



Black scurf of potato: Insights into biology, diagnosis, detection, host-pathogen interaction, and management strategies

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Abstract

Black scurf/stem canker disease, caused by the basidiomycetous fungus *Rhizoctonia solani* Kühn, became one of the major constraints to potato production worldwide. *R. solani* isolates of AG-3 are considered the main causal organism of black scurf, characterized by the presence of sclerotial bodies on the surface of potato tubers. *R. solani* limits the potato plants growth by developing cankers on sprouts, stems and tubers which make tubers ugly due to the appearance of corky spots and elephant hide symptoms on the tubers. To stop the establishment of disease, early detection and precise identification of pathogens are important components of an integrated disease management system. The present review summarizes the current knowledge about symptomology and epidemiology of black scurf, methods for early and accurate detection of black scurf pathogen/s, and molecular basis of potato–*R. solani* interaction. Elaborative and up-to-date information on various management options including cultural, chemical, biological, genetic manipulation and nanotechnological approaches and their effectiveness for managing black scurf are discussed. Genetic approaches that show promise for the control of black scurf include the development of transgenic lines by overexpressing or silencing pathogenesis-related (PR) genes and genome editing to develop lines with lower susceptibility to the disease is discussed.

Keywords Biological control · Genome editing · Integrated disease management · Molecular detection · *Rhizoctonia solani* · *Solanum tuberosum* pathosystem · Transgenic potato

Introduction

Potato (*Solanum tuberosum* L.) is an important non-grain vegetable food crop and ranked fourth after maize, paddy and wheat in total production and consumption (Lal et al. 2019). Worldwide total potato production was estimated at 359.07 million tonnes in 2020 and India placed second after China with 51.3 million tons (FAOSTAT 2022). The world population increasing exponentially is putting further pressure on agricultural lands, water and other resources. Therefore, farmers have to increase their output to feed the

growing population (Chaudhary et al. 2020a). In that scenario, potatoes have great importance in the global food system, strengthening global food security and alleviating poverty. The potato crop is susceptible to various fungal, bacterial, viral diseases and many other disorders (Chaudhary et al. 2020b). Among the fungal diseases, black scurf/stem canker caused by the ubiquitous fungus *Rhizoctonia solani* Kühn (teleomorph: *Thanatephous cucumeris* Frank (Donk)) is a serious problem in various potato growing regions in the world, including India. *Rhizoctonia* diseases in potatoes can cause a reduction in yield as well as quality (Das et al. 2014). The quantitative yield losses resulted from the infection of stems and underground portions that reduce the size and number of potato tubers (Carling et al. 1989). In contrast, qualitative losses occur mainly owing to mishappening of the tubers and sclerotial formation on the tuber surface (James and McKenzie 1972). The estimated yield loss due to *Rhizoctonia* diseases was reported up to 25% in India (Sharma 2015), 30% in Canada and 50% in other countries (Woodhall et al. 2008). The marketable yield loss of potatoes due to *Rhizoctonia* spp. reached up to 30%

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(Tsror 2010). Black scurf/stem canker disease of potatoes is difficult to control due to the prolonged survivability of the fungus as a dormant structure called sclerotia and its wide host range. In the present review, we provide up-to-date information regarding black scurf/stem canker disease caused by *Rhizoctonia* spp. Information is arranged under headings: pathogen, disease symptoms, anastomosis groups (AGs), detection & diagnosis and current control practices. The information can be useful for the better management of the disease.

The pathogen

The soil-borne pathogen *Rhizoctonia solani* AG-3 is considered the main causal organism of *Rhizoctonia* diseases of potatoes (Banville et al. 1996; Virgen-Callaros et al. 2000). Based on rDNA internal transcribed spacer (ITS) sequences variation the members of AG-3 were divided into three subgroups: AG-3PT (potato type), AG-3TB (tobacco type) and AG-3TM (tomato type) (Kuninaga

et al. 2000; Misawa and Kuninaga 2010). *R. solani* is unable to produce asexual structures and exists in the form of mycelia, sclerotia, or basidiospores (sexual spores) (Keijer 1996). Anamorphic classification of *Rhizoctonia* spp. is based on the cell's nuclear condition (multi, bi, or uni-nucleate) and the ability of hyphal anastomosis with tester strains of designated anastomosis groups (AGs) (Sneh et al. 1991). To date, thirteen AGs (AG1-AG13) and AGB1 have been identified based on phenotypic and genotypic characteristics including cultural, morphological, host range, virulence, nutritional requirements, molecular and biochemical characteristics (González et al. 2016). Generally, on potato dextrose agar (PDA) medium *R. solani* AG-3 isolates grew slower than AG1-I subgroup isolates (Chaudhary et al. 2023a) with whitish to light brown mycelial colour during early growth which turn brown as colony become aged (Fig. 1a). Microscopically, hyphal branch originates from distal dolipore septum with a characteristic constriction at the branching point (Ajayi-Oyetunde and Bradley 2018; Chaudhary et al. 2023b).

Fig. 1 Symptoms and causal organism of black scurf and stem canker disease of potato (a) Culture petriplate of *Rhizoctonia solani*, the causal organism of black scurf/stem canker disease; (b) Characteristic symptom of black scurf; (c) Corky spot symptom/ Eyeless or blind tuber; (d) Elephant hide symptom; (e) Damage on underground main stem; (f) *Rhizoctonia* lesions on stolons (g) Stunting and rosetting of plant tops; curled leaves; (h) White sheet of mycelia on stem; (i) Formation of Aerial tubers



Disease symptoms

Shortly after planting, necrosis on germinating sprouts are the typical symptoms of stem canker which results in the late emergence of potato plants in the field. Black scurf symptoms (Fig. 1b) appear later in the cropping season when sclerotial bodies start to cover the progeny potato tubers (Banville 1989). Generally, *R. solani* does not penetrate or damage the potato tubers; however, tuber mishappening may occur (Weinhold et al. 1982). Additionally, in severe infection, atypical symptoms including cracking, corky lesions, and elephant hide may also be observed on tubers (Campion et al. 2003; Muzhinji et al. 2014) (Fig. 1c, d). Reddish-brown to sunken grey lesions are formed on the newly developing sprouts, resulting girdle the young sprout (Fig. 1e). Below the affected area secondary sprouts are formed and if these secondary sprouts also infected, tertiary sprouts may be developed from non-affected lower buds. This process may be repeated several times. Sprouts will fail to emerge or wilt after emergence, resulting in uneven or irregular emergence and in severe cases may lead to a poor crop stand. Reddish-brown to brown lesions appear underneath the stems and on the stolons (Fig. 1f). As these lesions mature, they become rough and brown cankers and have craters, cracks or cracks or both (Banville 1978).

Infection of the stem causes stunting and rosetting of plant tops resulting in curling of the upper leaves which sometimes turn red or yellow (Fig. 1g) (Wharton et al. 2007). In a recent study, Ito et al. (2017) observed that leaf curling is not a direct symptom of *Rhizoctonia*. Still, prior infection with the Potato leaf roll virus enhanced the severity of *Rhizoctonia* diseases. At the base of stems and on the plant parts that are in contact with soil a greyish-white, felt-like mycelium mat can be observed (Fig. 1h), which is caused by the perfect stage (*T. cucumeris*) of the fungus (Banville and Carling 2001). Aerial tubers could be formed in the leaf axils of stems due to the interference of carbohydrate movement (Beukema and van der Zang 1990). These are green to reddish-purple round to bottle-shaped transformations of lateral shoots in the axils, with a few small leaves at the top (Fig. 1i).

Occurrence of *R. solani* anastomosis group (AGs) in potato

Rhizoctonia solani AG-3 is considered the most prevalent AG causing black scurf/stem canker in potatoes (Woodhall et al. 2007; Lehtonen et al. 2008a). However, other AGs such as AG2-1 (Woodhall et al. 2007; Lehtonen et al. 2008a), AG4 (Virgen-Calleros et al. 2000), AG4 HG-I, AG4 HG-III (Muzhinji et al. 2014; 2015), AG4 HG-II (Woodhall et al. 2012) and AG5 (Bandy et al. 1988), AG-8

(Balali et al. 1995), AG-9 (Yanar et al. 2005) have also been reported in potato fields at a lower frequency around the world. Besides, binucleate *Rhizoctonia* (BNR) isolates were also recovered from potato plants (Carling et al. 1986a). Farrokhi-Nejad et al. (2007) collected 12 BNR isolates (out of 58) that cause mild symptoms in potato sprouts. BNR AG A and AG R causing stem canker, black scurf and tuber defects were reported in South Africa (Muzhinji et al. 2015; Zimudzi et al. 2017). Recently, Shuai et al. (2022) reported that AG2-2IV causes black scurf in potatoes in Heilongjiang province, China.

