



# Potato dry rot disease: current status, pathogenomics and management

Rahul Kumar Tiwari<sup>1,2</sup> · Ravinder Kumar<sup>1</sup> · Sanjeev Sharma<sup>1</sup> · Vinay Sagar<sup>1</sup> · Rashmi Aggarwal<sup>2</sup> · Kailash Chandra Naga<sup>1</sup> · Milan Kumar Lal<sup>1,2</sup> · Kumar Nishant Chourasia<sup>1</sup> · Dharmendra Kumar<sup>1</sup> · Manoj Kumar<sup>1</sup>

Received: 6 August 2020 / Accepted: 19 October 2020 / Published online: 3 November 2020  
© King Abdulaziz City for Science and Technology 2020

## Abstract

Potato dry rot disease caused by *Fusarium* species is a major threat to global potato production. The soil and seed-borne diseases influence the crop stand by inhibiting the development of potato sprouts and cause severe rots in seed tubers, table and processing purpose potatoes in cold stores. The symptoms of the dry rot include sunken and wrinkled brown to black tissue patches on tubers having less dry matter and shriveled flesh. Fungal infection accompanied by toxin development in the rotten tubers raises more concern for consumer health. The widespread dry rot causing fungal species (*Fusarium graminearum*) is reported to have a hemibiotrophic lifestyle. A cascade of enzymes, toxins and small secreted proteins are involved in the pathogenesis of these hemibiotrophs. With the availability of the genome sequence of the most devastating species *Fusarium sambucinum*, it is important to identify the potential pathogenicity factors and small secreted proteins that will help in designing management strategies. Limited resistant cultivars and the emergence of fungicide-resistant strains have made it more threatening for potato cultivation and trade. Several novel fungicide molecules (Azoxystrobin, chlorothalonil and fludioxonil), are found very effective as tuber treatment chemicals. Besides, many beneficial bioagents and safer chemicals have shown antibiosis and mycoparasitism against this pathogen. Germplasm screening for dry rot resistance is important to assist the resistance breeding program for the development of resistant cultivars. This review aims to draw attention to the symptomatology, infection process, pathogenomics, the role of toxins and management approaches for potato dry rot disease, which is very much critical in designing better management strategies.

**Keywords** *Fusarium* dry rot · Pathogenomics · Tuber · Toxins · Potato · Management

## Introduction

Potato (*Solanum tuberosum* L.) ranks first as a non-cereal food crop for human consumption and has a great potential in ensuring food security in developing nations (FAOSTAT 2019). The diverse distribution pattern and major cultivation as a cash crop in areas having a high level of hunger and malnutrition make it a global crop in sustainable food availability (Haverkort et al. 2013; Devaux et al. 2020; Lal et al. 2020a). The food and agriculture organization (FAO) declared the year 2008 as the international year of the

potato. Presently, potato is grown over 19 million hectares area with an annual production of 388 million tons worldwide (FAOSTAT 2019). Around 1.3 billion people consume fresh potatoes as a staple food (50 kg per person annually) in India and China. The consistent increase in potato production in the developing world exceeding developed nations indicates its importance as a source of food, income and employment especially in Asia, Africa and Latin America (Devaux et al. 2020). The greater productivity and nutrition quality improvement is the prime goal for potato breeders, at the same time minimization of losses in the field due to pest, diseases and adverse environmental conditions and better post-harvest management is also critical. Poor crop and post-harvest management, field and storage diseases, frost and heavy rains are some of the most important factors for yield loss and nutritional profile deterioration in potato (Delgado et al. 2017; Lal et al. 2020b; Tiwari et al. 2020a). There are more than 40 pathogens, such as viruses, fungus,

✉ Ravinder Kumar  
chauhanravinder97@gmail.com

<sup>1</sup> ICAR-Central Potato Research Institute, Shimla, Himachal Pradesh 171 001, India

<sup>2</sup> ICAR-Indian Agricultural Research Institute, New Delhi 110012, India

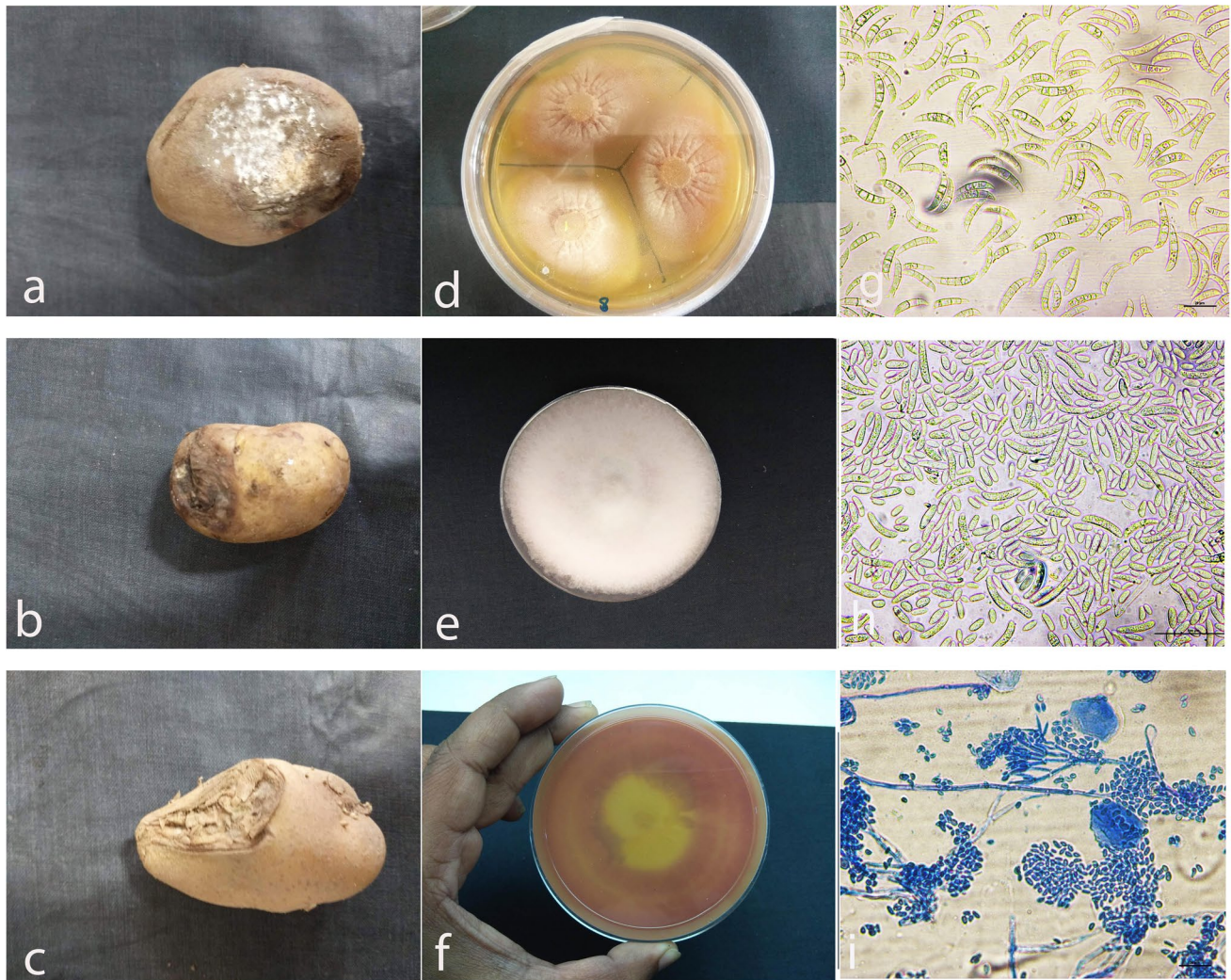
nematode, insects and bacteria which cause damage to foliar parts and tubers in potato (Fiers et al. 2012; Kumar et al. 2019, 2020). These biotic agents cause up to 22% direct or indirect losses in the potato production system and threaten the tuber quality and yield (International Potato Center, Lima, Peru <https://www.cipotato.org/>; Food and Agriculture Organization, United Nations <https://www.fao.org/>). Potato tubers comprise more than 70% water content which makes them vulnerable to galls, blemishes and rots after harvest during handling, transportation and storage. Earlier, the rots in potato were considered as minor and inevitable, but with changing consumer preferences, these are now a major concern for potato growers which deteriorate seed tuber and table purpose potatoes in cold stores (Bojanowski et al. 2013). Rots affect the tuber flesh deeply and are mainly classified either as soft rot or dry rot. The soft rot is a bacterial disease showing wet slimy lesions on tubers that engross the whole tuber within a few days of infection. However, dry rot is a fungal disease where a pattern of shrinking, shriveling and non-slimy lesion development is observed on the surface of tubers (Fiers et al. 2012). Potato dry rot is a devastating fungal disease caused by *Fusarium* worldwide. Soil and seed-borne inoculum can affect the plants in the field but the main damage occurs during storage. Dry rot affects the crop stand by inhibiting the development of potato sprouts and cause losses up to 25% with infection as high as 60% during storage (Wharton et al. 2007). The damage becomes more serious when other diseases, such as soft rot and late blight accompany dry rot during storage. An estimated loss due to this disease in the United States is US\$100–250 million annually (<https://www.ars.usda.gov>). In the Gansu Province of China loss due to dry rot is 88% of total post-harvest losses (Suqin et al. 2004; Du et al. 2012). More than 50% of seed lots in Michigan are reported to have dry rot infections (Gachango et al. 2012). The yield loss of 25–60% is highly dependent on the inoculum level in soil (Stevenson 2001; Heltoft et al. 2016). Worldwide, more than 13 *Fusarium* species are causing dry rot disease in potato (Cullen et al. 2005). *Fusarium sambucinum* is considered the most aggressive pathogen for this disease in major parts of Europe, China and North America (Secor and Salas 2001; Du et al. 2012). In Britain, *Fusarium coeruleum* (Libert) Sacc. is the most prevalent fungus in cold stores (Peters et al. 2008a). *Fusarium graminearum* (Schwabe) along with *F. sambucinum* was reported to be the most frequent species causing dry rot in potato in North Dakota (Estrada et al. 2010). Similarly, in Michigan, the *Fusarium oxysporum* is the most common fungus causing dry rot while *F. sambucinum* is the most aggressive. Apart from being pathogenic, *Fusarium* species are also known for producing mycotoxins in food products and dry rot causing species also to produce mycotoxins; sambutoxin, trichothecene, fusarin C, fusaric acid, zearalenone and deoxynivalenol (Desjardins

2006; Daami-remadi 2012; Bojanowski et al. 2013). Some of these toxins also act as pathogenicity factors in developing rots in tubers. Symptoms of the dry rot include sunken and wrinkled brown to black tissue patches on tubers having less dry matter and shriveled flesh. The wrinkled patches during prolong storage produces cottony white, purple, pink or brick orange spore and mycelial mass which survive in soil or rotten tuber debris (Stevenson 2001; Vatankhah et al. 2019). The information on the disease epidemiology is very elusive. The fungus can survive well at 4 °C and 10 °C, therefore, poses an equal threat to seed tubers and potatoes used for processing. The aggressiveness of different species depends upon the storage conditions and cultivars types. The management strategy mainly includes the use of resistant cultivars, disease-free seed potato, cultural practices, bio-agents, chemical treatment and storage microenvironment management (Bang 2007; Peters et al. 2008a; Al-Mughrabi et al. 2013; Bojanowski et al. 2013; Jiang et al. 2019). The current scenario demands an exhaustive screening of available cultivars and potato germplasms to identify the source of resistance and to frame a suitable breeding program. Also with the availability of the genome sequence of *F. sambucinum* (Patil et al. 2017), it is important to identify the potential pathogenicity factors and small secreted proteins that can be targeted in developing dsRNA based therapeutic biomolecules for seed tuber treatment. The role of multifunctional phytoprotectant, such as melatonin and strigolactones is also need to be explored which is highly effective in managing post-harvest losses in horticultural crops (Tiwari et al. 2020b). This review aims to draw attention to the symptomatology, infection process, pathogenomics, role of toxins and management approaches for this pathogen which is very much critical in designing better management strategies.

