actively pursued since their use eliminates the occurrence of any residues in the treated product and they generally have a minimal environmental impact (Usall et al. 2016). Among the variety of physical treatments that have been explored, the use of ultraviolet-C light (UV-C, 190–280 nm) has shown significant application due to its ability to directly inhibit pathogen growth and also induce defense mechanisms in host tissues (Romanazzi et al. 2016). The use of UV-C and fluorescent lights provided control of soft rot in potato caused by *P. carotovorum* subsp. *carotovorum* without inducing sprouting. UV-C and fluorescent light have been shown to induce the accumulation of antifungal substances in potato which may contribute to disease control (Rocha et al. 2015). UV-C irradiation was reported to completely prevent the development of both dry rot (*F. solani*) and soft rot (*Erwinia carotovora*) in potatoes stored at 8 °C for 3 months (Ranganna, Kushalappa, and Raghavan 1997). A

recent study by Jakubowski and Królczyk (2020) also used UV-C radiation to successfully reduce postharvest rots in stored potato tubers.

Harvesting, processing and storage conditions have a significant impact on the incidence and severity of many storage diseases of potato (Bojanowski et al. 2013). Potatoes are prone to be contaminated with 4,15-diacetoxyscirpenol when they are infected by *F. sambucinum*. The level of 4,15-diacetoxyscirpenol (DAS), a type A trichothecene, was reduced by 26% when infected potatoes were cooked for 1 h at 100 °C and by 100% when cooked for 4 h at 121 °C (Shams et al. 2011). *Fusarium* spp. only infects tubers through wounds, so considerable effort should be placed on using practices that minimize tuber bruising and wounding. It is best to harvest potatoes when conditions will allow the tubers to remain at temperatures between 10 and 18 °C. Tubers should also be harvested 1–2 weeks after the above-ground potato plants have died to ensure maturation of tuber skin (epidermis) (Knowles and Plissey 2008). Potato tubers should be exposed to conditions favoring wound healing after they are harvested. Good conditions for rapid wound healing in storage are high humidity (95–99%), a tuber pulp temperature between 13 and 16 °C, and adequate ventilation to prevent condensation on the tubers. After the wound-healing period (7–10 days), temperature and relative humidity should be decreased to 2–5 °C (10 °C for processing tubers) and 90–95% RH. Seed tubers should be warmed before they are cut into seed pieces after storage to promote rapid healing (Bojanowski et al. 2013).

Genetic enhancement utilizing CRISPR

Genome-editing utilizing the Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/Cas9 system for targeted genome modifications has emerged as a powerful approach to genetic engineering, due to the ability to design and construct gene-specific single guide RNA (sgRNA) vectors. The CRISPR/Cas9 system offers an alternative approach to conventional genetic engineering and is expected to revolutionize the ability to produce superior genotypes of crops with economically-important traits such as disease resistance, better nutritional value, and stress resistance, in a manner that is safe and acceptable to regulatory agencies and consumers. A potato reference genome has been assembled (Potato Genome Sequencing Consortium 2011) that will facilitate the application of CRISPR technology in potato. Butler et al. (2015) initially tracked the generation and inheritance of targeted mutations in potato using the CRISPR/Cas9 system, which provided a foundation for future genetic manipulation of potato. Since then, several genome editing projects have been conducted in potato using the CRISPR/Cas9 system (Khromov et al. 2018; Nadakuduti et al. 2019). CRISPR/Cas9 was used to deliver ribonucleoproteins to potato protoplasts by targeting the gene encoding a starch granule-bound starch synthase (Andersson et al. 2018). Agrobacterium-mediated transformation was used to deliver a CRISPR/Cas9 cytidine base editor (Veillet et al. 2019). CRISPR/Cas9-mediated editing was used to modify genes encoding rgs-CaM-like proteins

in transgenic potato plants (Osmani et al. 2019). Hameed et al. (2019) reviewed the potential of using the CRISPR-Cas system to confer pathogen-derived or host-mediated resistance against phytopathogenic RNA viruses in potatoes and other crop plants. A multiplexed CRISPR-Cas13a methodology was also proposed to combat Potato virus Y (PVY), a globally diverse phytopathogen infecting multiple crops. Zhan et al. (2019) demonstrated that transgenic potato lines expressing Cas13a/sgrRNA constructs exhibited lower PVY accumulation and disease symptoms than wild-type plants. The levels of viral resistance were correlated with the expression level of the Cas13a/sgrRNA construct in the transgenic potato plants. Appropriately designed sgrRNAs can specifically interfere with multiple PVY strains, while having no effect on unrelated viruses, such as PVA or Potato virus S. In addition to virus resistance, Makhotenko et al. (2019) utilized a bioballistic approach to deliver gold or chitosan microparticles coated with a complex consisting of the Cas9 endonuclease and a short guide RNA into apical meristem cells of potato. Editing of at least one allele of the coilin gene considerably increased the resistance of the edited lines to infection by the potato virus Y and also increased the tolerance of potato plants salt and osmotic stress. It is evident that this genome-editing technology holds great promise for the development of potato genotypes with increased resistance to fungal pathogens, including causal fungi for postharvest rots. Barrangou and Ntebebaart (2019) stated in their review that many CRISPR tools can be used to manipulate food microbiomes from farm to fork. Various pathogenic bacteria and spoilage organisms can be targeted and controlled with the use of CRISPR-based antimicrobials. The properties of beneficial bacteria, such as starter cultures and probiotics, can also be enhanced using CRISPR-based genome editing. Implementation of CRISPR tools in foods, however, will require regulatory approval and consumer acceptance. The need for the development of technical and ethical guidelines, at all levels, and the establishment of laws on the bioethical issues associated with genetic manipulation of genomes, have also been emphasized (Li, Bian, et al. 2019).

Future trends

There is increasing need to develop eco-friendly, effective methods that manage postharvest losses caused by microbial pathogens. As the population of the world continues to increase, the ability to prevent the loss of harvested crops to postharvest diseases has become even more critical (Wisniewski and Droby 2019). More recently, Kusstatscher et al. (2020) reported that high microbial diversity and resilient microbial networks are linked to fruit and vegetable health, while diseased products exhibit severe dysbiosis. Field management practices and postharvest handling of fruits and vegetables have been shown to affect the composition of the indigenous microbiome of fruits and vegetables and have a substantial impact on their storability. Microbiome tracking could be implemented as a tool to evaluate postharvest processes, and their potential impact on fruit and vegetable health. The review by Kusstatscher et al.

(2020) presents new insights into postharvest microbiome dynamics and suggests that modulation of the microbiome provides a new approach for the development of new, sustainable disease control strategies as previously postulated by Droby and Wisniewski (2018).

In addition, the utilization of mycoviruses as biocontrol agents and CRISPR technology to control dry rot in potato are areas deserving greater research. Fungal pathogens infected with a mycovirus, exhibit a decreased ability to infect host tissues, and often accompanied by decrease in mycelial growth, sporulation, etc. A novel dsRNA mycovirus was isolated from *F. oxysporum* (Lemus-Minor et al. 2015), while a new botybirnavirus was isolated from *A. alternata* (Ma et al. 2019). Complete genome sequences of both mycoviruses have been reported. Elucidating the mechanisms underlying the interaction between mycovirus - fungal pathogen - potato host, will greatly facilitate the discovery of other mycoviruses that can be effectively used to manage potato storage diseases. Whether mycoviruses affect mycotoxin production and whether they are safe to humans will require further research. Using CRISPR technology, the molecular breeding of potato utilizing CRISPR technology for resistance to seed-borne fungal diseases and their related postharvest rots has great future potential.

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