Disease cycle and epidemiology

Rhizoctonia infection on potato crops can be initiated through seed-borne or soil-borne inoculum *viz.*, either sclerotia or runner hyphae from the plant debris. *R. solani* may survive as dormant sclerotia for over the years in soil and stubbles and can re-infect healthy potato plants in the subsequent crop season (Keijer et al. 1996) (Fig. 2). After successful attachment of vegetative growing hyphae to the surface of plant the T-shaped branches are formed within 12 h (Lehtonen et al. 2008b). *R. solani* enters the plant tissue and produces RS toxin, a mixture that includes N-acetyl glucosamine, N-acetyl galactosamine, glucose and mannose (Vidhyasekaran et al. 1997) along with pathogen effectors (Zheng et al. 2013). Penetration into the epidermis and cortex takes place with lobate appressoria or infection cushion or both from which the infection peg grows and enters the host (Marshall and Rush 1980; Singh and Subramanian 2017). Further, inter- or intra-cellular growth of mycelium triggers extracellular enzyme secretion, resulting in the infected tissue's collapse and forming brownish lesions called stem canker (Banville et al. 1996). This condition develops mainly before the formation of daughter tubers. The mycelium continues to grow on stolons and roots and develops sclerotial structures on them, which stimulated the senescence at the end of the growing season. Consequently, sclerotia are developed on daughter tubers known as black scurf. At the maturity of the potato crop, sclerotia remaining in the soil serve as the source of primary inoculum which infects the host plants in the next growing season (Scholte 1989). Environmental conditions like temperature and relative humidity are important for the infection and initiation of *Rhizoctonia* disease in potatoes. Low temperatures with high soil moisture and neutral to acidic soil (pH 7 or less) are favourable for stem cankers. Initiation of sclerotia formation on daughter tubers started late in the cropping season, mainly after harm cutting, but sclerotia can be seen at mid of the cropping season.

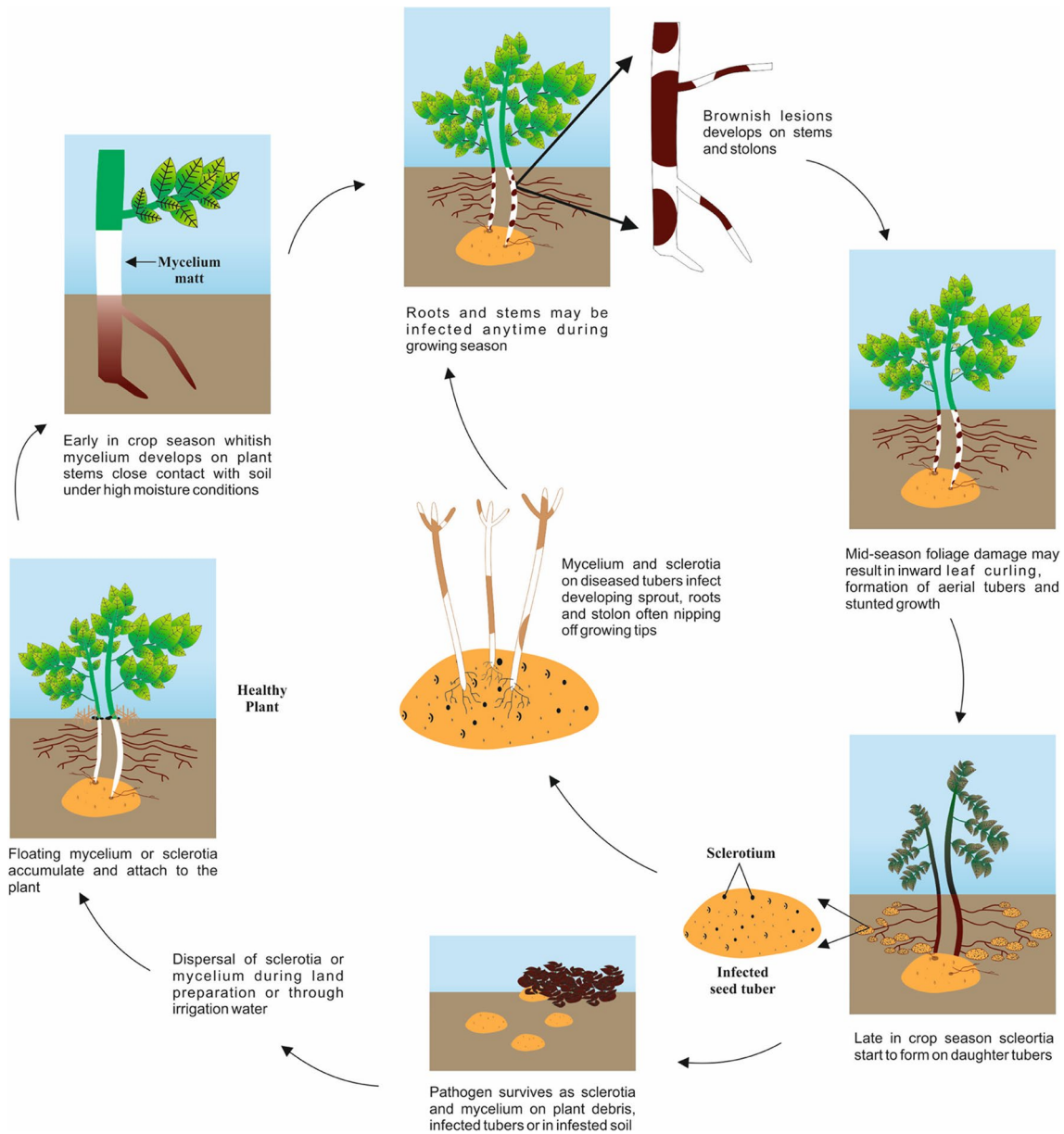


Fig. 2 Disease cycle of *Rhizoctonia* disease in potato showing different phases of sclerotia formation and disease symptoms

Molecular mechanism of Potato - *R. solani* AG3 interaction

Presently, there is limited information about the molecular responses of *R. solani* AG3-PT during pathogenic interaction with potato plants (Zrenner et al. 2020). The published complete whole genome sequence assemblies of AG-3 *R. solani* isolates (Cubeta et al. 2014; Wibberg et al. 2017; Patil et al. 2017) and potatoes (Xu et al. 2011) can be utilized for understanding the key mechanisms of *R. solani* infection and disease development (Table 1).

There is some information on phytotoxins (3-methylthiopropionic acid (3-MTPA) and 3-methylthioacrylic acid

(3-MTAA)) produced by *R. solani* AG3 with relation to disease symptoms, and concentration of the phytotoxin was correlated with pathogenicity (Kankam et al. 2016a, b). In rice sheath blight, three potential secreted effectors (such as glycosyltransferase, cytochrome C oxidase CtaG/cox11 and peptidase inhibitor I9) correlate with the virulence of *R. solani* AG1-IA (Zheng et al. 2013). In a study, Rioux et al. (2011) isolated and compared ESTs from AG1-IA infected rice leaves and AG-3 infected potato sprouts. Of 25 mRNAs from AG1-IA and AG3 showed significant similarity, 12 were associated with the pathogenesis processes. The six putative pathogenesis-related genes *viz.*, pyruvate carboxylase (PC), ABC-transporter (ABC), glycosyl-transferase

Table 1 List of sequenced *Rhizoctonia solani* from different hosts with their genomic characteristics

S.N.	Anastomosis group	Strain name	Host	Seq. Size (Mb)	Contings	GC Content (%)	Genes Predicted	Gene Density (genes/10 Kbp)	tRNA	rRNA	Reference
1	AG1-IA	B275	Rice	37.80	2,648	47.61	10,489	2.8	153	18	Zheng et al. (2013)
2	AG1-IA	1802/KB	Rice	28.93	1,517	46.99	10,037	-	117	2	Nadarajah et al. (2017)
3	AG1-IB	7/3/14	Soybean	52.74	23,355	48.10	12,616	2.4	187	22	Wibberg et al. (2013); Wibberg et al. (2015a)
4	AG8	WAC10335	Lupin	35.92	-	48.80	13,964	3.9	105	20	Hane et al. (2014)
5	AG2 IIIB	BBA69670	Sugar Beet	56.02	5,826	48.34	11,897	2.1	135	15	Wibberg et al. (2015b)
6	AG3	Rhs-1AP	Potato	52.50	6,040	48.40	12,726	2.4	-	17	Cubeta et al. (2014)
7	AG3-PT	RS-20	Potato	55.85	30,594	48.30	11,431	2.1	181	31	Patil et al. (2017)
8	AG3-PT	Ben3	Potato	51.00	27,078	48.58	12,567	-	-	-	Wibberg et al. (2017)

(GTF), kappa-family glutathione-S-transferase (GLU), Rab-type GTPase (RAB), and Nic96-type nucleoporin (NIC) had similar expression patterns in the AG1/rice and AG3/potato pathosystems. However, expression patterns of the putative AAA-type ATPase gene (AAA) and MFS were quite different between AG1 and AG3 which underscores the potential differences in *R. solani* pathogenesis mechanisms utilized in these two pathosystems (Subterranean vs. Foliar). In a recent transcriptomic analysis of AG3- potato interaction, various genes transcribed proteins with diverse hydrolase and peptidase activities have been predicted that were expressed differentially with due course of time response (Zrenner et al. 2020), while an additional increase of expression of hydrolases and genes coding various integral membrane proteins with transporter function was lined to interaction progression.