## Symptomatology and etiology of potato dry rot disease

The tubers and roots are the main plant parts that are directly affected by dry rot disease. The pattern of shrinking and shriveling along with lesion development on the outer surface of tubers and roots are common. Simultaneously, the black or brown rot occurs in the internal tissues. The wounds act as the main entry point for the pathogen from where they cause the rotting of the internal tissue giving black, brick orange, whitish or brownish tissue. The tubers showing typical symptoms of dry rot collected from different states of India have been shown (Fig. 1a–c). The indirect effect of infection can be observed as necrotic lesions on the damaged primary and secondary roots of the potato plant (Fig. 2). The first-ever study on potato dry rot by Martius in 1842 revealed that the disease is caused by a fungus named *Fusisporium* at that time which was later on identified as





**Fig. 1** a–c Typical symptoms of dry rot showing shriveled and mummified tubers, d–f Pure culture of *Fusarium sambucinum*, *Fusarium solani*, *Fusarium oxysporum*, g–i Respective fungal spores and mycelia as observed under a compound microscope (40 × magnification)



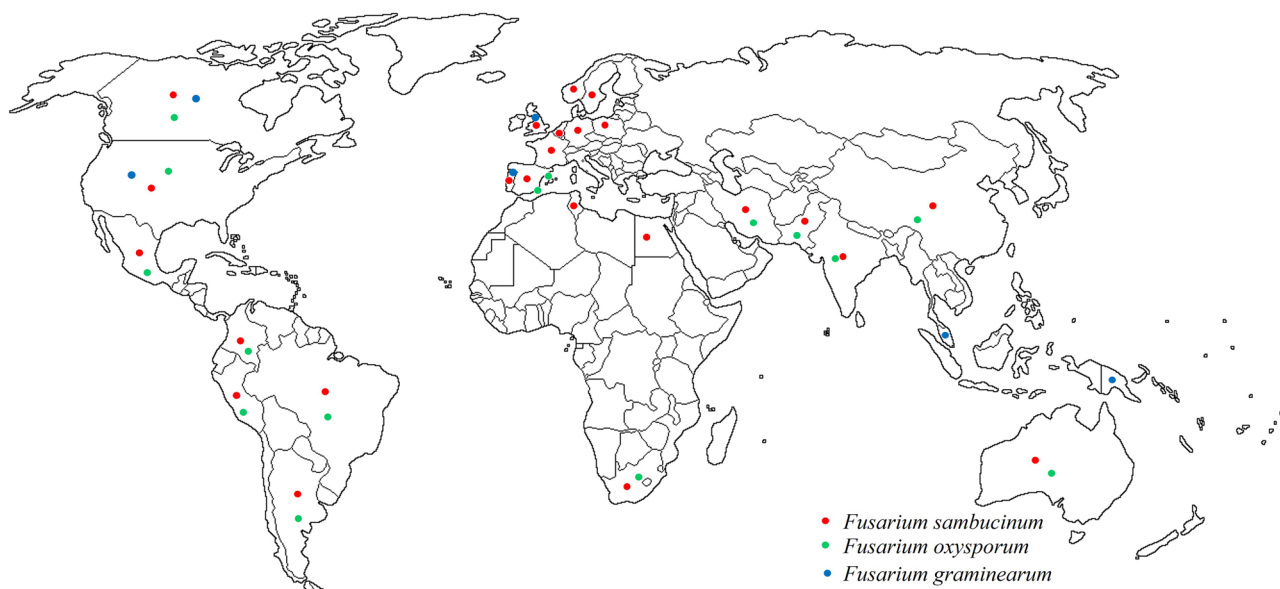
**Fig. 2** a, b Typical dry rot symptoms showing necrotic lesions on the damaged primary and secondary roots of the potato plant

*Fusarium oxysporum* (Saccardo and Traverso 1882). Presently, 13 different *Fusarium* species cause potato dry rot worldwide (Cullen et al. 2005). These are namely *F. sulphureum* Schlechtend. (syn. *F. sambucinum* Fuckel), *F. coeruleum* (Libert) Sacc. (syn. *F. solani* var. *coeruleum*), *F. avenaceum* (Fr.:Fr.) Sacc., *F. culmorum* (Wm. G. Sm.) Sacc., *F. oxysporum* Schlechtend. Fr., *F. acuminatum* Ellis & Everh., *F. crookwellense* L. W. Burgess, P. E. Nelson & T. A. Tousoun, *F. equiseti* (Corda) Sacc., *F. graminearum* Schwabe, *F. scirpi* Lambotte & Fautrey, *F. semitectum* Berk. & Ravenel, *F. sporotrichioides* Sherb. and *F. tricinctum* (Corda) Sacc. However, this list is still not complete and needs much more exhaustive survey and sampling to identify more *Fusarium* species involved, such as *F. ciliatum*, *F. torulosum*, *F. reticulatum* and *F. verticillioides* (Gachango et al. 2012). The spore and colony morphology of three most common dry rot causing fungus have been shown in Fig. 1 (d-i) from the part of our ongoing research work.

### Distribution pattern based on frequency and aggressiveness of *Fusarium* species

*Fusarium* species are the world's most devastating fungus infecting almost all grown crops and potato is no exception (Estrada et al. 2010). In potatoes, pathogens are responsible for wilt and vascular discoloration and causing rots and seed decay in tubers during storage. The most devastating and frequent species are *F. sambucinum*, *F. solani* and *F. oxysporum* based on geographic location and prevailing atmospheric

conditions (Stefańczyk et al. 2016). In the USA (Secor and Salas 2001) and Great Britain (Peters et al. 2008c) *F. sambucinum* and *F. coeruleum* are the two most frequent fungus causing potato dry rot respectively along with *F. avenaceum* and *F. culmorum* as minor rot causing fungi. However, several reports consider *F. sulphureum* as the most frequent fungus in North America and Europe (Recep et al. 2009; Gachango et al. 2012). *F. solani* and *F. oxysporum* are the main fungi associated with dry rots in south Africa (Theron and Holz 1990). The higher incidence and aggressiveness of *F. sulphureum* and *F. solani* has been observed in predominant potato cultivars in Iran. Interestingly, *F. graminearum* the cereal fungus has been reported as the dominant dry rot agent in North Dakota (Estrada et al. 2010), Tunisia (Daami-remadi 2012) and Canada (Peters et al. 2008b). This indicates the host adaptation in *Fusarium* fungus as wheat and potato crop rotation is common in the cropping system. The worldwide spatial distribution *F. sambucinum* has been depicted in Fig. 3. In India, a study reported nine species of *Fusarium* have been associated with dry rots but there is no further study of diversity and distribution of this fungus in storage and fields (Singh et al. 1987). However, the first report of *F. sambucinum* came from cold stores of Madhya Pradesh (Sagar et al. 2011) and it gave an alarming signal to carry out countrywide surveys and assess the prevalence of this threatening species in cold stores. In China also, the *F. sambucinum* is the most notorious fungus in major potato growing regions along with four minor species as *F. oxysporum*, *F. avenaceum*, *F. acuminatum* and *F. equiseti* (Du et al. 2012). More recently in Egypt, the *F. sambucinum*



**Fig. 3** The map indicates the spatial distribution of dry rot caused by *Fusarium* sp across the world. On the map, dots with red, green and blue colour denotes *Fusarium sambucinum*, *Fusarium oxysporum* and *Fusarium graminearum*, respectively



was identified as the predominant fungus followed by *F. oxysporum*, *F. verticillioides* and *F. incarnatum* (Gherbawy et al. 2019).

## Pathogenomics of *Fusarium* dry rot

Pathogenomics is a high-resolution strategy to develop and analyze the whole genome sequences of pathogenic agents (Fungi, bacteria and viruses) for the identification of pathogenesis and virulence determinants and the regulators of various metabolic activities. It is a modern tool for a better understanding of host–pathogen interactions and to identify the potential targets for efficient chemical control (Rampersad 2020). The genome of more than 12 *Fusarium* species has already been sequenced during the last two decades (Table 1). An analysis from the genomic studies revealed that the majority of the *Fusarium* species possess a hemibiotrophic association with the host and they shift from biotrophic to necrotrophic phase within the host depending upon the prevalent microenvironment and host adaptations (Perfect and Green 2001; Ma et al. 2013). A cascade of enzymes, toxins and small secreted proteins are involved in the pathogenesis of these hemibiotrophs. A study reported that virulent *F. sambucinum* strains can detoxify the sesquiterpene phytoalexins produced by potato (Desjardins and Gardner 1989). These phytoalexins are mainly rhisitin and lumbimin. High virulence was associated with loci designated as *Rim1* through meiotic recombinational analysis. Fleisner et al. 2002 investigated the mechanism which allows the *F. sambucinum* to tolerate phytoalexins. Their findings strongly suggested the role of ATP-binding cassette multidrug-resistant transporter in secreting toxic substances out of the cells. The gene *Gpabc1* codes for this transporter and provides tolerance to phytoalexins. The pathogenicity of this fungus was also correlated with host nonspecific phytotoxin trichothecenes and the disruption of trichidiene synthase gene lead to reduced virulence in *F. sambucinum*. Another gene enniatin synthase 1 (*ESYN1*) responsible for mycotoxin production was correlated with the regulation of virulence in *F. sambucinum* (Eranthodi et al. 2020). The disruption of *ESYN1* leads to reduced virulence and reduced lesion size on inoculated tubers. Similar findings are reported in *F. avenaceum* mediated dry rot disease. Recently autophagy which is a natural mechanism occurring in plants, animals and fungi has been correlated with the regulation of fungal growth, development and virulence. A study by Khalid et al. (2019a) revealed that the autophagy-related gene (*ATG 3*) is a potential regulator of conidial growth and development and pathogenicity of *F. oxysporum* in potato. While previously they have reported that *ATG22* gene is involved in the pathogenicity of the fungus (Khalid et al. 2019b). The deletion mutant

of *F. oxysporum* showed reduced conidiation and mycelial growth along with reduced lesion size in inoculated tubers. The novel finding demands more researches in this regard to elucidating the vital role of autophagy in dry rot fungus pathogenicity. Cutinase enzymes are actively involved in the pathogenicity of *F. solani* in potato. These enzymes can be used as markers to identify the pathogenic *F. solani* isolates. The role of *Fusarium* specific specialized effectors and pathogenicity genes, such as “Secreted In Xylem” (*SIX*) genes and *Fusarium* transcription factor (*FTF*)-encoded genes (*FTF1* and *FTF2*) has already been established in *F. oxysporum* f. sp. *lycopersici* (*FOL*) mediated tomato infection and it will be interesting to explore similar aspects in potato. Likewise, the function of *Fgl1* gene, a secreted lipase has been established as a virulence factor of *F. graminearum* of barley, maize and wheat, and its function in potato is still not explored. Recently the *F. graminearum* is emerging as major species involved in dry rot in potato. An insight into the genome of this fungus reveals that there is high genetic diversification in infection-related genes and that’s the main factor for its environmental adaptability (Paper et al. 2007; Kamran et al. 2020). This could also be the main reason for shifting of this fungus from wheat to potato host. Further, researches are needed in this direction to analyze the host shift and adaptation strategies of this fungus which will aid in restricting the survival of pathogen and provide management options. The genome sequence of most devastating species, *F. sambucinum* is available and further studies are now focused on improved understanding of (i) pathogenicity and virulence determinants (structures and functions), (ii) shift of biotrophic to necrotrophic life style, (iii) molecular basis of infection process, (iv) genetic diversity and species complex due to specific genomic regions (v) prediction of disease outbreak due to new strains (vi) emergence of fungicide-resistant strains.