R. solani produces phenylacetic acid (PAA), three hydroxy (OH⁻) and a 3-methoxy (3-MeO⁻) derivative of PAA, which are important in the parasitism and infection process in plants (Mandava et al. 1980). In a study, Bartz et al. (2012) demonstrated the involvement of the PAA metabolic complex in *Rhizoctonia* disease development in tomatoes and also suggested that the production of these compounds is not the primary or the only determinant of pathogenicity. Reactive Oxygen Species (ROS) are very active and highly toxic to biological molecules and important growth regulators which are involved in limiting pathogen spread, induction of cell death and cell signalling in host-plant interactions (Torres 2010; Barna et al. 2012). It was also reported that fungi also produce ROS during pathogenic interactions (Daub and Ehrenshaft 2000; Samsatly et al. 2018). Therefore, the regulation of ROS in fungal cells and tolerance to external ROS produced by the host plant represent a balanced control and detoxification by both partners which can govern the fate of disease development (Heller and Tudzynski 2011). To maintain this balance, plant and fungal cells possess a complex array of protective mechanisms such as oxalic acid or the NADPH oxidase RBohD (Torres et al. 2005; Kadota et al. 2015), or ROS-quenching molecules including vitamin B6 (VB6) and various antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione-S-transferase (GST), and glutathione reductase (Zhang et al. 2015; Girard et al. 2017). Little information are reported on ROS scavenging systems in *R. solani* and to date the up-regulation of *R. solani* genes particularly, PYRIDOXALREDUCTASE (PLR AKR8; DW520695) and PYRIDOXAL-5-PHOSPHATASES and TRANSAMINASES of the vitamin B6 (VB6) salvage biosynthetic pathway was reported in *R. solani* hyphae in association with a mycoparasite or an antagonistic bacterium, respectively (Chamoun and Jabaji 2011; Gkarmiri et al. 2015). Samsatly et al. (2015) characterized two genes of the de-novo VB6 biosynthetic pathway;

RsolPDX1 (KF620111.1) and RsolPDX2 (KF620112.1), and one gene RsolPLR (KJ395592.1) of the VB6 salvage biosynthetic pathway of AG3. Recently, in a study Samsatly et al. (2020) provided indirect evidence on the functionality of RsolPDX1 and RsolPDX2 of AG3 and their involvement in VB6 de-novo biosynthesis pathway of the yeast *Saccharomyces cerevisiae* and showed that the antioxidant genes encoding VB6 (*i.e.*, PDX, PLR), CAT and, GST of AG3 and potato are differentially induced and transcriptionally regulated at the infection site (*i.e.*, necrotic tissues, and surrounding areas) during AG3- potato sprout interaction.

To defend themselves against phytopathogens like bacteria, fungi, viruses and insect herbivores, a complex defence system is induced in plants (Glazebrook 2005). Defence mechanisms can either be performed or induced. In response to necrotrophic fungi like *R. solani*, defence mechanisms attributed to ethylene (ET) and jasmonic acid (JA) signalling are known to be induced but not the salicylic acid (SA) signalling which plays an important role in plant resistance against biotrophic/hemibiotrophic pathogens (Tsuda et al. 2013). Recently, Kouzai et al. (2018) reported on the discovery of SA-dependent resistance of *Oryza sativa* and *Brachypodium distachyon* towards *R. solani* suggesting the existence of a pseudo biotrophic phase during the interaction with these two host species. The importance of SA-mediated defences plant defences in the AG3-potato pathosystem was further underlined by Genzel et al. (2017). Currently, no qualitative resistance has been reported, it assumed that a general response to AG3- potato infection is more probable and different pathways are involved in pathogen-associated molecular patterns (PAMP)-triggered immunity (PTI), previously identified as being induced by necrotrophs (Genzel et al. 2017).

It is well documented that pathogenesis-related (PR) genes become activated by induction of the systemic acquired resistance (SAR) pathway (Sanz-Alf erez et al. 2008). The PR proteins form a group of at least 17 structurally and functionally distinct protein families that are ubiquitous in plants (Liu and Ekramoddoullah 2006). The expression levels of five PR genes *viz.*, PR-1 (1,3- β -glucanase), PR-3 (chitinase), PR-10, glutathione-S-transferase (GST) and phenylalanine ammonia-lyase (PAL) gene were found to be induced in potatoes at different time points of *P. infestans* infection indicating the involvement of SAR activation (Vleeshouwers et al. 2000; Gallou 2011). Further, microarray analysis revealed a systemic transcriptional induction of PR-2, PAL, and PI2 (PR-6) associated with JA and abscisic acid (ABA) pathways in potato sprouts in response to AG3-potato infection (Lehtonen et al. 2008b). The expression of PR-10 is also described to be induced by the plant hormones JA and ABA (Liu and Ekramoddoullah 2006). In addition, while attacking the host plants, several fungi produce extracellular proteinases and protease inhibitors (PIs) (Kim et al.

2005). In turn, plants synthesize proteases and PIs as a way to defend themselves and recognise fungal derived proteinases (Jashni et al. 2015). It has been reported that Solanaceous plants have high contents of proteinase inhibitors. In a study, Gvozdeva et al. (2006) revealed that potato plants synthesize various proteinases which can suppress trypsin-like extracellular proteinases of *R. solani* in vitro.

For *R. solani*-potato interaction study, another critical area is the investigation of adaptive alterations in the metabolic profile of potato plants upon *R. solani* AG-3 infection. Although, limited studies have been conducted to reveal the involvement of metabolic changes during the period of potato response to the *R. solani* attack. In a study, Aliferis and Jabaji (2012) studied the accumulation of metabolites in potato sprouts at the *R. solani* infection site and they observed differential accumulation of phenolics, amino acids, alkaloids, fatty acids and organic acids in infected and mock infected sprout tissue. Further, carboxylic acids and sugars were increased during AG-3 infection, whereas host cell wall precursors and protein amino acids decreased. Also, the *R. solani*-derived virulence factor phenylacetic acid was quantified in infected sprouts (Bartz et al. 2012).

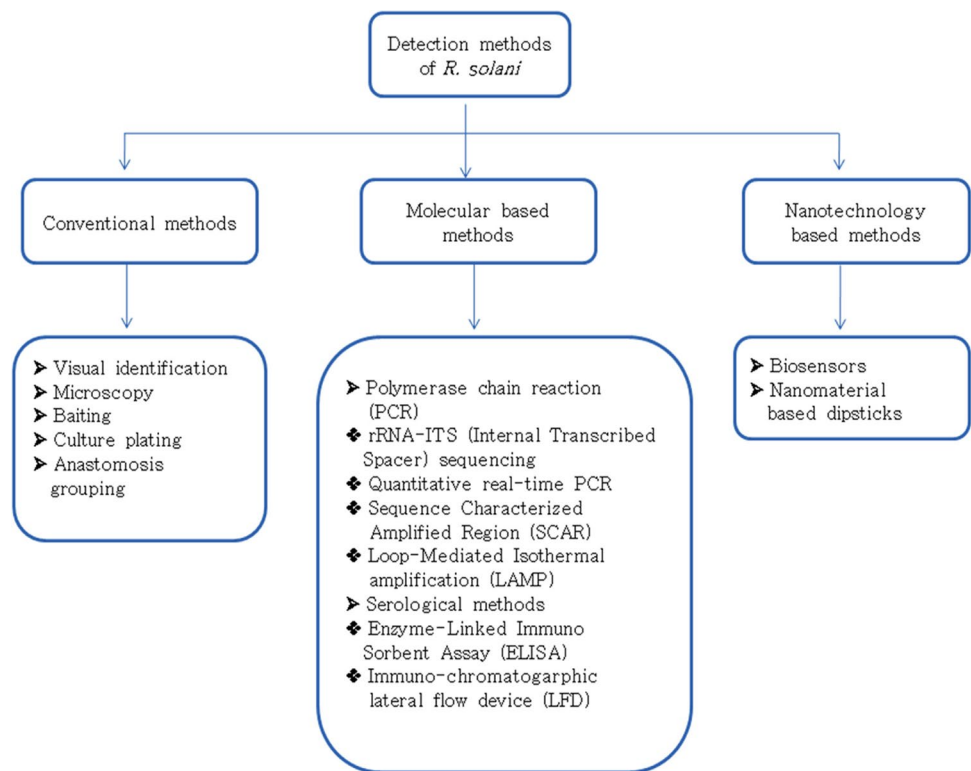
Detection and diagnosis

Detection and diagnosis of phytopathogens in crop plants and other host plant species may be required to monitor the presence and quantitative level of the pathogen(s) in a crop for preventive and curative measures. Various methods used for *R. solani* detection are outlined in Fig. 3.

Conventional approaches

Plant infection or the presence of phytopathogens can be determined by the visual inspection of disease symptoms followed by isolation of putative pathogen on a suitable nutrient medium. The isolated pathogen can be identified and characterized based on microscopic observations and taxonomic characteristics. However, conventional methods are nonspecific and not so much reliable due to their inability to differentiate among closely related species (Narayanasamy 2001). Additionally, the detection of pathogens becomes more difficult when disease symptoms are indefinite, low pathogen levels, absence of fruiting bodies, latent infection, etc. (Agrios 2005). Various detection techniques *i.e.*, bait method using susceptible host material (Weinhold 1977; Paulitz and Schroeder 2005; Spurlock et al. 2015), culture plating (Anderson and Huber 1965; Ko and Hora 1971; Vincelli and Beaupre 1989), wet sieving and direct microscopic observation (Boosalis and Scharen 1959), incubating immersion tubes in soil (Martinson 1963), wooden toothpicks (Paulitz and Schroeder 2005) and anastomosis test (Ogoshi 1987) have been developed for monitoring *R.*

Fig. 3 Various methods used for the detection of *R. solani*



solani in soil. The addition of tannic acid (300 ppm) as a marker to water agar was useful for the isolation, identification and quantification of *R. solani* (Hsieh et al. 1996). Although quite effective, these methods are time-consuming, labour-intensive and require considerable knowledge of fungal taxonomy.

Molecular approaches

The advancement in molecular biology techniques has provided new insights into the detection and cataloguing the soil-borne fungal pathogens like *R. solani* and can identify unknown species or strains from their DNA sequences.

PCR (Polymerase chain Reaction) based

For the detection of *R. solani* AG1-IA (Matsumoto 2002; Lal et al. 2020), AG-1-IB (Grosch et al. 2007), AG-2 and subgroups (Salazar et al. 2000), AG-3 (Bounoua et al. 1999), AG-4 and AG-8 (Brisbane et al. 1995) PCR-based methods have been used. Bounoua et al. (1999) used restriction endonuclease, XhoI to construct PCR-based restriction map for the detection of AG-3 from plants and soil samples. Recently, Irandukunda et al. (2022) used a multiplex PCR for the rapid detection of *R. solani* AG-3PT from potato tubers and soil.

rRNA-ITS (Internal Transcribe Spacer) sequence-based method

The internal transcribed spacer (ITS) region of nuclear DNA (rDNA) has been widely used for evolutionary studies and phylogenetics of fungal genus (Cubeta et al. 1996). The ITS region presents in several hundred copies in the genome and each unit is comprised of three genes viz., 18S (Small Subunit Ribosomal DNA, or SSU), 5.8S and 28S (Large Subunit Ribosomal DNA, or LSU) (Capote et al. 2012). Because ITS1 and ITS2 regions have not transcribed any protein, they are less affected by evolutionary pressure and therefore, highly variable among different isolates. By analyzing sequence differences of these regions, *Rhizoctonia* spp. can be grouped into clades having phylogenetic relationships. The 5.8S region of *R. solani* rDNA gene is highly conserved. The 18S and 28S subunits are used to differentiate high taxonomic levels such as family and genera while ITS allows the characterization of organisms at the species level (Gardes and Bruns 1993). The ITS sequence (ITS1-5.8S-ITS2) database of *R. solani* is extensively available at the NCBI GenBank (<http://www.ncbi.nlm.nih.gov/genbank>) which facilitates phylogenetic analysis. The rDNA-ITS sequences available at NCBI contained a conserved 5.8S region but showed variation in ITS1 and ITS2 regions (Carling et al. 2002; Amaradasa et al. 2013). Kanetis et al. (2016) performed an rDNA-ITS sequence analysis of 68 isolates collected from potato tubers. Sequence analysis of ITS regions

of rDNA confirmed the prevalence of AG3. Additionally, the phylogenetic analysis found that AG3 isolates were of the potato type, distinctly separated from the AG3 tobacco type.

Quantitative real-time PCR

Currently, the qPCR (Quantitative PCR) technique is an important advanced method used for diagnosing and detecting phytopathogens. Visual examination of *Rhizoctonia* disease at the early stages of infection does not provide a reliable estimation of the level of disease infection. A real-time quantitative (Q) PCR method was developed for the detection and quantification of *R. solani* AG3-PT DNA from tuber and soil samples. A specific primer based on the rDNA-ITS region of *R. solani* was designed. The assay produced amplicons with AG3-PT, and non-specific for the isolates from other AGs or subgroups of AG3 (Lees et al. 2002; Woodhall et al. 2013). Similarly, Zhao et al. (2014) designed specific primers for qPCR from rDNA-ITS region of *R. solani* and detected DNA as low as 100 fg from the infected tobacco tissues and soil samples. Shen et al. (2017) established the SYBR Green-I qPCR detection assay for the quantification of *R. solani* AG3 sclerotia from the soil. They reported that detecting sensitivity for the wet-sieving qPCR method was 10-fold higher than that of the conventional PCR.

DNA fingerprinting approaches

DNA fingerprinting is a technique that simultaneously detects many minisatellites in the genome to produce patterns unique to an organism. These methods are widely used to amplify the tandem repeats present in the random regions of the genome of an organism which helps to identify species-specific patterns when conserved genes do not have enough to differentiate the species (McCartney et al. 2003). In *R. solani* to assess the genetic variations among AG subgroups DNA fingerprinting techniques like Randomly amplified polymorphic DNA (RAPD) and DNA amplification fingerprinting (DAF) markers have been widely used (Stodart et al. 2007). Similarly, UP-PCR (Universally Primed PCR) markers were also very resembled RAPD (Bulat et al. 1998) which differentiates *R. solani* isolates belonging to different AGs and different subgroups (Lübeck and Lübeck 2005). Various DNA fingerprinting assays use only based on the same principle of DNA polymerase mediated amplification of DNA fragments to generate multiple copies of target genome sites. These techniques' difference depends primarily on the design or choice of primers and the level of stringency (Patil and Solanki 2016). However, AFLP (Amplified Fragment Length Polymorphism) technique is different from the above mentioned assays (Vos et al. 1995; Lübeck and Lübeck 2005). Ceresini et al. (2002) used AFLP analysis to differentiate AG-3 isolates from potato (AG-3 PT) and

tobacco (AG-3 TB). The findings revealed that analysed isolates from both hosts had distinct AFLP phenotypes. Thus, the AFLP technique has a very high discriminatory ability to facilitate intra-group variation.

SCAR (Sequence Characterized Amplified Region) approach

RAPD (Randomly amplified polymorphic DNA) markers may be used to differentiate target organisms from those of non-target organisms and unique specific bands with the target organism genomic DNA could be produced and cloned. Once the unique bands have been amplified and detected, they can be used as probes for the presence of similar DNA fragments in the related species. Further, after analysis, if the amplicons do not match, sequenced them, and species-specific SCAR (Sequence Characterized Amplified Region) markers could be developed (Ma and Michalides 2005) that selectively amplifies the marker and acts as a target site in diagnostic assays. Since *R. solani* is a species complex, SCAR markers are necessary for identification at strain or AG subgroup level. Grosch et al. (2007) designed and used SCAR markers to produce species-specific probes and PCR primers in *R. solani*.

Loop-Mediated Isothermal Amplification (LAMP) assay

LAMP technique can be performed onsite in the field, resulting in a significant reduction in time required to detect and diagnose the diseases. The LAMP method can be carried out inexpensively using simple water or heating block. A positive reaction is recognized by the accumulation of a visible product appearing as a white precipitate (Notomi et al. 2000). The products can be detected by agarose gel electrophoresis, by the use of spectrophotometry to measure turbidity (Mori et al. 2004), in RT-LAMP using intercalating fluorescent dyes (Oscorbin et al. 2016), or by visualize the turbidity through naked eyes or colour changes (Iwamoto et al. 2003; Mori et al. 2001). The LAMP method was integrated with lateral flow devices (LFDs) to improve the efficiency for in-field detection of *R. solani* in plant tissues, seeds, and propagules. LAMP primers based on the internal transcribed spacer (ITS) DNA sequences were used for the detection of anastomosis groups of *R. solani*. The LAMP-LFD procedure effectively detected *R. solani* in several infected plant species belonging to diverse families and has the potential for onsite diagnosis of *R. solani* in plants, seeds, propagules, and soils.

The detection limit of the LAMP-LFD protocol (10 fg) was comparable to that of qRT-PCR format (Patel et al. 2015). LAMP assay was utilized by Lu et al. (2015) for the detection and diagnosis of *R. solani* (ITS-Rs-LAMP) and

Macrophomina phaseolina (ITS-Mp-LAMP) in diseased soybean tissues in the field. The detection limit of the ITS-Rs-LAMP assay was 10 pg/μl of genomic DNA, and that of the ITS-Mp-LAMP assay was 100 pg/μl of genomic DNA.