The transcriptome analysis is a significant tool for understanding host–pathogen interactions and identifying the genes responsible for the virulence of pathogen and resistance or susceptibility of the host. A transcriptomic analysis involving *F. solani* f. sp. *eumartii* a tolerant potato cultivar “Spunta” has revealed the activation of inducible defense responses (Ippolito et al. 2010). The involvement of several PR proteins, chitinases and peroxides has been largely demonstrated in this study. However, the upregulation of a wide range of MAPK (mitogen-activated protein kinase), such as CIPK (calcineurin B-like protein-interacting protein kinase), SAPK8 (osmotic stress/ABAe activated protein kinase 8), CTR1-like kinase and shaggy related kinase denotes the complex level of physiological remodeling in response to fungus attack in potato. Interestingly, some of the RNA processing proteins, such as zinc finger motif RNA binding proteins, Glycine-rich RNA-binding proteins, DEAD-box RNA helicase, mRNA splicing factor (*STA1*),

**Table 1** Sequenced genomes of *Fusarium* species infecting potato and other hosts

S. no.	<i>Fusarium</i> sp.	Strain	Chromosomes	Scaffolds	Platforms	Genome size <sup>a</sup> (Mb)	(%) GC Content <sup>b</sup>	Predicted genes <sup>c</sup> Nos	BioProject/Accession Nos	References
1	<i>F. graminearum</i> *	PH-1	4	31	Sanger	36.60	48.33	13,332	PRJNA13839 PRJNA243	Cuomo et al. (2007)
2	<i>F. oxysporum</i> f. sp. <i>lycoperic</i>	4287	15	113	Sanger	61.36	48.40	17,735	PRJNA342688 PRJNA18813	Ma et al. (2010)
3	<i>F. verticillioides</i>	7600	11	36	Sanger	41.78	48.70	14,179	PRJNA245136 PRJNA15553	Brown et al. (2008)
4	<i>F. fujikuroi</i>	IMI58289	12	12	Pyro-sequencing	43.90	48.30	14,813	PRJNA322155	Wiemann et al. (2013)
5	<i>F. sambucinum</i> *	F-4	Unknown	18	454	42.00	47.8	12,845	PRJNA274729	(Patil et al. 2017)
6	<i>F. solani</i> f. sp. <i>pisi</i>	77-13-4	17	209	Sanger	51.28	50.78	15,707	PRJNA16586	Coleman et al. (2009)
7	<i>F. virguliforme</i>	Mont-1	Unknown	11	454	51.00	50.60	14,845	PRJNA63281	Srivastava et al. (2014)
8	<i>F. circinatum</i>	FSP34	Unknown	3457	454	45.24	47.30	15,713	PRJNA226125	Maphosa et al. (2016) map
9	<i>F. oxysporum</i> 5176	5176	Unknown	3395	454	55.00	47.60	17,817	AFQF00000000	Thatcher et al. (2012)
10	<i>F.pseudograminearum</i>	CS3096	Unknown	655	Illumina	37.00	47.75	12,488	PRJNA242845 PRJNA66583	Gardiner et al. (2012)
11	<i>F.proliferatum</i> *	ET1	Unknown	32	Illumina	45.21	48.5	16,136	PRJNA576857 PRJEB9885	Niehaus et al. (2016)
12	<i>F. culmorum</i> *	UK99	05	06	Illumina	41.92	45.66	12,378	PRJEB12835	Kulik et al. (2015)

\*On potato as host plant

have also been found up-regulated in active defense response which needs exhaustive studies as the role of these transcription factors are poorly understood. A series of studies involving *F. solani* f. sp. *eumarti* and potato cultivar Spunta have already reported the role of cyclophilin coding StCyp, transcriptional coactivator StMBF1, St-ACO3 coding for an ACC oxidase and MAP kinase StMPK1 in induced defense response in potato tubers (Blanco et al. 2006; Zanetti et al. 2002; Godoy et al. 2001). Some of these identified genes are involved in tolerance of many abiotic and pathogen stresses in different crops and further study in this regard may lead to a successful management strategy against combined biotic and abiotic stresses in crop plants.

The comparative genomics studies between dry rot causing *Fusarium* spp. revealed that *F. sambucinum* possesses perfect microsatellites while *F. verticilloides* microsatellites are in the compounded form (Patil et al. 2017). There are very limited genes characterized in *F. sambucinum*, such as major facilitator superfamily (MSF) genes which were confirmed within the genome sequence. An one-way average nucleotide identity (ANI) among *Fusarium* spp. by comparing 100 housekeeping gene sequences revealed the closest association between *F. sambucinum* (Strain FS-4) and *F. graminearum* (Strain PH-1) (99.12%) (Patil et al. 2017). However, the least relationship was observed with *F. verticillioides* (Strain 7600) (97.81%). The phylogeny based on the Translation Elongation Factor 1 $\alpha$  (TEF1 $\alpha$ ) gene depicted a close evolutionary relationship between *F. sambucinum* and *F. culmorum*, causal agent of foot, stalk and root rot, seedling and ear blight in cereals and grasses. An exhaustive comparative analysis of recently sequenced genome with other *Fusarium* spp. genomes will provide greater understandings of evolutionary relationships, fungus origins and pathogenicity.

### Infection-related to dry rot and the life cycle of the *Fusarium* species

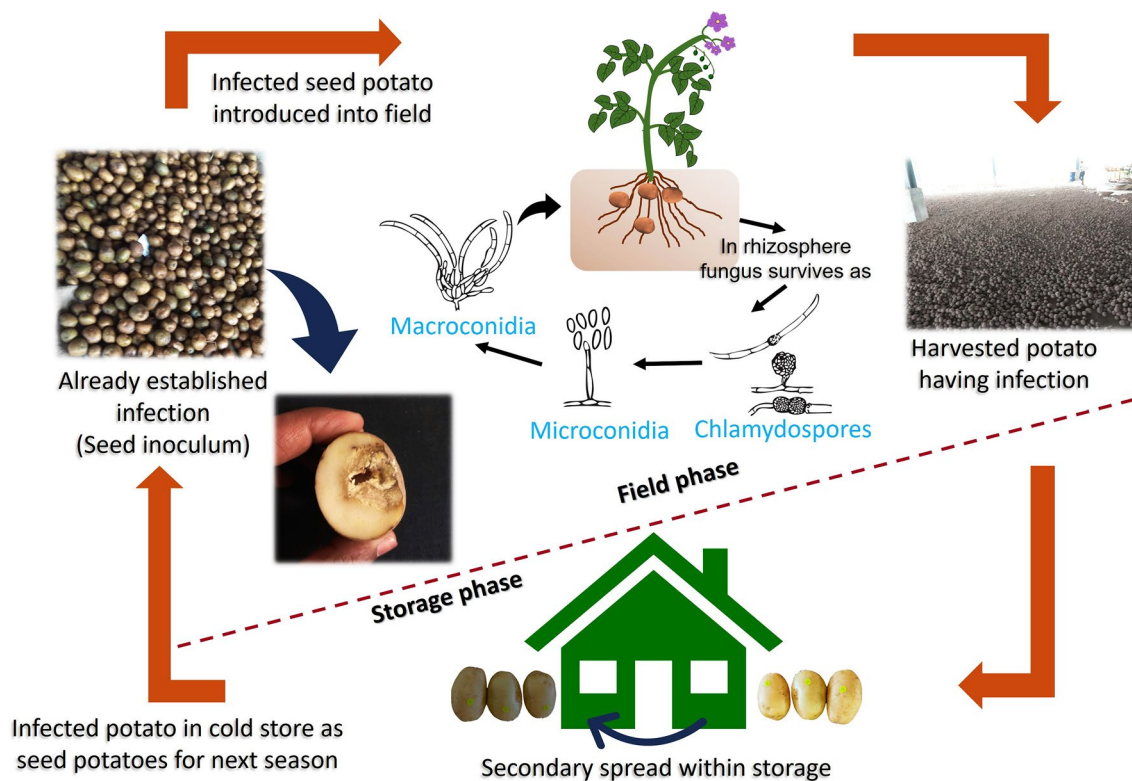
The dry rot causing *Fusarium* species are both seed and soil borne. Although the dry rot is considered a major threat for tubers in storage, but its ill effects can also be observed in the field in the form of wilting and root degradation of potato plants (Mahdavi et al. 2009). There are also some indications that fungal isolates differ in their ability to cause wilt symptoms and dry rots in potato (Secor and Salas 2001). This is an important matter of investigation as very few studies highlight the *Fusarium* wilt in potato plants and the majority of researches focus on *Fusarium*-induced dry rot of tubers. The wounds developed on the tubers during harvesting, handling and transportation become the entry point for fungal spores and these infested tubers initiate the dry rot in storage. The fungus can initiate infection only

when the tuber skin is ruptured. The infection hypha grows in intercellular spaces in live cells and becomes intracellular only when the cell is dead. But this also varies with species as *F. coeruleum* shows both intercellular and intracellular growth pattern while *F. avenaceum* kills the penetrated cells and grows intracellular right from the beginning of infection (Stevenson 2001; Bojanowski et al. 2013).

The survival of *Fusarium* spores in soil and on plant debris acts as the main reservoir of inoculum and major source of tubers infections in the field (Peters et al. 2008c; Cullen et al. 2005). The surviving spores in soil cause rotting in progeny tubers only after wounds developed due to intercultural operations (Bojanowski et al. 2013). The transmissions of fungal spores from mother tubers to progeny tubers also depends upon the *Fusarium* sp. involved in causing these rots. It has been observed that different *Fusarium* sp. have a different rate of sporulation belowground and hence the extent of infection also varies accordingly (Cullen et al. 2005; Bojanowski et al. 2013). It was observed that *F. sulphureum* transmission is greater from contaminated seed tuber while *F. coeruleum* transmits more readily from rotten mother tuber. *F. sulphureum* preferably sporulates on stem bases whereas *F. coeruleum* rapidly sporulates outside rotten tubers (Choiseul et al. 2001; Cullen et al. 2005; Bojanowski et al. 2013). The optimum temperature for mycelial growth of *F. sambucinum*, *F. graminearum*, *F. oxysporum*, *F. solani* and *F. culmorum* is 20–25 °C whereas for sporulation 25–30 °C temperature is required. *F. solani* var. *coeruleum* needs 25–30 °C and 20–25 °C, respectively for growth and sporulation. Usually, in cold stores, a temperature above 10 °C increases the *Fusarium* growth while < 5 °C is known to reduce infection (Secor and Salas 2001). However, *F. sambucinum* and *F. graminearum* have shown mycelial growth below 5 °C, which is the main reason for dry rot development even at extremely low temperatures (Daami-remadi 2012). Temperature above 40 °C completely restricts the growth of all the fungal species involved in dry rot disease. A pictorial representation of the occurrence and spread of dry rot in field and storage has been illustrated in Fig. 4.

### Toxins in disease development

Mycotoxins play a critical role in host–pathogen interactions (Aiko and Mehta 2016; Nagaraja et al. 2016). These toxins are considered as a secondary determinant of pathogenicity and the main weapon of *Fusarium* species in developing dry rots in potato. These *Fusarium* toxins have been classified as trichothecene and non-trichothecene mycotoxins and reported in many hosts affected by this genus (Mills 1990; Bojanowski et al. 2013; Nagaraja et al. 2016). Trichothecens are the sesquiterpenes causing toxicity in plants



**Fig. 4** An illustration of the dry rot disease cycle consisting of storage and field phase. The disease is initiated from the soil and/or seed borne inoculum under field conditions. The tubers harvested from

infected plants may possess the inoculum and under ambient storage conditions cause severe rots in tubers kept in cold stores

as well as mycotoxicosis in animals and humans (Desjardins 1995; Bojanowski et al. 2013). *Fusarium* species infecting potato and cereal grains mainly produce non-macrocytic trichothecenes categorized as type A (includes diacetoxyscirpenol [DAS] and T-2 toxin) and type B (includes nivalenol [NIV] and deoxynivalenol [DON]) (Desjardins 2006; Delgado et al. 2010). Much dry rot causing *Fusarium* species (*F. sambucinum*, *F. coeruleum*, *F. oxysporum*, *F. equiseti*, *F. graminearum*) produce trichothecenes DON, DAS, NIV and T-2 toxin in tissues of rotten tubers as previously documented (Bojanowski et al. 2013). Fumonisin, zearalenones (ZEA), sambutoxin, fusaric acids, fusarin C and enniatins are the major non-trichothecene mycotoxins associated with dry rots (Bojanowski et al. 2013; Eranthodi et al. 2020). The occurrence of this group of toxins in rotten tubers is concerning as these toxins are associated with deadly animal diseases, such as ZEA cause estrogenic syndromes in swine, Fumonisin have carcinogenic and hepatotoxic effects, sambutoxins are associated with hemorrhage in the stomach and intestines of rats (Kim and Lee 1994; Desjardins 2006; Bojanowski et al. 2013).

Earlier it was observed that these toxins are produced not only in rotted tissues of the infected tubers but also on distant healthy-looking tissues which were a matter of

great concern for consumers as normally the rotted tissue is removed and the rest part is used for cooking. However, Delgado et al. (2010) reported that the tissue surrounding the rotted lesions by *F. graminearum* accumulates a non-lethal amount of toxins within 7 months of storage. This aspect also warrants exhaustive researches as the type of cultivar and prevalent *Fusarium* species in a particular area might be the factor for toxin distribution in the rotted and healthy tissues. The effect of cooking on the inactivation of trichothecenes in potato infected with *F. sambucinum* indicates that thermal treatment is unable to completely inactivate these toxins and it needed more than 4 h of cooking to eliminate these toxins. This is another future line of work to safeguard the health of the consumers. The data regarding the effect of these toxins on the health of consumers is also lacking. The toxins associated with dry rot causing *Fusarium* species are described in Table 2.

## Genetic resistance and molecular breeding

Worldwide, most of the commonly growing potato cultivars are susceptible to *Fusarium* dry rot (Daami-remadi 2012; Bojanowski et al. 2013; Heltoft et al. 2015; Chen et al.