Serological diagnostics

In the serological techniques, specific antibodies are used to detect their respective antigens in the test samples. Every antibody is specific for a particular antigen and binds to it, usually foreign proteins, complex carbohydrates, polynucleotides, or lipopolysaccharides. Enzyme-Linked Immuno Sorbent Assay (ELISA) is a valuable serological technique used for plant fungal pathogens detection (Johnson et al. 1982). Polyclonal antibodies (PABs) and monoclonal antibodies (MABs) have been produced against fungal antigens present in whole cells, cell fractions, extracellular components, and culture filtrates. Methods of production of PABs and MABs, principles of immunological reactions, and applications of various immunoassays have been discussed (Narayanasamy 2001, 2005). Using PABs and MABs in immunodiffusion tests attempts have been made to distinguish anastomosis groups of *R. solani* (Benson 1992; Thornton et al. 1999). For the detection of *R. solani* and related species, a one-step immuno-chromatographic lateral flow device (LFD) was developed. Antigens from representative isolates of *R. solani* AGs 1, 2-1, 2-3, 2-t, 3, 4, 5, 6, 7, 8, 9, 10, 11, and BI gave a positive response in LFD tests (Thornton et al. 2004).

Isozymes-based method

Isozymes are defined as multiple molecular forms of a single enzyme and these forms have similar enzymatic properties but slightly different amino acid sequences. The genetic locus may be monomorphic (expressed in a single allele). When the genetic locus is polymorphic the isozymes formed by the expression of different alleles are called allozymes. Isozyme analysis is a powerful biochemical technique that can be used to detect, differentiate and identify morphologically similar or closely related species, varieties and forma specialis. Liu et al. (1990) studied the genetic relationship among 14 isolates of *R. solani* AG-2 group by evaluating data derived from 11 enzyme systems. Pannecoucq et al. (2008) used pectic zymograms to group and subgroup *R. solani* isolates from Belgian cauliflower fields. Isozyme polymorphism was also profiled to analyze the genetic diversity of Indian *R. solani* isolates of AG1-IA (Neeraja et al. 2003), and Iranian *R. solani* isolates of AG1 subgroups infecting cotton (Mohammadi et al. 2003). Its use for population genetics investigation is limited in a predominantly asexual organism like *R. solani*.

Biosensor

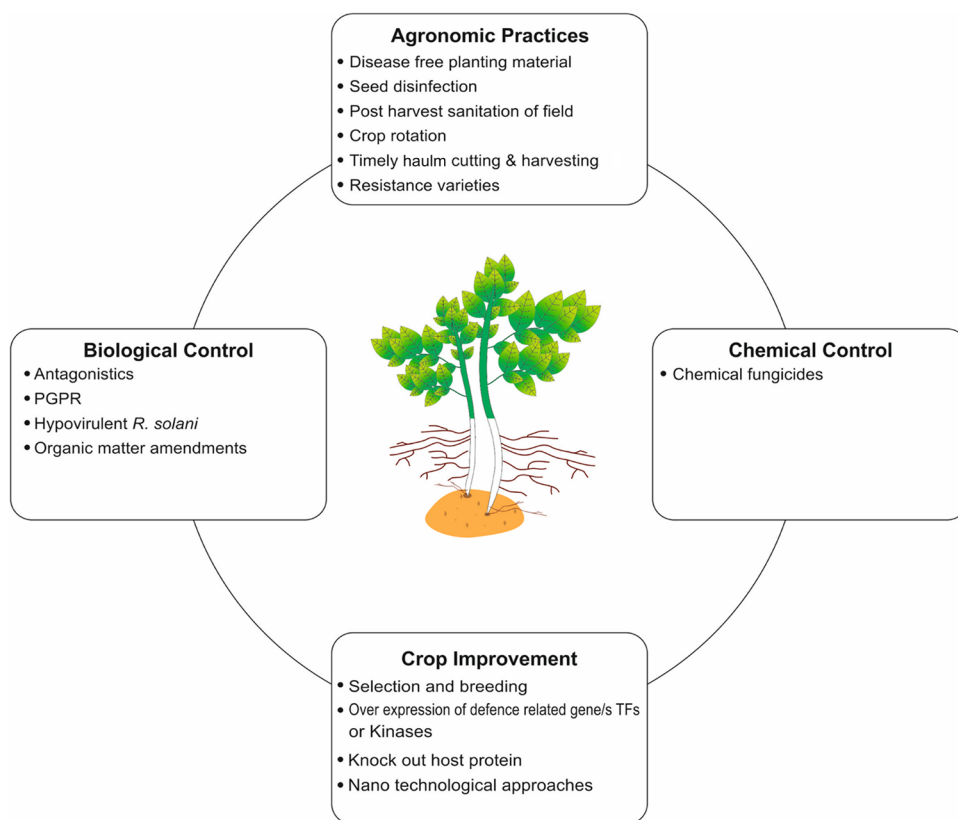
Biosensors are analytical devices that use a biological sensing element integrated into a physiochemical transducer and produce an electrical signal when in contact with the analyte (pathogen). During the last decade, numerous biosensors have been reported, and many have shown high sensitivity and low detection limits (Ray et al. 2017). The specificity and sensitivity of the biosensors can be enhanced by the use of enzymes, antibodies, DNA probes and bacteriophages as the specific recognition elements (Fang and Ramasamy 2015). Nanomaterials like nanoparticles and quantum dots (QDs) etc. have emerged as essential tools for the faster detection of particular biological entities with extreme accuracy. Presently, on-site detection is gaining importance for plant disease diagnosis. The need for on-site detection has led to development the advance, rapid and sensitive detection devices and kits which can be used in-field for disease detection. Singh et al. (2010, 2014) developed a nano-Au-based dipstick to detect Karnal bunt disease in wheat rapidly. Few devices or kits are currently available as commercial products such as Alert test kits and Pocket diagnostic test kits from Neogen Corp. and La Chandra Bioscience, respectively, are available for pathogenic fungi, such as *Pythium*, *Phytophthora* and *R. solani* detection (Ray et al. 2017). Biosensors would become a promising and attractive alternative to other time-consuming and tedious assays such as ELISA, but there is a need for some modifications, improvements and proper validation for in-field application.

As the black scurf organism is a widespread seed and soilborne pathogen. *R. solani* has a large host range and survives in the soil for a long time; therefore, it is difficult to manage with any single practice. Integrated disease management (IDM) strategies and knowledge of each stage are required for the effective control of this disease. Current management approaches are discussed below and can be considered related to cultural practices, chemical and biological control, crop improvement and nanotechnological approach (Fig. 4).

Cultural practices

Cultural practices *i.e.*, planting diseased free seed tubers, soil disinfection, non-host crop rotation, haulm cutting, tuber harvesting time, soil management, plant residues and irrigation influence the development of *Rhizoctonia* diseases in potatoes (Lal et al. 2022a). Black scurf can be managed by planting certified seeds free from any *R. solani* inoculums, therefore black scurf incidence monitoring is the first line of prevention of the disease. Furthermore, it would minimize the chance of establishing pathogens in the field. Non-host crop rotation is important for reducing the inoculum level of pathogenic microbes that require living hosts for survival

Fig. 4 Disease management strategies for *Rhizoctonia* diseases of potato



(Peters et al. 2003). The crop rotation strategy is less effective with pathogens such as *Pythium* spp., *Sclerotinia sclerotiorum*, *Sclerotium rolfsii* and *R. solani* having broad host ranges and long term survival characteristics. Even though, *R. solani* can survive through multi-year rotations, increasing the time between potato crops can lower the inoculum level in the soil resulting in less disease severity and incidence (Hopkins et al. 2004). Honeycutt et al. (1996) observed that *Rhizoctonia* diseases were observed more severe in continuous potato cropping than in potatoes cultivated in rotation with non-host crops. Rotations of 3-5 years are often recommended to effectively reduce the disease severity of black scurf. The use of crops with known disease-suppressive capabilities, such as *Brassica* spp., cereals, millets, Sun-hemp and non-solanaceous crops may provide additional resources for reducing disease through improved cropping systems. Field crops belonging to the *Brassica* family used in crop rotations and as green manures have been associated with reductions in soil-borne pathogens. These reductions could be due to the volatile sulfur compounds production through a process known as biofumigation and to change the structure of soil microbial density (Larkin and Griffin 2007). The mustard mixture reduced *Rhizoctonia* and common scab diseases of potatoes (Larkin et al. 2011). Maize, green gram, sun hemp and cowpea were evaluated as green manure crops for managing black scurf. Various other plant

species (including weeds) have been shown to sustain *R. solani* (Jager et al. 1982; Carling et al. 1986b) and should be considered in crop rotation and weed control. Crop rotation may have some beneficial effects, but the fungus has such a wide host range and so easily reintroduced as sclerotia on seed potatoes that it is not very effective. In three cropping sequences viz., potato-wheat-paddy, potato-onion-maize & potato-green gram-groundnut, the highest incidence of black scurf was recorded in the potato-onion-maize cropping sequence (CPRI 2019).