**Table 2** The major trichothecene and non-trichothecene toxins of dry rot causing species

Toxins	Molecular weight (g/mol) and chemical formula	<i>Fusarium</i> species	References
<b>Non-trichothecene toxins</b>			
Fusaric acid	179.2157 (C <sub>10</sub> H <sub>13</sub> NO <sub>2</sub> )	<i>F. sambucinum</i> , <i>F. crookwellense</i> , <i>F. oxysporum</i>	Bacon et al. (1996), Venter and Steyn (1998)
Fumonisin	721.83 (C <sub>34</sub> H <sub>59</sub> NO <sub>15</sub> )	<i>F. sambucinum</i> , <i>F. equiseti</i> , <i>F. oxysporum</i>	El-Hassan et al. (2007)
Fusarin C	431.5 (C <sub>23</sub> H <sub>29</sub> NO <sub>7</sub> )	<i>F. crookwellense</i>	Golinski et al. (1988), Sydenham et al. (1991)
Sambutoxin	453 (C <sub>28</sub> H <sub>39</sub> NO <sub>4</sub> )	<i>F. sambucinum</i> , <i>F. oxysporum</i> ,	Kim and Lee (1994)
Enniatins	639.8 (C <sub>33</sub> H <sub>57</sub> N <sub>3</sub> O <sub>9</sub> )	<i>F. acuminatum</i> , <i>F. avenaceum</i> , <i>F. oxysporum</i> , <i>F. sambucinum</i> , <i>F. scirpi</i> ,	Herrmann et al. (1996), Song et al. (2008)
Beauvericin	783.95 (C <sub>45</sub> H <sub>57</sub> N <sub>3</sub> O <sub>9</sub> )	<i>F. sambucinum</i> , <i>F. equiseti</i> , <i>F. oxysporum</i> <i>F. acuminatum</i> , <i>F. avenaceum</i> ,	Song et al. (2008), Logrieco et al. (1998)
Zearalenones	318.364 (C <sub>18</sub> H <sub>22</sub> O <sub>5</sub> )	<i>F. crookwellense</i> , <i>F. equiseti</i> , <i>F. graminearum</i> , <i>F. oxysporum</i> , <i>F. sambucinum</i>	Sydenham et al. (1991), Burlakoti et al. (2008), El-Hassan et al. (2007)
<b>Trichothecene toxins</b>			
Deoxynivalenol	296.32 (C <sub>15</sub> H <sub>20</sub> O <sub>6</sub> )	<i>F. culmorum</i> , <i>F. coeruleum</i> <i>F. equiseti</i> ,	El-Banna et al. (1984), Latus-Ziętkiewicz et al. (1987), Delgado et al. (2010)
3-acetyldeoxynivalenol	338.4 (C <sub>17</sub> H <sub>22</sub> O <sub>7</sub> )	<i>F. graminearum</i> , <i>F. oxysporum</i> , <i>F. sambucinum</i>	
15-acetyldeoxynivalenol	338.4 (C <sub>17</sub> H <sub>22</sub> O <sub>7</sub> )		
Nivalenol	312.31 (C <sub>15</sub> H <sub>20</sub> O <sub>7</sub> )	<i>F. culmorum</i> , <i>F. equiseti</i> , <i>F. graminearum</i> , <i>F. sambucinum</i> <i>F. crookwellense</i>	El-Banna et al. (1984), Nielsen Thrane (2001), Sydenham et al. (1991)
HT-2 toxin	424.5 (C <sub>22</sub> H <sub>32</sub> O <sub>8</sub> )	<i>F. coeruleum</i> , <i>F. sambucinum</i>	Desjardins and Gardner (1989), El-Banna et al. (1984)
Fusarenone	354.4 (C <sub>17</sub> H <sub>22</sub> O <sub>8</sub> )	<i>F. culmorum</i> , <i>F. equiseti</i> , <i>F. graminearum</i> , <i>F. crookwellense</i>	Nielsen Thrane (2001)
T-2 toxin	466.5 (C <sub>24</sub> H <sub>34</sub> O <sub>9</sub> )	<i>F. equiseti</i> , <i>F. graminearum</i> , <i>F. sambucinum</i> , <i>F. oxysporum</i>	El-Hassan et al. (2007)
4-acetyl-monoacetoxyscirpenol, 15-acetyl-monoacetoxyscirpenol,	324.4 (C <sub>17</sub> H <sub>24</sub> O <sub>6</sub> )	<i>F. equiseti</i> , <i>F. sambucinum</i>	Nielsen Thrane (2001), El-Hassan et al. (2007)
Diacetoxyscirpenol	324.4 (C <sub>17</sub> H <sub>24</sub> O <sub>6</sub> )		
Neosolaniol	366.4 C <sub>19</sub> H <sub>26</sub> O <sub>7</sub> 382.4 (C <sub>19</sub> H <sub>26</sub> O <sub>8</sub> )	<i>F. sambucinum</i>	Nielsen Thrane (2001)

2020). In China, Du et al. 2012 screened 21 cultivars and 46 breeding lines against *F. sambucinum* (NM5-1-S). All these 67 potato clones were found susceptible to dry rot disease. However, the most tolerant cultivar against *F. sambucinum* was Desiree (Du et al. 2012). Cultivar susceptibility varied based on the dominance of *Fusarium* species in a location-specific manner. In Tunisia, cultivar Mondial and Spunta showed less susceptibility to *F. sambucinum* and *F. oxysporum* f. sp. *tuberosa* whereas cultivar Liseta was less susceptible to *F. oxysporum* and *F. graminearum* (Trabelsi et al. 2016). In Iran, 43 potato cultivars were screened against *F. sulphureum*, *F. solani* and *F. oxysporum* and cultivar Saturna was found resistant among all the tested cultivars (Esfehiani 2005). Cultivar Owyhee Russet had shown significant

resistance to dry rots as compared with Russet Burbank. Owyhee Russet was moderately resistant to *F. solani* var. *coeruleum* but susceptible to *F. sambucinum* (Yilma et al. 2012). While screening the potato cultivars against dry rots it is important to consider storage temperatures, as some reports have highlighted the role of storage temperature in the susceptibility of cultivars against several *Fusarium* species. Also, the aggressiveness of the *Fusarium* species varies according to storage temperatures (Daami-remadi 2012). Cultivars placed in less susceptible groups against *F. sambucinum* at temperature 30 °C moved to highly susceptible groups at 15 °C (Mejdoub-Trabelsi et al. 2012). Breeding for dry rot resistant potato cultivars is presently not very efficient due to laborious phenotyping (Chen et al. 2020).

The inoculation technique has also been constantly evolved to facilitate the screening of tubers of resistant cultivars and germplasm. Different inoculum methods include delivery of spore suspension of mycelia plug in the wounded tuber using the micrometer-type syringe, a cork borer, steel pin tools, a drill or a metal cylinder (Ayers and Robinson 1954; Peters et al. 2008b; Estrada et al. 2010; Sagar et al. 2011; Chen et al. 2020). Recently Chen et al. (2020) developed a simple and efficient cross-contamination-free technique denoted as plastic screw wounding which will aid in screening potato lines against *Fusarium* dry rot. Due to variability in disease response of host tubers depending on storage and prevalent species, ongoing studies should focus on ranking the resistance of cultivars based on these factors. The effect of mixed infections of *Fusarium* species should also be considered in such studies as tubers in field and storage face several of these species at a time. The occurrence of soft rot also influences the resistance of given potato tubers against dry rot therefore correlations also need much more elaborative studies to understand the underlying mechanism of dry rot and wet rot occurrence in potato.

## Management of *Fusarium* dry rot disease

### Cultural practices and storage conditions

Good and careful cultural practices along with optimization of storage conditions are the most crucial factors which influence the incidence and severity of any storage rot and potato dry rot is no exception. Planting disease-free seed tubers, avoiding tuber injuries during harvesting, providing appropriate conditions for wound healing through curing are the crucial factors that provide good control to dry rot (Stevenson 2001). At most care is required at the time of harvesting to minimize and bruises and wounds on the harvested tubers which restricts the entry and germination of the fungal spores and prevent major rotting. A 10–18 °C temperature of the pulp is the right stage for tuber harvesting (Knowles and Plissey 2008). This temperature along with high humidity (95–99%) and good ventilation is crucial for wound healing in tubers right after harvest. There should be an interval of 1–2 weeks in vine killing and harvesting which gives enough time for healing and reduce the chances of pathogen attack (Knowles and Plissey 2008). Planting certified seed tubers having < 2% disease symptoms is recommended (Secor and Johnson 2008). The diseased tubers should be discarded and seed treatment is applied to the remaining tubers before planting. Proper disinfection of storage facilities and implements used in handling and cutting of tubers is also mandatory. Physiological maturation of the tuber is another important factor that affects dry rot development. A study by Heltoft et al. (2015) indicated that early

maturing cultivars are much more susceptible to *F. sambucinum* than the late maturing cultivars. Moreover the immature tubers having high sucrose content, poor skin set and low dry matter content were more vulnerable to *Fusarium* species (Heltoft et al. 2015). The correlation of sucrose and dry matter content in dry rot development needs much more focused studies to identify any direct or indirect relations which will aid in disease resistance breeding program. Harvesting potatoes with a high level of maturity minimize the chance of rotting in storages. Harvest date is an important factor affecting *F. coeruleum* mediated dry rot development (Carnegie et al. 2001).

Crop rotation which is the most advised cultural practice in managing soil-borne diseases is not very effective in potato dry rot management (Bojanowski et al. 2013). Potato crop rotations with Italian ryegrass, red clover and barley did not show any significant reduction in the incidence and severity of dry rots in 2–3 years. The long-term survival of *Fusarium* spores in soil and its broad host range makes it a difficult pathogen to manage using crop rotation. Moreover, there are reports of crop infectivity of *Fusarium* isolates in potato, clover and cereal crops which indicates that crop rotation may favor the survival of pathogenic strains rather than controlling them (Peters et al. 2008b). Soil solarization which harnesses the solar energy in moist soil with the aim of thermal inactivation of the pathogen propagules is found effective in managing *Fusarium* dry rot in fields. It reduced the population density of fungus up to a greater extent within 6 weeks of solarization. However, this is only possible in areas with high solar intensity over a longer duration to maintain a sufficient soil temperature for inactivation of microbes (Saremi et al. 2011).

Before storage, a thorough examination of tubers is necessary for any wounds, pests and disease appearance. Even a single rotted and damaged tuber may destroy the whole lot during storage and that is the reason for proper grading before storage (Pinhero et al. 2009). During storage, proper circulation of cool air is very important as respiration in stored potatoes generates excessive CO<sub>2</sub> and heat which may facilitate the growth of adhering fungal spores. The CO<sub>2</sub> level in a well-maintained storage facility ranges from 1200 to 1500 ppm. The CO<sub>2</sub> concentration above 5000 ppm indicates storage rots and/or insufficient ventilation in the storage which needs immediate attention (Gottschalk and Ezhekiel 2006; Pinhero et al. 2009).

### Chemical control

During the potato growth cycle, the management of dry rot is possible in two phases (i) seed piece decay management before planting and (ii) post-harvest treatments of tubers before storage. The most popular and effective fungicide used for dry rot management in both pre- and post-harvest

management belongs to the benzimidazole group. Thiabendazole is the most effective and extensively used benzimidazole fungicide against most of the dry rot causing *Fusarium* species (Daami-remadi 2012; Gachango et al. 2012; Bojanowski et al. 2013). Thiophanate-methyl (benzimidazole group) is used in Canada to control seed tuber piece decay. Extensive uses of thiabendazole lead to the appearance of resistant strains especially against *F. sambucinum*, but the rest of the *Fusarium* species viz. *F. solani*, *F. oxysporum*, *F. culmorum*, *F. equiseti*, *F. sporotrichioides*, *F. acuminatum* and *F. avenaceum* were still sensitive to this fungicide with few reports of fungicide resistance (Ocamb et al. 2007; Gachango et al. 2012; Bojanowski et al. 2013).

The appearance of thiabendazole-resistant strains led to the exploration of other synthetic chemicals to manage dry rots. The alternative chemicals found effective against dry rot have been very well documented by Bojanowski et al. (2013). Some new generation fungicides belonging to “low-risk fungicide” groups, such as fludioxonil (phenylpyrroles) and azoxystrobin (strobilurins) are also found effective in managing dry rots (Daami-remadi 2012). To reduce tuber seed piece decay and sprout rot, Fludioxonil can be used as a protectant fungicide. Likewise, difenoconazole is also very effective against most of the *Fusarium* species in managing seed piece decay (Gachango et al. 2012). Azoxystrobin, chlorothalonil and fludioxonil effectively reduced the severity of dry rot up to 50% as compared to control during 21 days of storage at 25–27 °C. These chemicals can be utilized to manage benzimidazole-resistant *F. sambucinum* strains (Daami-remadi 2012). Several treatment combinations have also been tried to manage multiple rots causing pathogens. Fungicides mixture of metalaxyl + mancozeb or maneb is found effective in controlling tuber diseases where rotting was reduced by 50 and 91% on tubers inoculated with *F. sambucinum* and *P. erythrosetica* + *F. sambucinum*, respectively. Fludioxonil with mancozeb as seed tuber treatment was found effective against dry rot (Wharton et al. 2007).

The consistent increase in fungicide resistance and ill effects of synthetic chemicals on human and animal health demands a sustainable management approach that is eco-friendly, less hazardous and friendly to the potato growers. In this direction, several inorganic and organic salts, essential oils and phytohormones have been tested in sustainably managing these rots. The generally recognized as safe (GRAS) salts, potassium metabisulfite and sodium metabisulfite have shown 100% control of dry rot while magnesium sulfate, potassium sulfate, ammonium sulfate, sodium carbonate, sodium sulfate, calcium phosphate and potassium phosphites significantly reduced the infection percentage (Kolaei et al. 2013). Sodium silicate inhibited the pathogenic activity against *F. sulphureum* in vitro and reduced dry rot lesions of tubers in vivo (Li et al. 2009). Other GRAS

compounds, such as essential oils and plant extracts have also shown a good in vitro and in vivo inhibition of dry rot causing fungi in the form of seed treatment or fumigation (Baturó-Ciesniewska et al. 2015; Hay et al. 2019; Raigond et al. 2019). Garlic (*Allium sativum* L.) essential oil found effective in reducing the severity of dry rot disease caused by *F. solani* (Bång 2007). Vapors of cineole and menthol contributed to limit the rots induced by two strains of *F. sambucinum* (Vaughn and Spencer 1994). Thyme (*Thymus capitatus*), oregano (*Origanum vulgare* L.), marjoram (*Origanum majorana* L.) essential oils completely inhibited the mycelial growth of *F. coeruleum* (Daferera et al. 2003). In addition, essential oils of fennel (*Foeniculum vulgare* Mill.) and peppermint (*Mentha piperita* L.) were found highly toxic to *F. oxysporum* and controlled the tuber decay when applied as a protective emulsifiable concentrate (Mahmoud et al. 2010). The most aggressive *F. sambucinum* is also sensitive to aqueous extracts of cinnamon (*Cinnamomum verum* J. Presl) and dry rot was significantly reduced with its application (Mvuemba et al. 2009). Recently, the cinnamaldehyde which is a predominant constituent of cinnamon essential oil was found highly effective against *F. sambucinum* (Wei et al. 2020). The study on the underlying mechanism revealed that a concentration of 3 and 4 mM inhibited spore germination by restricting the ergosterol biosynthesis, enhancing reactive oxygen species accumulation and hence disrupting cell membrane integrity. The downregulation of ergosterol biosynthetic genes (ERG11, ERG6 and ERG4) and 67.94% reduction of ergosterol content were analyzed by quantitative real-time PCR and high-performance liquid chromatography (HPLC), respectively. The methanol extract of pomegranate peels significantly inhibited dry rot development on tubers inoculated with *F. sambucinum* as preventive applications (Elshebriny et al. 2016). Chlorogenic acid was the main phenolic compound identified in the extract through HPLC. A phloroglucinol compound dryocrassin ABBA form *Dryopteris crassirhizoma* (fern) controlled dry rot of potato tubers by suppressing the fungal growth along with the induction of defense responses. There was increased antioxidant enzyme activity along with the upregulation of plant lipid-transfer proteins which collectively restricted the *F. solani* var. *coeruleum* in causing rots in tubers. Some essential oils directly inhibited toxin production as palmarose (*Cymbopogon martinii* (Roxb.) Wats) and clove (*Syzygium aromaticum* (L.) oils inhibited DON and ZEA production in *F. graminearum* (Velluti et al. 2004). More elaborative studies are needed to explore the potential of these essential oils and plant extracts on inactivation of toxins released by *Fusarium* species during dry rot infection. The role of essential oils and botanicals as sustainable alternative to synthetic chemicals needs further investigations for their on-farm efficacy.

The use of chitosan as GRAS food additive is approved by the United States Food and Drug Administration



(Romanazzi et al. 2017). This natural nontoxic biopolymer can be a safe alternative to harmful chemicals as it exhibits good antifungal activity when applied as edible coatings. A recent study showed that a concentration of 0.25% chitosan completely inhibits *F. sambucinum* growth and prevents the other physiological losses in tubers. Chitosan was effective in managing dry rots in a dose-dependent manner in potato cultivar Kufri Jyoti and Kufri Chipsona (Raigond et al. 2019). Further studies are also going on regarding the chitosan mediated induced defense response in potato plant and its role in regulating other physiological processes in potato tubers. A similar antifungal effect of chitosan has also been reported against *F. sulphureum* and *F. solani* (Sun et al. 2008). Recently, cationic amylose–hexadecyl ammonium chloride inclusion complex used as antimicrobial thin film significantly inhibited up to 99% *F. sambucinum* damage to wounded tubers (Hay et al. 2019). These kinds of safe coating materials should be promoted for the management of post-harvest pathogens in potato and other crops.

### Use of nanotechnology

Silver nanoparticles (AgNPs) are the emerging group of phytoprotectant that have shown immense potential in ameliorating the fungal and bacterial infections in crop plants (Shen et al. 2020). Recently, these silver nanoparticles have shown high efficacy in mitigating *Fusarium* species complex incited dry rots. A concentration of 10 mg/l was completely fungicidal and transmission electron microscopy showed a clear disruption of the cell membrane of the fungal spore and mycelia. Further transcriptomic analysis elucidated that AgNPs induced apoptosis in fungal cells by disrupting energy and substance metabolism suppressed the fatty acid and carbohydrate metabolism during 6–12 h of treatment. Similar results of the antifungal effect of AgNPs against *F. sambucinum* in potato cultivar Kufri Jyoti have also been observed (Unpublished data). AgNPs are much safer alternatives to manage this disease as compared to synthetic chemical pesticides. There is a plethora of researches available for AgNPs efficacy in medical and plant sciences, but exhaustive investigations are still needed for its mechanism of action on plant pathogens and any side effects to the plants or other beneficial microbes.

### Biological control

Indiscriminate use of fungicide driven environmental deterioration and the emergence of fungicide-resistant strains have emphasized the exploration of antagonistic microbes which can inhibit dry rot causing *Fusarium* species through antibiosis, mycoparasitism or hyperparasitism (Kishan et al. 2017a, b). A comprehensive review by Bojanowski et al. 2013 highlighted the role of these antagonistic microbes,

such as *Pseudomonas*, *Enterobacter*, *Pantoea* (Schisler and Slininger 1994), *Trichoderma harzianum* (Sadfi et al. 2001), *Bacillus cereus* (Sadfi et al. 2002), *P. fluorescens* (Slininger et al. 2003), *B. cepacia* (Recep et al. 2009), *Glomus irregular* mycorrhizza (Ismail and Hijri 2012) in mitigation of potato dry rot diseases. Some bio-pesticides Bio-save 10LP and 11LP (*Pseudomonas syringae*) are also registered in the USA to control dry rots and silver scurf in potato (Al-Mughrabi et al. 2013). After 2013, some of the bioagents found promising in managing this disease have been discussed here.

A talc-based formulation of *P. fluorescens* VUPf506 was found effective for in situ management of *F. solani* (Vatankhah et al. 2019). It restricted the fungal development up to 79.8% as compared to control. Use of osmoprotectant (trehalose or fructose) with Kenite<sup>®</sup> 700 and HYFLO<sup>®</sup> as carrier *Pseudomonas fluorescens* strains P22Y05 reduced *Fusarium* dry rot by more than 60% (Schisler et al. 2016). The isolates of *T. viride* VG18, *T. harzianum* TZ16, *T. virens* KB31, *T. asperellum* ÖT1 and *T. inhamatum* KEB12 controlled *F. sambucinum* in inoculated tubers stored at 24 °C for 4–6 weeks (Aydın 2019). *Paecilomyces lilacinus* and *T. polysporum* significantly reduced the dry rot caused by *F. oxysporum* (Kubar et al. 2019). The role of nonpathogenic endophytes associated with potato phyllosphere and rhizosphere is also positive in dry rot suppression. The identified *Aspergillus*, *Penicillium*, *Colletotrichum* and *Trichoderma* strains were effective in suppressing *F. sambucinum* and *F. solani*. The use of aqueous extract from brown algae *Sargassum vulgare* reduced dry rot severity by 55% as compared to control (Nawaim et al. 2017). The quest of finding some bioagents and chemicals for induced resistance led to the finding of T2-Toxin produced by *Fusarium* species which developed inherent resistance in potato against *F. sulphureum*. The T2-Toxin (1 mg L<sup>-1</sup>) with its elicitor like activity enhanced the production of ROS and new phenylpropanoid metabolites (Xue et al. 2019).

### Host-induced gene silencing

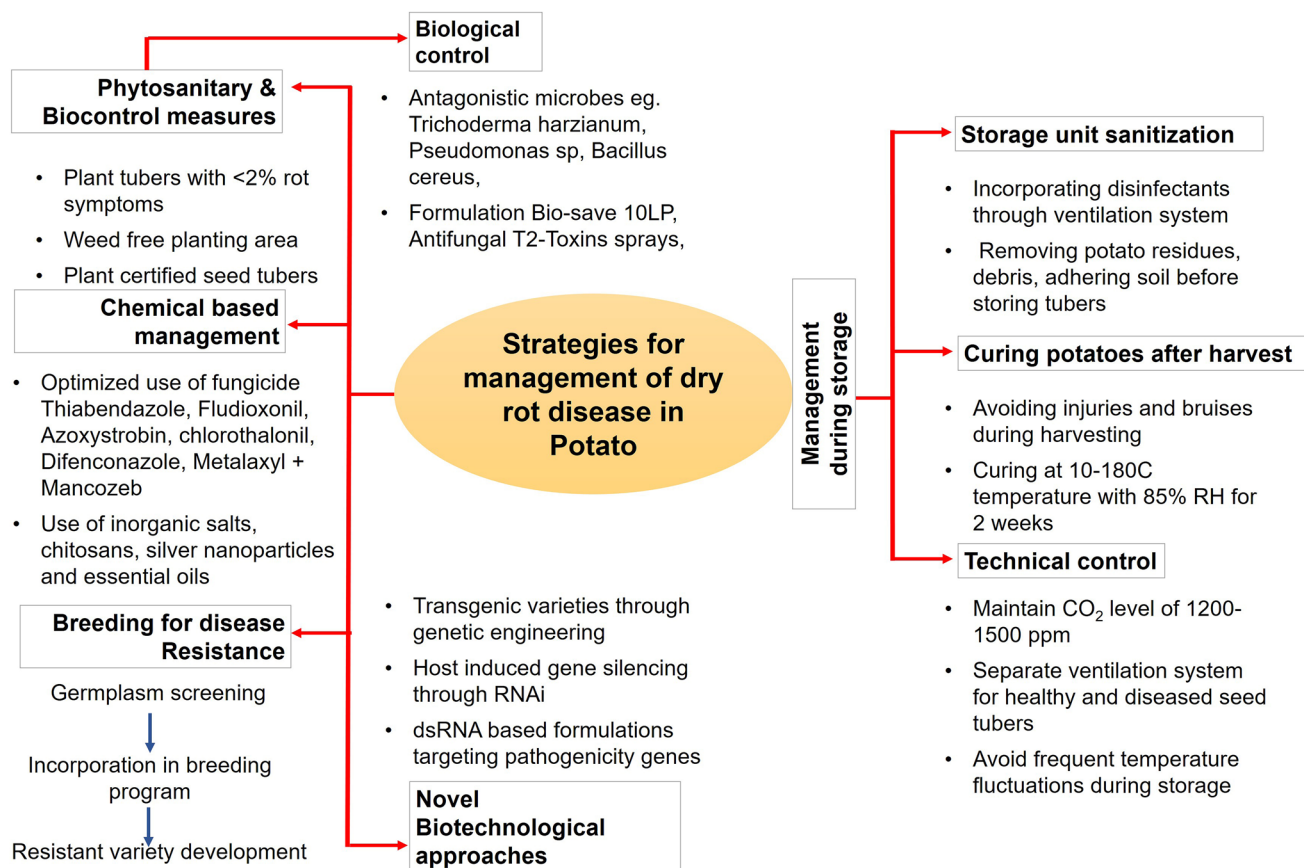
Host-induced gene silencing (HIGS) conferred through an RNAi-based mechanism restricting the expression of selected genes of the pathogen has the potential to control *Fusarium* diseases of economically important crop plants (Rampersad 2020). There are good examples of RNAi-mediated silencing of targeted genes as in wheat against *F. culmorum* (Chen et al. 2016) and *F. graminearum* (Koch et al. 2016; Kamran et al. 2020), banana against *F. oxysporum* f. sp. *cubense* (Ghag and Ganapathi 2019), tomato against *F. oxysporum* f. sp. *lycopersici* (Singh et al. 2020; Tetorya and Rajam 2018), barley against *F. graminearum* (Koch et al. 2016) and tobacco against *F. verticillioides* (Tinoco et al. 2010). Unfortunately, there is not a single report of

RNAi-mediated disease suppression in dry rots in potato. This warrants the need for exploration of these aspects which will give a valuable management option for this disease. The phytoprotectant melatonin is emerging as an environmentally friendly chemical to manage post-harvest biotic stresses in horticultural crops (Tiwari et al. 2020b; Moustafa-farag et al. 2020). There is a need to explore the role of novel phytohormones in dry rot suppression. The major strategies to manage potato dry rot disease are highlighted in Fig. 5.