Chemical control

The application of chemical fungicides is the most frequently used and effective method for managing the *Rhizoctonia* diseases in potatoes. Fungicides are chemically toxic compounds having unique mechanisms of action applied to eliminate or inhibit the growth of pathogens (Gullino et al. 2000). Fungicides prevent the *Rhizoctonia* disease development by several means like damaging the cell membrane of fungus, acts as enzyme inhibitors, disrupts the processes such as respiration or energy production or altered the metabolic pathways regulates the cell wall synthesis (Singh et al. 2019). As there is more than one AG responsible for *Rhizoctonia* disease of potatoes, these AGs have varying sensitivity to fungicides. Therefore, the identification of the group(s)

causing disease in any particular field is crucial to fungicide selection (Kataria and Gisi 1996, 1999). Isolates of *Rhizoctonia* AGs 1, 3 and 5 were affected moderately by fungicides having aromatic hydrocarbon, whereas AGs 2-1, 4, 7 and 8 isolates were least sensitive. *R. solani* isolates showed high sensitivity levels against penicuron, flutolanil and iprodione, except isolates of AG-5 (Campion et al. 2003). Commonly used available fungicides against *R. solani* in potatoes with active ingredients and action mechanisms are presented in Table 2.

Tuber-borne *R. solani* is easily manageable as compared to its soil-borne counterpart due to its accessibility to control agents. For controlling the black scurf of potatoes, seed tubers treatment with 3% acetic acid was found effective. (Dutt 1979). Potato variety ‘Kurfi Chandramukhi’ dipped in a mixture of acetic acid 1% + zinc sulphate 0.05% for 15 min before or after cold storage successfully controlled the *R. solani* (Somani 1986). Seed tubers treated with boric acid (3%) as dip treatment before cold storage (Singh et al. 2002) and with penicuron as spray and dip treatments at planting time (Arora 2013; Thind et al. 2002) for controlling seed inoculums was followed to manage *Rhizoctonia* disease. Two chemicals viz., boric acid and penicuron are frequently used by Indian farmers to control the potato black scurf disease (Khurana et al. 2001). In an in-vitro study, *R. solani* AG-3 was inhibited completely by tolclofos-methyl and Penicuron, whereas in-field experiment, penicuron and azoxystrobin controlled the sclerotial development on potato tubers (Virgen-Calleros et al. 2000). In India, few fungicide products viz., Penflufen 22.43% FS, Penicuron 22.9% SC, Thifluzamide 24% SC, Carbendazim 25% + Mancozeb 50% WP, Carbendazim 12% + Mancozeb 63% WP, Carboxin 37.5% + Thiram 37.5% WS, Thiophanate-methyl 450g/l + Pyraclostrobin 50g/l w/v FS and Tebuconazole 15% + Zineb 57% WDG are registered under Central Insecticide Board and Registration Committee (CIB and RC) for control of *Rhizoctonia* disease in potato. Fluxapyroxad 333 FS is also registered in India for the management of potato black scurf disease (<http://crop-protection.basf.in/en/fungicide>). Recently, Arora et al. (2022) evaluated the efficacy of fluxapyroxad 333 FS at 0.08, 0.1 and 0.12% as tuber dip treatment and reported that these doses were statistically at par for managing black scurf. Some naturally derived fungicides like β -methoxyacrylates (also known as strobilurins) or QoI (Quinone outside Inhibitors) extracted from *Strobilurus tenecellus* (wild mushroom) were found effective against *R. solani* (Bag et al. 2016). Tuber seeds treated with a mixture of sodium hypochlorite and thiophanatemethyl at the pre-planting stage reduced black scurf severity at harvesting and after storage (Errampalli and Johnston 2001).

Dusting seed tubers with tolclofos-methyl, or penicuron spraying, gave control equal to that achieved by dipping in formaldehyde (Wicks et al. 1995). Acetaldehyde (5.0 ml/L)

and Benzaldehyde (10.0 ml/L) in addition to fungicide (Basamid) @ 50 g/m² of soil significantly reduced the disease incidence of black scurf (Abd-Alla et al. 2013). Chemical control is the highly effective and most widely used method for controlling field crop disease caused by fungus. However, the regular and continued application of a chemical fungicide increases the risk of the evolution of new highly pathogenic and fungicide-resistant races (Materatski et al. 2019). Mutations may occur in the genome of the fungus resulting in the alteration of the target site for molecular binding, target protein production can be increased and reduced uptake or metabolic breakdown of the fungicide may also increase (Gullino et al. 2000). Therefore, farmers and producers must either choose more specialized and long-lasting fungicides that increase the production expense or increase the frequency of fungicide application to control the fungal diseases. Another concern over fungicide application is related to hazards to the environment and human health (Kim et al. 2017). The fungicides application may also lead to adverse impacts on the terrestrial and aquatic ecosystems, soil organisms (e.g., earthworms, microorganisms) and poses a risk to the long-term fertility of the soil (Komarek et al. 2010). Therefore, research and development activities have to be established for searching the best alternatives to chemical fungicides such as the introduction of biocontrol agents to control *Rhizoctonia* diseases in potato crop.

Biological control

Biocontrol is the action of microbes, predators or parasites to minimize the population density of pathogenic organisms and is considered an eco-friendly and cost-effective component of an integrated disease management program (Verma et al. 2019; Kumar et al. 2022). Microbes such as PGPRs (plant growth promoting rhizobacteria) are the residents of the rhizosphere that are known to be involved in the synthesis of phytohormones, enhance nitrogen uptake, cause phosphorus/zinc/potassium solubilization and induced systemic resistance (Mustafa et al. 2019). The PGPRs that were found effective against *R. solani* included *Pseudomonas* spp., *Bacillus* spp. and *Enterobacter* spp. (Tabassum et al. 2017). In a greenhouse experiment, the interaction of potato seeds with *Bacillus* spp. showed 30-41.45% disease reduction of black scurf and 28.50-40.25% of stem canker caused by *R. solani* (Kumar et al. 2012). *Pseudomonas* sp. strain (S8.Fb11) reduced the proportion of infected tubers by *R. solani* to 40% for cv. Spunta and to 74% for cv. Nicola (Mraabet et al. 2013). Recently, Lal et al. (2022b) reported that talc formulation of *Pseudomonas* sp. strain (Pf14) enhanced agronomical characters and inhibited black scurf severity by up to 68% in a field experiment. In an in-vitro study, *B. subtilis* (V26) strain was found effective against *R. solani* and reduced disease incidence up to 63% and 81% of root

Table 2 Commonly used chemical fungicides for the control of *Rhizoctonia* disease in potato

Trade name	Active ingredient	Formulation	Mode of action	References
Monceren	Pencycuron 250 SC	Suspension concentrate	Inhibits fungal cell division and spindle microtubules assembly	Thind et al. (2002)
Emesto prime	Penflufen 22.43% SC	Suspension concentrate	Targets succinate dehydrogenase enzyme in electron transport system and inhibits mitochondrial respiration	Lal et al. (2014)
Pulsor	Thiifluzamide 24% SC	Suspension concentrate	Targets succinate dehydrogenase complex II in the tricarboxylic acid cycle and affect the fungal respiration	Lal et al. (2017a); Bhandari et al. (2017)
Zen	Carbendazim 50 WP	Wettable powder	Disrupts β -tubulin assembly during mitosis and inhibits development of the germ tubes, formation of appressoria, and the growth of mycelia	Kulkarni & Chavhan (2017)
Indofil M-45	Mancozeb 75 WP	Wettable powder	Multisite contact activity, chelates metal cations, interferes with the vital thiol compounds in the fungal cell wall	Goswami et al. (2018)
Amistar 25 SC	Azoxystobin 22.9% SC	Suspension concentrate	Disrupts the electron transport chain, prevents ATS synthesis by binding to the Qo site of complex III within the mitochondria and affect the fungal respiration	Wharton & Wood (2013); Goswami et al. (2018)
Topsin-M	Thiophenate methyl 70WP	Wettable powder	Inhibits β -tubulin assembly during mitosis and spindle microtubules assembly	Malik et al. (2014)
Triton	Validamycin 10 SL	Suspension concentrate	Inhibits an important carbohydrate energy source <i>i.e.</i> trehalase in fungi	Malik et al. (2014)
Vitavax	Carboxin 37.5% + Thiram 37.5% WP	Wettable powder	Dual action (systemic and contact); Carboxin inhibits succinate cytochrome c reductase, succinate coenzyme Q reductase and succinate dichlorophenolindophenol (DCIP) in mitochondria, Thiram inhibits metal-dependent and sulfhydryl enzyme systems in fungi	Lal et al. (2018)
Xelora	Thiophanate methyl 45% + Pyraclostrobin 5% SC	Suspension concentrate	Dual action (systemic and contact); Thiophanate inhibits β -tubulin assembly during mitosis and spindle microtubules assembly, Pyraclostrobin targets electron transfer system by binding to the ubihydroquinone oxidation centre of the mitochondrial bc1 complex (complex III) and inhibits mitochondrial respiration	Lal et al. (2017b)

Table 2 (continued)