## Conclusion and future thrust

Globally, *Fusarium* dry rot is a disease having economic importance. There are more than 13 species of dry rot causing *Fusarium* reported worldwide and the genetic diversity varies depending upon the geographical location. The frequency of occurrence and aggressiveness of dry rot causing *Fusarium* strains also differ depending upon the prevalent cultivars and environmental conditions in a location-specific manner. It is very important to screen the available cultivars

and newly developed germplasm against the pathogen to develop a ranking for susceptibility and resistance. The susceptibility/resistance of a particular cultivar varies depending upon *Fusarium* species and storage temperature; hence, it should be considered for designing a breeding program. Marker-assisted selection is the need of the hour to identify certain resistant QTLs for this disease. There is a dire need to formulate unique forward genetic approaches for identifying and overexpressing genes that inactivate or detoxify mycotoxins. It will help to develop tolerant cultivars against toxin-producing *Fusarium* species. The development of an integrated disease management approach that includes the use of certified disease-free seeds, preventing the injury of tubers during harvesting, curing and transportation, optimum storage conditions and applying the recommended dose of registered chemicals can efficiently manage the disease. The emergence of fungicide-resistant strains demands the use of GRAS compounds, microbial antagonists and silver nanoparticles in managing the disease with less environmental hazard and minimum pest resurgence. Novel phytohormones like melatonin and strigolactones should also



**Fig. 5** The flow chart highlights the major strategies to manage dry rot disease of potato in field and storage conditions. The disease management in cold stores relies on proper curing and handling of the harvest coupled with storage unit sanitization. Management in field

conditions is possible through adopting adequate phytosanitary measures, applying suitable chemical and bioagents and planting tolerant cultivars

be tried in potato plants and/or tubers as these biochemicals have given promising results in managing post-harvest diseases of commercial crops. The availability of genomic data demands further functional analysis and proteomics of pathogenicity genes only then these genes can be targeted for designing non-transgenic and transgenic management approaches. The *Fusarium* species are having versatile and novel combinations of virulence determinants and pathogenicity factors. Host-induced gene silencing has demonstrated a good potential in mitigating *Fusarium* diseases in some important commercial crops and it will be interesting to explore its role in dry rot suppression in potatoes. The successful management of dry rot will depend upon the additional research on the identified gaps and collaborative efforts of stakeholders (scientists, industrialists and farmers) in formulating an integrated management approach from farm to storage.

**Acknowledgements** This study was supported by the Indian Council of Agricultural Research, New Delhi, India.

**Author contributions** RKT, RK and MKL designed the outline of the article, composed the manuscript and figures. KCN, KNC and DK searched the literature and related information, SS, VS, RA and MK provided scientific feedback and critical comments to revise the content.

## Compliance with ethical standards

**Conflict of interest** There is no conflict of interest by the co-authors.

**Ethical approval** No human subjects were used in the writing of the manuscripts.

## References

- Aiko V, Mehta A (2016) Prevalence of toxigenic fungi in common medicinal herbs and spices in India. *3 Biotech* 6:1–10. <https://doi.org/10.1007/s13205-016-0476-9>
- Al-Mughrabi KI, Vikram A, Peters RD et al (2013) Efficacy of *Pseudomonas syringae* in the management of potato tuber diseases in storage. *Biol Control* 64:315–322. <https://doi.org/10.1016/j.biocontrol.2012.11.011>
- Aydın MH (2019) Evaluation of some *Trichoderma* species in biological control of potato dry rot caused by *Fusarium sambucinum* Fuckel isolates. *Appl Ecol Environ Res* 17(1):533–546. [https://doi.org/10.15666/aer/1701\\_533546](https://doi.org/10.15666/aer/1701_533546)
- Ayers GW, Robinson DB (1954) An inoculation technique for the study of dry rot of potatoes. *Am Potato J* 31:278–281. <https://doi.org/10.1007/BF02861635>
- Bacon CW, Porter JK, Norred WP, Leslie J (1996) Production of fusaric acid by *Fusarium* species. *Appl Environ Microbiol* 62(11):4039–4043
- Bang U (2007) Screening of natural plant volatiles to control the potato (*Solanum tuberosum*) pathogens *Helminthosporium solani*, *Phoma foveata* and *Rhizoctonia solani*. *Potato Res* 50:185–203. <https://doi.org/10.1007/s11540-008-9044-y>
- Baturo-Ciesniewska A, Lenc L, Grabowski A, Lukanowski A (2015) Characteristics of polish isolates of *Fusarium sambucinum*: molecular identification, pathogenicity, diversity and reaction to control agents. *Am J Potato Res* 92:49–61. <https://doi.org/10.1007/s12230-014-9410-z>
- Blanco FA, Zanetti ME, Casalongué CA, Daleo GR (2006) Molecular characterization of a potato MAP kinase transcriptionally regulated by multiple environmental stresses. *Plant Physiol Biochem* 44(5–6):315–322
- Bojanowski A, Avis TJ, Pelletier S, Tweddell RJ (2013) Management of potato dry rot. *Postharvest Biol Technol* 84:99–109
- Brown DW, Butchko RAE, Proctor RH (2008) Food additives and contaminants genomic analysis of *Fusarium verticillioides*. Genomic analysis of *Fusarium verticillioides*. *Food Addit Contam* 25:1158–1165. <https://doi.org/10.1080/02652030802078166>
- Burlakoti RR, Ali S, Secor GA et al (2008) Population biology genetic relationships among populations of *Gibberella zeae* from barley, wheat, potato, and sugar beet in the upper midwest of the United States. *Am Phytopath Soc* 98:969. <https://doi.org/10.1094/PHYTO-98-9-0969>
- Carnegie SF, Cameron AM, Haddon P (2001) The effect of date of haulm destruction and harvest on the development of dry rot caused by *Fusarium solani* var. *coeruleum* on potato tubers. *Ann Appl Biol* 139(2):209–216
- Chen W, Kastner C, Nowara D, Oliveira-Garcia E, Rutten T, Zhao Y, Deising HB, Kumlehn J, Schweizer P (2016) Host-induced silencing of *Fusarium culmorum* genes protects wheat from infection. *J Exp Bot* 67(17):4979–4991
- Chen D, Nahar K, Bizimungu B et al (2020) A simple and efficient inoculation method for *Fusarium* dry rot evaluations in potatoes. *Am J Potato Res*. <https://doi.org/10.1007/s12230-020-09774-4>
- Choiseul JW, Allen L, Carnegie SF (2001) The role of stem inoculum in the transmission of *Fusarium sulphureum* to potato tubers. *Potato Res* 44:165–172. <https://doi.org/10.1007/BF02410103>
- Coleman JJ, Rounsley SD, Rodriguez-Carres M et al (2009) The genome of *Nectria haematococca*: contribution of supernumerary chromosomes to gene expansion. *PLoS Genet* 5(8):e1000618. <https://doi.org/10.1371/journal.pgen.1000618>
- Cullen DW, Toth IK, Pitkin Y et al (2005) Use of quantitative molecular diagnostic assays to investigate *Fusarium* dry rot in potato stocks and soil. *Phytopathology* 95:1462–1471. <https://doi.org/10.1094/PHYTO-95-1462>
- Cuomo CA, Güldener U, Xu JR, Trail F, Turgeon BG, Di Pietro A, Walton JD, Ma LJ, Baker SE, Rep M, Adam G (2007) The *Fusarium graminearum* genome reveals a link between localized polymorphism and pathogen specialization. *Science* 317(5843):1400–1402
- Daami-Remadi M (2012) Potato *Fusarium* dry rot in tunisia: current status and future prospects. *Pest Technol* 6:15–22
- Daferera DJ, Ziogas BN, Polissiou MG (2003) The effectiveness of plant essential oils on the growth of *Botrytis cinerea*, *Fusarium* sp. and *Clavibacter michiganensis* subsp. *michiganensis*. *Crop Prot* 22:39–44. [https://doi.org/10.1016/S0261-2194\(02\)00095-9](https://doi.org/10.1016/S0261-2194(02)00095-9)
- Delgado JA, Schwarz PB, Gillespie J et al (2010) Trichothecene mycotoxins associated with potato dry rot caused by *Fusarium graminearum*. *Phytopathology* 100:290–296. <https://doi.org/10.1094/PHYTO-100-3-0290>
- Delgado L, Schuster M, Torero M (2017) Reality of food losses: a new measurement methodology. IFPRI discussion paper 1686. International Food Policy Research Institute (IFPRI), Washington, DC. <https://ebrary.ifpri.org/cdm/ref/collection/p15738coll2/id/131530>
- Desjardins AE (1995) Population structure of *Gibberella pulicaris* (Anamorph *Fusarium sambucinum*) from potato tuber dry rot in North America and Europe. *Am Potato J* 72:145–156. <https://doi.org/10.1007/BF02849350>