Trade name	Active ingredient	Formulation	Mode of action	References
Rizolex	Tolclofos-methyl 50 WP	Wettable powder	Inhibits the biosynthesis of phospholipids and affects cellular motile function resembling cytochalasin A	Virgen-Calleros et al. (2000)
Frownicide	Fluazinam	Wettable powder	Interrupts the fungal cell's energy production by an uncoupling effect on oxidative phosphorylation in mitochondria	
Prodione 500 SC	Iprodione	Suspension concentrate	Inhibits spore germination by interrupting the DNA and RNA synthesis and inhibits the NADH cytochrome c reductase activity, thereby preventing lipid and membrane synthesis and ultimately mycelium growth	Muzhinji et al. (2018)
Celest 100 FS	Fludioxonil	Suspension concentrate	Inhibits transport-associated phosphorylation of glucose and glycerol synthesis, which reduces mycelium growth	
Moncut	Flutolanil 99.5% WP	Wettable powder	Inhibits succinate dehydrogenase (SDH) activity in mitochondrial complex II and disrupts the Krebs cycle and the mitochondrial electron transport chain	Zhao et al. (2019)

canker and black scurf, respectively as well as enhanced plant growth in-planta (Khedher et al. 2015). *Trichoderma* and *Gliocladium* have also been reported as biocontrol agents against plant pathogens. *Trichoderma* spp. and *Gliocladium* spp. reduce the growth of *R. solani* employing different mechanisms, such as competition for nutrients and space, antibiosis and by mycoparasitism (Harman 2007). Volatile antibiotics (e.g. 6-pentyl- α -pyrone and isocyanide derivatives), hydrophilic compounds (e.g. heptelic acid or koningic acid) and amphipathic polypeptides (e.g. peptaibiotics and peptaibols) produced by *Trichoderma* spp. are the major antifungal secondary metabolites (Lorito et al. 2010, Bailey and Lumsden 2014). Tsrer et al. (2001) reported that the application of *T. harzianum* to the soil surface had a relatively small effect compared to the in-furrow treatments. Wilson et al. (2008) documented that application of *T. harzianum*, either in-furrow or in combination with flutolanil applied to seed tubers, increased marketable tuber yield (from 35% to 60%), and reduced black scurf incidence on progeny tubers from 31% to 11%, which could not be achieved using flutolanil alone. In a study, Hicks et al. (2014) reported that isolates of *Trichoderma* spp. (*T. virens*, *T. atroviride* and *T. barbatum*) reduced the percentage of diseased stolon by 41–46% in-planta. Recently, in a pot experiment, Walid et al. (2022) treated the potato seed with *T. harzianum* and observed the reduced severity of black scurf. Rahman et al. (2014) evaluated *Trichoderma* spp. against *R. solani* on potatoes and suggested that integrated or combination approaches could be effective for controlling black scurf. Brewer and Larkin (2005) demonstrated that a mixed formulation of *B. subtilis* and *T. virens* control stem canker well than each organism alone. In a field trial study, tuber treatment with 2% boric acid along with *T. viride* @ 10 g/kg seed recorded the lowest disease incidence (15.33%) and index (0.38) with the highest yield (324.68 q/ha) (Patel and Singh 2021). Despite the promising results with antagonists, the introduction of new biocontrol agents involves various considerations such as the tedious work of selection and screening, optimization of the mode of application to achieve the best results (Tabassum et al. 2017), the shelf life of the bioagents, efficacy in the field experiments, eco-friendly measures, and registration to be used as a PGPR (Etesami and Maheshwari 2018).

Hypovirulent *R. solani* strains show potential as new biocontrol agents against soil-borne potato diseases. Hypovirulent properties in these isolates are due to the presence of specific M2 cytoplasmic double-stranded (ds) RNA elements (Liu et al. 2003). In these strains, the dsRNA elements might be involved in the up-regulation of quinic acid pathway or down-regulation of the shikimic acid pathway, resulting in the drastic reduction in the phenyl acetic acid (PAA) production responsible for pathogenicity and virulence of *R. solani* (Bartz et al. 2012). In a field experiment, Rhs1AI,

a hypovirulent strain of *R. solani* AG-3 had the potential to reduce *Rhizoctonia* disease incidence and severity up to 65% (Bandy and Tavantzis 1990; Larkin and Tavantzis 2013). However, in another study, where hypovirulent isolate Rhs1A1 did not show any reduction in black scurf severity when it was applied in combination with compost amendment with crop rotation (Bernard et al. 2014). More recently, Larkin (2020) tested two *R. solani* hypovirulent isolates (Rhs1AI and Bs69) combined with *B. subtilis* (GB03) and reported a reduction in disease incidence and severity of black scurf by 25–30% and 30–47%, respectively. The hypovirulent *R. solani* isolates may endow comparable or superior control of *Rhizoctonia* diseases of potatoes, than the existing bioagents, however, conjugations of hypovirulent strains with compatible bioagents having different modes of action are a matter of concern.

Nanotechnological approaches

The use of nanomaterials in plant disease management has created great interest (Kah et al. 2019), which may be very effective in the future with the progress of the application aspect of nanotechnology. Carbon, silver, silica and alumina-silicates-based nanoparticle were used for controlling plant disease. Recently, nanotechnology has a great effectiveness against numerous phytopathogens using silver nanoparticles (AgNPs). Interactions of AgNPs with microbes increase because of their larger surface area-to-volume ratio and thus more ability to permeate (Liao et al. 2019). When aqueous silver (Ag⁺) ions were exposed to a filtrate of *Vitis vinifera*, they reduced in solution resulting in the formation of stable AgNPs with 10–80 nm size which inhibited the growth of pathogenic bacteria (Chaudhary et al. 2012). Min et al. (2009) assayed the fungistatic and fungicidal effect of AgNPs against sclerotium-forming phytopathogenic fungi, *R. solani*, *Sclerotinia sclerotiorum* & *Sclerotinia minor* and documented that the AgNPs strongly inhibited the growth of fungal colonies and sclerotial germination. Nanosized silica-silver was effectual in the suppression of the growth of many fungi including *R. solani* and showed 100% growth inhibition at 10 ppm concentration (Park et al. 2006). Silica–silver nanoparticles are potentially effective against *B. cinerea*, *B. sorokiniana*, *C. gloeosporioides*, *M. grisea*, and *R. solani* (Jo et al. 2009). Kaur et al. (2012) examined the fungicidal properties of nano-size silver/chitosan nanoformulation against seed-borne plant pathogens viz., *R. solani*, *A. flavus* and *A. alternata*. It was documented that AgNPs concentration @ 15 mg exhibited excellent growth inhibition potential against *A. alternata*, *S. sclerotiorum*, *Macrophomina phaseolina*, *R. solani*, *B. cinerea* and *Curvularia lunata* (Krishnaraj et al. 2012). Elgorban et al. (2015) evaluated the different concentrations of AgNPs against six anastomosis groups (AGs) of *R. solani* infecting cotton and reported the

antifungal properties to control *R. solani* AGs. Nejad et al. (2017) documented that AgNPs @ 50 ppm were effective against *R. solani* causing sheath blight in rice in both *in-vitro* and *in-vivo* conditions and showed the highest inhibition of sclerotia formation and mycelia growth and suppressed the lesion development on leaves.

The *in-vitro* antifungal potential of various nanoparticles has been examined against phytopathogenic fungi namely *A. alternata*, *M. phaseolina* and *R. solani*. Among the various formulations of nanoparticles, Cu-chitosan nanoparticles were found most effective at 0.1% concentration (Saharan et al. 2013). Recently, Cui et al (2020) developed dual-functionalized polylactide (PLA) nanocapsules loaded with two fungicides validamycin and thifluzamide which showed better spreading performance on foliage application against *R. solani* compared with commercial fungicide formulations. However, several aspects of nanoparticles with relation to plants and the environment viz., their half-life in soil, their toxic effect on plants and animals and the optimum dosage for *in-field* application need to be determined. There are a few questions remaining to be addressed, viz., the exact mechanism of interaction of nanoparticles with fungal cells and how the surface area of nanoparticle influences the killing mechanism.

Genetic improvement of potato for *Rhizoctonia* resistance

Resistant germplasm is the most effective and environmental friendly way to control plant diseases. The conventional breeding approaches in potatoes can be coupled with modern biotechnology techniques to develop improved disease-resistant germplasms. Here the various strategies which can be implemented in the genetic improvement of potatoes against *R. solani* are discussed.