- Desjardins AE (2006) *Fusarium* mycotoxins: chemistry, genetics, and biology. American Phytopathological Society (APS Press), St. Paul
- Desjardins AE, Gardner HW (1989) Genetic analysis in *Gibberella pulicaris*: Rishitin tolerance, rishitin metabolism, and virulence on potato tubers. *Mol Plant Microbe Interact* 2:26–34
- Devaux A, Goffart J-P, Petsakos A, et al. (2020) Global food security, contributions from sustainable potato agri-food systems. In: The potato crop. Springer International Publishing, pp 3–35
- Du M, Ren X, Sun Q et al (2012) Characterization of *Fusarium* spp. causing potato dry rot in china and susceptibility evaluation of chinese potato germplasm to the pathogen. *Potato Res* 55:175–184. <https://doi.org/10.1007/s11540-012-9217-6>
- El-Banna AA, Scott PM, Lau PY (1984) Formation of trichothecenes by *Fusarium solani* var. *coeruleum* and *Fusarium sambucinum* in potatoes. *Appl Environ Microbiol* 47:1169–1171. <https://doi.org/10.1128/aem.47.5.1169-1171.1984>
- El-Hassan KI, El-Saman MG, Mosa AA, Mostafa MH (2007) Variation among *Fusarium* spp. the causal of potato tuber dry rot in their pathogenicity and mycotoxins production. *Egypt J Phytopathol* 35(2):53–68
- Elsherbiny EA, Amin BH, Baka ZA (2016) Efficiency of pomegranate (*Punica granatum* L.) peels extract as a high potential natural tool towards *Fusarium* dry rot on potato tubers. *Postharvest Biol Technol* 111:256–263. <https://doi.org/10.1016/j.postharvbio.2015.09.019>
- Eranthodi A, Schneiderman D, Harris LJ et al (2020) Enniatin production influences *Fusarium avenaceum* virulence on potato tubers, but not on durum wheat or peas. *Pathogens*. <https://doi.org/10.3390/pathogens9020075>
- Esfahani MN (2005) Susceptibility assessment of potato cultivars to *Fusarium* dry rot species. *Potato Res* 48(3–4):215–226
- Estrada R, Gudmestad NC, Rivera VV, Secor GA (2010) *Fusarium graminearum* as a dry rot pathogen of potato in the USA: prevalence, comparison of host isolate aggressiveness and factors affecting aetiology. *Plant Pathol* 59:1114–1120. <https://doi.org/10.1111/j.1365-3059.2010.02343.x>
- FAOSTAT (2019) Food and agriculture data. <https://www.fao.org/faostat/en/#data/QCinfo>
- Fiers M, Edel-Hermann V, Chatot C et al (2012) Potato soil-borne diseases. A review. *Agron Sustain Dev* 32:93–132
- Fleisner A, Sopalla C, Weltring KM (2002) An ATP-binding cassette multidrug-resistance transporter is necessary for tolerance of *Gibberella pulicaris* to phytoalexins and virulence on potato tubers. *Mol Plant Microbe Interact* 15:102–108. <https://doi.org/10.1094/mpmi.2002.15.2.102>
- Gachango E, Hanson LE, Rojas A et al (2012) *Fusarium* spp. causing dry rot of seed potato tubers in Michigan and their sensitivity to fungicides. *Plant Dis* 96:1767–1774. <https://doi.org/10.1094/PDIS-11-11-0932-RE>
- Gardiner DM, McDonald MC, Covarelli L et al (2012) Comparative pathogenomics reveals horizontally acquired novel virulence genes in fungi infecting cereal hosts. *PLoS Pathog*. <https://doi.org/10.1371/journal.ppat.1002952>
- Ghag SB, Ganapathi TR (2019) RNAi-mediated protection against banana diseases and pests. *3 Biotech* 9:1–8
- Gherbawy YA, Hussein MA, El-dawy EGA et al (2019) Identification of *Fusarium* spp. associated with potato tubers in upper egypt by morphological and molecular characters. *Asian J Biochem Genetics Mol Biol* 2:1–14. <https://doi.org/10.9734/AJBGM/B/2019/v2i330062>
- Godoy AV, Zanetti ME, Segundo BS, Casalongué CA (2001) Identification of a putative *Solanum tuberosum* transcriptional coactivator up-regulated in potato tubers by *Fusarium solani* f. sp. *eumartii* infection and wounding. *Physiol Plant* 112:217–222. <https://doi.org/10.1034/j.1399-3054.2001.1120210.x>
- Golinski P, Vesonder RF, Latus-Zietkiewicz D, Perkowski J (1988) Formation of fusarenone X, nivalenol, zearalenone, alpha-trans-zearalenol, beta-trans-zearalenol, and fusarin C by *Fusarium crookwellense*. *Appl Environ Microbiol* 54(8):2147–2148
- Gottschalk K, Ezhekiel R (2006) Food Products Press, New York, pp 489–522
- Haverkort AJ, De Ruijter FJ, Van Evert FK, Conijn JG, Rutgers B (2013) Worldwide sustainability hotspots in potato cultivation. 1. Identification and mapping. *Potato Res* 56(4):343–53.
- Hay WT, Fanta GF, Rich JO et al (2019) Antifungal activity of a fatty ammonium chloride amylose inclusion complex against *Fusarium sambucinum*; control of dry rot on multiple potato varieties. *Am J Potato Res* 96:79–85. <https://doi.org/10.1007/s12230-018-9683-8>
- Heltoft P, Molteberg EL, Nærstad R, Hermansen A (2015) Effect of maturity level and potato cultivar on development of *Fusarium* dry rot in Norway. *Potato Res* 58:205–219. <https://doi.org/10.1007/s11540-015-9300-x>
- Heltoft P, Brierley JL, Lees AK et al (2016) The relationship between soil inoculum and the development of *Fusarium* dry rot in potato cultivars Asterix and Saturna. *Eur J Plant Pathol* 146:711–714. <https://doi.org/10.1007/s10658-016-0946-2>
- Herrmann M, Zocher R, Haese A (1996) Enniatin production by fusarium strains and its effect on potato tuber tissue. *Appl Environ Microbiol* 62(2):393–398
- Ippólito SD, Laura M, Florencia M et al (2010) Physiological and molecular plant pathology transcriptome profiling of *Fusarium solani* f. sp. *eumartii* -infected potato tubers provides evidence of an inducible defense response. *Physiol Mol Plant Pathol* 75:3–12. <https://doi.org/10.1016/j.pmpp.2010.09.002>
- Ismail Y, Hijri M (2012) Arbuscular mycorrhisation with *Glomus irregulare* induces expression of potato PR homologues genes in response to infection by *Fusarium sambucinum*. *Funct Plant Biol* 39(3):236–245
- Jiang H, Wang B, Ma L et al (2019) Benzo-(1, 2, 3)-thiadiazole-7-carbothioic acid s-methyl ester (BTH) promotes tuber wound healing of potato by elevation of phenylpropanoid metabolism. *Postharvest Biol Technol* 153:125–132. <https://doi.org/10.1016/j.postharvbio.2019.03.003>
- Kamran M, Anamika K, Tabinda P et al (2020) *Fusarium* head blight in wheat: contemporary status and molecular approaches. *3 Biotech* 3:1–17. <https://doi.org/10.1007/s13205-020-2158-x>
- Khalid AR, Lv X, Naeem M et al (2019a) Autophagy related gene (ATG3) is a key regulator for cell growth, development, and virulence of *Fusarium oxysporum*. *Genes (Basel)*. <https://doi.org/10.3390/genes10090658>
- Khalid AR, Zhang S, Luo X et al (2019b) Role of autophagy-related gene atg22 in developmental process and virulence of *Fusarium oxysporum*. *Genes (Basel)*. <https://doi.org/10.3390/genes10050365>
- Kim JC, Lee YW (1994) Sambutoxin, a new mycotoxin produced by toxic *Fusarium* isolates obtained from rotted potato tubers. *Appl Environ Microbiol* 60:4380–4386
- Kishan G, Kumar M, Tiwari R, Sharma P (2017a) Deciphering the mechanism of mycoparasitism of *Sclerotinia sclerotiorum* by *Trichoderma* spp. *Int J Pure App Biosci* 5:1246–1250. <https://doi.org/10.18782/2320-7051.5226>
- Kishan G, Tiwari R, Prakash G et al (2017b) Factors affecting mycoparasitism of *Sclerotinia sclerotiorum* by *Trichoderma* spp. *Indian Phytopathol* 70:397–399. <https://doi.org/10.24838/ip.2017.v70.i3.72494>
- Knowles NR, Plissey ES (2008) Maintaining tuber health during harvest, storage, and post-storage handling. In: Johnson DA (ed) Potato health management. St. Paul Minnesota, APS Press, pp 79–99

- Koch A, Biedenkopf D, Furch A et al (2016) An RNAi-based control of *Fusarium graminearum* infections through spraying of long dsRNAs involves a plant passage and is controlled by the fungal silencing machinery. *PLOS Pathog* 12:e1005901. <https://doi.org/10.1371/journal.ppat.1005901>
- Kolaei EA, Cenatus C, Tweddell RJ, Avis TJ (2013) Antifungal activity of aluminium-containing salts against the development of carrot cavity spot and potato dry rot. *Ann Appl Biol* 163:311–317. <https://doi.org/10.1111/aab.12056>
- Kubar AA, Nizamani MM, Kaleri AA et al (2019) Efficacy of different fungicides and bio control agents against *Fusarium oxysporum*, causal agent of potato dry rot. *Indian J Sci Technol* 12(1):1–12. <https://doi.org/10.17485/ijst/2019/v12i7/141007>
- Kulik T, Brankovics B, Sawicki J, van Diepeningen A (2015) The complete mitogenome of *Fusarium culmorum*. *Mitochondrial DNA* 27:2425–2426. <https://doi.org/10.3109/19401736.2015.1030626>
- Kumar R, Tiwari RK, Jeevalatha A, Kaundal P, Sharma S, Chakrabarti SK (2019) Potato viruses and their diagnostic techniques: an overview. *J Pharm Phytochem* 8(6):1932–1944
- Kumar R, Kaundal P, Arjunan J et al (2020) Development of a visual detection method for Potato virus S by reverse transcription loop-mediated isothermal amplification. *3 Biotech* 10:213. <https://doi.org/10.1007/s13205-020-02214-4>
- Lal MK, Kumar A, Kardile HB et al (2020a) Biofortification of Vegetables. In: Sharma TR, Deshmukh R, Sonah H (eds) *Advances in agri-food biotechnology*. Springer, Singapore. [https://doi.org/10.1007/978-981-15-2874-3\\_5](https://doi.org/10.1007/978-981-15-2874-3_5)
- Lal MK, Kumar A, Raigond P et al (2020b) Impact of Starch Storage Condition on Glycemic Index and Resistant Starch of Cooked Potato (*Solanum tuberosum*) Tubers. *Starch Stärke*. <https://doi.org/10.1002/STAR.201900281>
- Latus-Ziętkiewicz D, Perkowski J, Chelkowski J (1987) *Fusarium* species as pathogens of potato tubers during storage and their ability to produce mycotoxins. *Mycotoxin Res* 3(1):99–104
- Li YC, Bi Y, Ge YH et al (2009) Antifungal activity of sodium silicate on *Fusarium Sulphureum* and its effect on dry rot of potato tubers. *J Food Sci*. <https://doi.org/10.1111/j.1750-3841.2009.01154.x>
- Logrieco A, Moretti A, Castella G, Kostecki M, Golinski P, Ritieni A, Chelkowski J (1998) Beauvericin production by *Fusarium* species. *Appl Environ Microbiol* 64(8):3084–3088
- Ma LJ, Van Der Does HC, Borkovich KA, Coleman JJ, Daboussi MJ, Di Pietro A, Dufresne M, Freitag M, Grabherr M, Henrissat B, Houterman PM (2010) Comparative genomics reveals mobile pathogenicity chromosomes in *Fusarium*. *Nature* 464(7287):367–373
- Ma L-J, Geiser DM, Proctor RH et al (2013) *Fusarium* pathogenomics. *Annu Rev Microbiol* 67:399–416. <https://doi.org/10.1146/annurev-micro-092412-155650>
- Mahdavi-Amiri M, Razavi M, Sharifi K, Zare R (2009) Investigation on genetic diversity of *Fusarium oxysporum* causing potato *Fusarium* wilt by pathogenicity tests and RAPD markers. *Iran J Plant Path* 45(1):3–5
- Mahmoud GA, El-Tobgy KMK, Abo-El-Seoud MA (2010) Utilization of biocides for controlling pest attacks on potato tubers. *Arch Phytopathol Plant Prot* 43:251–258. <https://doi.org/10.1080/03235400701803812>
- Maphosa MN, Steenkamp ET, Wingfield BD (2016) Genome-based selection and characterization of *Fusarium circinatum*-specific sequences. *G3* 6:631–639. <https://doi.org/10.1534/g3.115.025817>
- Mejdoub-Trabelsi B, Jabnoun-Khiareddine H, Daami-Remadi M (2012) Effect of *Fusarium* species and temperature of storage on the susceptibility ranking of potato cultivars to tuber dry rot biocontrol of soilborne fungal diseases of vegetable crops. *Pest Technol* 6:41–46
- Mills JT (1990) Mycotoxins and toxigenic fungi on cereal grains in western Canada. *Can J Physiol Pharmacol* 68:982–986
- Moustafa-farag M, Almoneafy A, Mahmoud A et al (2020) Melatonin and its protective role against biotic stress impacts on plants. *Biomolecules* 10:54. <https://doi.org/10.3390/biom10010054>
- Mvumba H, Green S, Tsopmo A, Avis T (2009) Antimicrobial efficacy of cinnamon, ginger, horseradish and nutmeg extracts against spoilage pathogens. *Phytoprotection* 90(2):65–70
- Nagaraja H, Chennappa G, Poorna Chandra Rao K et al (2016) Diversity of toxic and phytopathogenic *Fusarium* species occurring on cereals grown in Karnataka state, India. *3 Biotech* 6:1–8. <https://doi.org/10.1007/s13205-016-0399-5>
- Nawaim A, Nefzi A, Jabnoun-Khiareddine H et al (2017) Control of *Fusarium* dry rot incited by *Fusarium oxysporum* f. sp. *tuberosi* using *Sargassum vulgare* aqueous and organic extracts biological control of soil borne pathogens. *Artic J Microb Biochem Technol* 9:200–208. <https://doi.org/10.4172/1948-5948.1000366>
- Niehaus EM, Münsterkötter M, Proctor RH, Brown DW, Sharon A, Idan Y, Oren-Young L, Sieber CM, Novák O, Pěňčík A, Tarkowská D (2016) Comparative “omics” of the *Fusarium fujikuroi* species complex highlights differences in genetic potential and metabolite synthesis. *Genome Biol Evol* 8(11):3574–3599
- Nielsen KF, Thrane U (2001) Fast methods for screening of trichothecenes in fungal cultures using gas chromatography–tandem mass spectrometry. *J Chromatogr* 929(1–2):75–87
- Ocamb CM, Hamm PB, Johnson DA (2007) Benzimidazole resistance of *Fusarium* species recovered from potatoes with dry rot from storages located in the Columbia Basin of Oregon and Washington. *Am J Potato Res* 84:169–177. <https://doi.org/10.1007/BF02987140>
- Paper JM, Scott-Craig JS, Adhikari ND et al (2007) Comparative proteomics of extracellular proteins *in vitro* and in planta from the pathogenic fungus *Fusarium graminearum*. *Proteomics* 7:3171–3183. <https://doi.org/10.1002/pmic.200700184>
- Patil VU, Vanishree V, Sagar V, Chakrabarti S (2017) Draft genome sequence of potato dry rot pathogen *Fusarium sambucinum* Fckl. F-4. *Am J Potato Res* 94:266–269. <https://doi.org/10.1007/s12230-016-9562-0>
- Perfect SE, Green JR (2001) Infection structures of biotrophic and hemibiotrophic fungal plant pathogens. *Mol Plant Pathol* 2(2):101–108
- Peters JC, Lees AK, Cullen DW et al (2008a) Characterization of *Fusarium* spp. responsible for causing dry rot of potato in Great Britain. *Plant Pathol* 57:262–271. <https://doi.org/10.1111/j.1365-3059.2007.01777.x>
- Peters RD, MacLeod C, Seifert KA et al (2008b) Pathogenicity to potato tubers of *Fusarium* spp. isolated from potato, cereal and forage crops. *Am J Potato Res* 85:367–374. <https://doi.org/10.1007/s12230-008-9037-z>
- Peters JC, Lees AK, Cullen DW, Sullivan L, Stroud GP, Cunnington AC (2008) Characterization of *Fusarium* spp. responsible for causing dry rot of potato in Great Britain. *Plant Pathol* 57(2):262–271
- Pinhero RG, Coffin R, Yada RY (2009) Post-harvest storage of potatoes. In: *Advances in potato chemistry and technology*. Elsevier, pp 339–370
- Raigond P, Sagar V, Mishra T et al (2019) Chitosan: a safe alternative to synthetic fungicides to manage dry rot in stored potatoes. *Potato Res* 62:393–409. <https://doi.org/10.1007/s11540-019-9421-8>
- Rampersad SN (2020) Pathogenomics and management of *Fusarium* diseases in plants. *Pathogens* 9(5):340. <https://doi.org/10.3390/pathogens9050340>
- Recep K, Fikrettin S, Erkol D, Cafer E (2009) Biological control of the potato dry rot caused by *Fusarium* species using PGPR strains.

- Biol Control 50(2):194–198. <https://doi.org/10.1016/j.biocontrol.2009.04.004>
- Romanazzi G, Feliziani E, Baños SB, Sivakumar D (2017) Shelf life extension of fresh fruit and vegetables by chitosan treatment. *Crit Rev Food Sci Nutr* 57:579–601. <https://doi.org/10.1080/10408398.2014.900474>
- Saccardo PA, Traverso GB (1882) *Sylloge Fungorum Omnium Hucusque Cognitorum* Sumptibus Coheredum Saccardo, vol 23, Abellini
- Sadfi N, Cherif M, Fliss I, Boudabbous A, Antoun H (2001) Evaluation of *Bacillus* isolates from salty soils and *Bacillus thuringiensis* strains for the biocontrol of *Fusarium* dry rot of potato tubers. *J Plant Pathol* 83:101–118. <https://doi.org/10.4454/jpp.v83i2.1118>
- Sadfi N, Chérif M, Hajlaoui MR, Boudabbous A (2002) Biological control of the potato tubers dry rot caused by *Fusarium roseum* var. *sambucinum* under greenhouse, field and storage conditions using *Bacillus* spp. isolates. *J Phytopathol* 150:640–648. <https://doi.org/10.1046/j.1439-0434.2002.00811.x>
- Sagar V, Sharma S, Jeevalatha A et al (2011) First report of *Fusarium sambucinum* causing dry rot of potato in India. *New Dis Rep* 24:5. <https://doi.org/10.5197/j.2044-0588.2011.024.005>
- Saremi H, Okhovvat SM, Ashrafi SJ (2011) *Fusarium* diseases as the main soil borne fungal pathogen on plants and their control management with soil solarization in Iran. *Afr J Biotechnol* 10:18391–18398. <https://doi.org/10.5897/AJB11.2935>
- Schisler DA, Slininger PJ (1994) Selection and performance of bacterial strains for biologically controlling *Fusarium* dry rot of potatoes incited by *Gibberella pulicaris*. *Plant Dis* 78:251–255. <https://doi.org/10.1094/PD-78-0251>
- Schisler DA, Slininger PJ, Olsen NL (2016) Appraisal of selected osmoprotectants and carriers for formulating gram-negative biocontrol agents active against *Fusarium* dry rot on potatoes in storage. *Biol Control* 98:1–10. <https://doi.org/10.1016/j.biocontrol.2016.03.009>
- Secor GA, Johnson SB (2008) Seed tuber health before and during planting. In: *Potato health management*. The American Phytopathological Society, St Paul pp 45–53
- Secor G, Salas B (2001) *Fusarium* dry rot and *Fusarium* wilt. In: Stevenson WR, Loria R, Franc GD, Weingartner DP (eds) *Compendium of potato diseases*, 2nd edn. The American Phytopathological Society, St. Paul, pp 23–25
- Shen T, Wang Q, Li C et al (2020) Transcriptome sequencing analysis reveals silver nanoparticles antifungal molecular mechanism of the soil fungi *Fusarium solani* species complex. *J Hazard Mater* 388:122063. <https://doi.org/10.1016/j.jhazmat.2020.122063>
- Singh BP, Nagaich BB, Saxena SK (1987) Fungi associated with dry rot of potatoes, their frequency and distribution. *Indian J Plant Pathol* 5:142–145
- Singh N, Mukherjee SK, Rajam MV (2020) Silencing of the ornithine decarboxylase gene of *Fusarium oxysporum* f. sp. *lycopersici* by host-induced RNAi confers resistance to *Fusarium* wilt in tomato. *Plant Mol Biol Rep* 3:1–1
- Slininger PJ, Schisler DA, Burkhead KD, Bothast RJ (2003) Postharvest biological control of potato sprouting by *Fusarium* dry rot suppressive bacteria. *Biocontrol Sci Technol* 13:477–494. <https://doi.org/10.1080/0958315031000140992>
- Song HH, Lee HS, Jeong JH, Park HS, Lee C (2008) Diversity in beauvericin and enniatins H, I, and MK1688 by *Fusarium oxysporum* isolated from potato. *Int J Food Microbiol* 122(3):296–301
- Srivastava SK, Huang X, Brar HK et al (2014) The genome sequence of the fungal pathogen *Fusarium virguliforme* that causes sudden death syndrome in soybean. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0081832>
- Stefańczyk E, Sobkowiak S, Brylińska M, Śliwka J (2016) Diversity of *Fusarium* spp. associated with dry rot of potato tubers in Poland. *Eur J Plant Pathol* 145:871–884. <https://doi.org/10.1007/s10658-016-0875-0>
- Stevenson WR (2001) *Compendium of potato diseases*. American Phytopathological Society, Saint Paul, p 143
- Sun XJ, Yang BI, Li YC, Han RF, Ge YH (2008) Postharvest chitosan treatment induces resistance in potato against *Fusarium sulphureum*. *Agric Sci China* 7(5):615–621
- Suqin H, Xiulin J, Zhouquan W, Tingyi Z, Xi D, Degong L (2004) Isolation and Identification of Pathogens Causing Dry Rot of Potato Tuber in Dingxi Prefecture of Gansu Province. *J Yunnan Agric Univ* 19(5):550–552
- Sydenham EW, Marasas WFO, Thiel PG et al (1991) Production of mycotoxins by selected *Fusarium graminearum* and *F. crookwellense* isolates. *Food Addit Contam* 8:31–41. <https://doi.org/10.1080/02652039109373953>
- Tetorya M, Rajam MV (2018) RNA silencing of *PEX6* gene causes decrease in pigmentation, sporulation and pathogenicity of *Fusarium oxysporum*. *Plant Pathol* 67:67–75. <https://doi.org/10.1111/ppa.12712>
- Thatcher LF, Gardiner DM, Kazan K, Manners JM (2012) A highly conserved effector in *Fusarium oxysporum* is required for full virulence on Arabidopsis. *Mol Plant Microbe Interact* 25:180–190. <https://doi.org/10.1094/MPMI-08-11-0212>
- Theron DJ, Holz G (1990) Effect of temperature on dry rot development of potato tubers inoculated with different *Fusarium* spp. *Potato Res* 33:109–117. <https://doi.org/10.1007/BF02358135>
- Tinoco MLP, DiasDall’Asta BBARC et al (2010) *In vivo* trans-specific gene silencing in fungal cells by in planta expression of a double-stranded RNA. *BMC Biol* 8:27. <https://doi.org/10.1186/1741-7007-8-27>
- Tiwari RK, Kumar R, Sharma S et al (2020a) Continuous and emerging challenges of silver scurf disease in potato. *Int J Pest Manag*. <https://doi.org/10.1080/09670874.2020.1795302>
- Tiwari RK, Lal MK, Naga KC, Kumar R, Chourasia KN, Subhash S, Kumar D, Sharma S (2020b) Emerging roles of melatonin in mitigating abiotic and biotic stresses of horticultural crops. *Sci Hortic* 272:109592
- Trabelsi BM, Abdallah RAB, Ammar N, Kthiri Z, Hamada W (2016) Bio-suppression of *Fusarium* wilt disease in potato using non-pathogenic potato-associated fungi. *J Plant Pathol Microbiol* 7:347–354. <https://doi.org/10.4172/2157-7471.1000347>
- Vatankhah M, Saberi Riseh R, Moradzadeh Eskandari M, Sedaghati E, Alaie H, Afzali H (2019) biological control of *Fusarium* dry rot of potato using some probiotic bacteria. *J Agric Sci Technol* 21(5):1301–1312
- Vaughn SF, Spencer GF (1994) Antifungal activity of natural compounds against thiabendazole-resistant *Fusarium sambucinum* strains. *J Agric Food Chem* 42:200–203. <https://doi.org/10.1021/jf00037a036>
- Velluti A, Sanchis V, Ramos AJ et al (2004) Impact of essential oils on growth rate, zearalenone and deoxynivalenol production by *Fusarium graminearum* under different temperature and water activity conditions in maize grain. *J Appl Microbiol* 96:716–724. <https://doi.org/10.1111/j.1365-2672.2004.02212.x>
- Venter SL, Steyn PJ (1998) Correlation between fusaric acid production and virulence of isolates of *Fusarium oxysporum* that causes potato dry rot in South Africa. *Potato Res* 41:289–294. <https://doi.org/10.1007/BF02358198>
- Wei J, Bi Y, Xue H et al (2020) Antifungal activity of cinnamaldehyde against *Fusarium sambucinum* involves inhibition of ergosterol biosynthesis. *J Appl Microbiol*. <https://doi.org/10.1111/jam.14601>
- Wharton P, Hammerschmidt R, Kirk W (2007) *Fusarium* dry rot. Michigan potato diseases series. Michigan State University, Michigan, pp 531–532



- Wiemann P, Sieber CMK, von Bargaen KW et al (2013) Deciphering the cryptic genome: genome-wide analyses of the rice pathogen *Fusarium fujikuroi* reveal complex regulation of secondary metabolism and novel metabolites. PLoS Pathog. <https://doi.org/10.1371/journal.ppat.1003475>
- Xue H, Bi Y, Prusky D et al (2019) The mechanism of induced resistance against *Fusarium* dry rot in potato tubers by the T-2 toxin. Postharvest Biol Technol 153:69–78. <https://doi.org/10.1016/j.postharvbio.2019.03.021>
- Yilma S, Vales MI, Charlton BA et al (2012) Owyhee russet: A variety with high yields of u.s. no. 1 tubers, excellent processing quality, and moderate resistance to *Fusarium* dry rot (*Fusarium solani* var. *coeruleum*). Am J Potato Res 89:175–183. <https://doi.org/10.1007/s12230-012-9239-2>
- Zanetti M, Terrile MC et al (2002) Isolation and characterization of a potato cDNA corresponding to a 1-aminocyclopropane-1-carboxylate (ACC) oxidase gene differentially activated by stress. J Exp Bot 53(379):2455–2457. <https://doi.org/10.1093/jxb/53/379/2455> (PMID: 12432039)