Selection and breeding

For determining the degree of host plant resistance against a pathogen, the maximum plant response to the pathogen must occur over a sufficient period under uniform selection pressure (Nelson and MacKenzie 1973). Monogenic host plant resistance, controlled by a single dominant gene is easily backcrossed into existing cultivars; however, this type of resistance may not be as durable as a resistance controlled by multiple genes. Resistance to *Rhizoctonia* diseases has existed in several wild *Solanum* species (Wastie 1994) and crosses with these wild cultivars have led to the conclusion that resistance to *Rhizoctonia* is under polygenic control and recessive (Li et al. 1995; Zeng et al. 2011). Screening tetraploid *Solanum* clones for resistance to *R. solani* has resulted in varied degrees of resistance to *Rhizoctonia*, which suggests that, even though not specifically selecting for resistance, breeders have incorporated some resistance by

selecting away from damage caused by this pathogen (Leach and Webb 1993). To date, the availability of potato germplasm showing high resistance to *R. solani* is very limited. Few potato varieties e.g., Portage, Mainstay, AC Belmont and AC Brador, are moderately resistant to *Rhizoctonia* infection (Reeves et al. 1995, 1997; Tarn et al. 1995a, b), but varietal resistance is not regarded as a solution for long term to black scurf and stem canker. In a study, Khandaker et al. (2011) reported 6 out of 25 potato germplasm show moderate resistance against black scurf in Bangladesh. In India, mostly the commercially cultivated varieties are susceptible to black scurf. However, varieties like *Kufri Dewa* and *K. Bahar* showed moderate susceptibility and *K. Sherpa* found resistance to *Rhizoctonia* disease (CPRI 1989, 1999). Recently, Singh et al. (2021) screened 18 potato varieties against black scurf, among them, *K. Ashok* and *K. Pukhraj* exhibited moderately and highly susceptible reactions, respectively. To date, no quantitative trait loci (QTL) has been well characterized for black scurf resistance. Furthermore, identification and annotation of black scurf and stem canker resistance genes in QTL loci, functional characterization and application in marker-assisted breeding will help to develop resistant potato cultivars against *Rhizoctonia*. However, resistance breeding for *Rhizoctonia* in potatoes is difficult due to the presence of two phases of the disease (black scurf and stem canker), pathogen population diversity, environmental factors and soil conditions (Leach and Webb 1993). This coupled with the limited availability of resistant germplasm has led to the search for alternatives like manipulating plant genomes to enhance resistance.

Genetic manipulation through biotechnology: Defense-related proteins

Besides traditional agricultural practices and integrated disease management (IDM), developing resistant cultivars either by genetic alteration or conventional breeding would be the best alternative for controlling plant diseases. Nowadays, the development of genetically modified plants is an easier and preferred strategy to the complex pre-breeding approaches, especially in potatoes for expressing the gene of interest for a particular desired phenotypic/genotypic trait/s. The non-availability of complete resistant germplasm of potato against *R. solani*, conventional breeding for this trait has not succeeded. Published references on rice and potato carrying active transgene/s against *Rhizoctonia* in-plant are listed in Table 3. Each transgene construct contained a promoter that controls the gene expression in plants fused to a coding region for a protein expected to have direct antifungal properties, activate host defense response, and inhibited the

fungal enzymes and virulence factors. Co-expression of two or more foreign genes was used in many studies.

On pathogen invasion, the accumulation of pathogenesis-related (PR) proteins is one important plant defence response. Transformation and expression of glycoside hydrolase proteins, which can degrade or lyse the cell wall of fungus and cell membrane, has been the most used method to develop fungal-resistant plants (Molla et al. 2020). Chitinases and glucanases are important antifungal proteins that hydrolyze or degrade chitin and glucan components of the fungal cell walls. Datta et al. (2001) introduced and overexpressed the PR genes *i.e.*, chitinase 11 (PR3 family) which hydrolyse and degrade the fungal cell wall resulting inhibited the growth of *R. solani* in rice plants. In potatoes, the transformation of chitinase (ChiC), from *Streptomyces griseus* along with a bialaphos resistance (*bar*) gene conferred resistance against *Alternaria solani* (Khan et al. 2008). However, in a study, Moravčíková et al. (2004) concluded that the cucumber class III (ChiC) gene could not enhance resistance against *R. solani* AG-3 to any considerable level. A class I chitinase gene *i.e.*, AF153195 from potato, was introduced into the tea genome and its overexpression resulted in an increased resistance against *Exobasidium vexans* (Singh et al. 2015). Similarly, in another study, the overexpression of chitinase gene LOC_Os11g47510 showed improved resistance against *R. solani* in rice plants (Richa et al. 2017). Other proteins with antifungal activity conferring enhanced tolerance to necrotrophic phytopathogens include small antimicrobial peptides (AMP) that disrupt fungal membrane integrity. The thaumatin-like proteins (TLP), osmotins, lysine-rich dermaseptins, cysteine-rich defensins and thionins, are acted by forming pores in the fungal membranes and causing cell lysis. Defensins attack fungal plasma membrane ceramide components and inhibit the transport of K^+ and Ca^{2+} , with host-specific effects on hyphal branching and tip extension (Jha & Chattoo 2010). Snakin-1 (SN-1) is a basic, cysteine-rich AMP encoded by a small gene family that confer tolerance to *R. solani* when transferred in potato (Almasia et al. 2008). Transgenic potato minitubers with genes encoding dermaseptin, the osmotin AP24 and lysozyme gave rise to foliage showing reduced necrosis against *R. solani* in detached leaf assays (Rivero et al. 2012). In an experiment, M'hamdi et al. (2013) integrated a ribosome-inactivating protein (*rip30*) gene from barley into the potato genome and observed that transgenic clones showed reduced black scurf disease incidence and severity.

Recent gene editing techniques can provide platforms for precise transgene-free genome editing. CRISPR/Cas9 (clustered regularly interspaced short palindromic repeats) technique has been successfully implemented in potatoes for targeted mutagenesis to generate knockout mutations (using nonhomologous end-joining) and gene targeting to edit an endogenous gene (by homologous recombination) (Wang

Table 3 Transgenes having *in plants* activity against *Rhizoctonia solani* in rice and potato

Host tissue	Fungal Pathogen	Gene product(s)	Activity	References
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice thaumatin-like protein (PR-5)	Enhanced resistance against sheath blight	Datta et al. (1999)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice chitinase (<i>Chi11</i>)	Restrict the growth of pathogen	Datta et al. (2000)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice chitinase (<i>RC7</i>)	Enhanced resistance against sheath blight	Datta et al. (2001)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice chitinase (<i>RCH10</i>)	Increased resistance to sheath blight	Kim et al. (2003)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice chitinase (<i>Ch11</i>)	Reduced no. of infection cushions, Increased resistance against sheath blight	Kumar et al. (2003)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice chitinase (<i>Chi11</i>)	Enhanced resistance against sheath blight	Sridevi et al. (2003)
<i>O. sativa</i> sheath	<i>R. solani</i> AG1-IA	Chitinase11 thaumatin-like protein	Reduced no. of infection cushions, lesion size in detached leaves; reduced lesion length, delayed lesion formation in intact sheaths	Maruthasalam et al. (2007)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice chitinase (<i>RC7</i>)	Enhanced resistance against sheath blight	Nandakumar et al. (2007)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice chitinase (<i>Chi11</i>) glucanase	Reduced disease severity <i>in planta</i>	Sridevi et al. (2008)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Defensin AFP2	Reduced no. of infected plants; reduced no. of lesions on leaves	Jha & Chattoo (2010)
<i>S. tuberosum</i> plant	<i>R. solnai</i> AG-3	Cucumber chitinase Tobacco glucanase	Reduced disease severity <i>in planta</i>	Moravčíková et al. (2004)
<i>S. tuberosum</i> plant	<i>R. solnai</i> AG-3	Rape chitinase; Rubber tree glucanase	Healthy root development; degrade the pathogen cell wall, restrict further fungal penetration	Chye et al. (2005)
<i>S. tuberosum</i> plant	<i>R. solnai</i> AG-3	<i>Snakin-1</i>	Enhanced damping-off survival	Almasia et al. (2008)
<i>S. tuberosum</i> minituber	<i>R. solani</i> , <i>P. infestans</i>	Antifungal peptide AP24 dermaseptin lysozyme	Inhibited growth <i>in vitro</i> ; reduced necrosis in detached leaves	Jha and Chattoo (2010)
<i>S. tuberosum</i> tuber	<i>R. solani</i> AG-3	Ribosome inactivating protein rip30	Reduced % tuber surface covered with sclerotia	M'hamdi et al. (2013)
<i>S. tuberosum</i> plant	<i>R. solani</i> AG-3	<i>S. marcescens</i> chitinase (<i>ChiA</i>)	Reduced disease severity <i>in planta</i>	M'hamdi et al. (2012)
<i>S. tuberosum</i> tuber	<i>R. solani</i> AG-3	<i>T. atroviride</i> chitinase (<i>chit 42</i>) <i>T. virens</i> glucanase (<i>bgn13.1</i>)	Enhanced antifungal activity	Esfahani et al. (2010)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Chitinase (<i>Chit11</i>)	Reduced disease severity <i>in planta</i>	Rajesh et al. (2016)
<i>O. sativa</i> plant	<i>R. solani</i> AG1-IA	Rice Chitinase	Reduced disease severity <i>in planta</i>	Richa et al. (2017)

et al. 2015; Butler et al. 2016). CRISPR/Cas9 system has been utilized to install mutation in OsSWEET11 gene, leading to improved tolerance against rice sheath blight (Gao et al. 2018). More recently, González et al (2020) used CRISPR/Cas9 system to induce mutation in the StPPO2 gene to produce potato tubers with reduced PPO activity and enzymatic browning. Rapid advancements in technologies would ease genome modification and subsequently aid in developing disease-resistant potato plants.

Conclusion and recommendations

Globally, black scurf is an important disease in potatoes having economic importance. Various inoculum sources like; soil, infected seed tubers, crop residues and wider host range, diverse genetic and pathogenic variability contribute to the difficulty in successful control of black scurf. Modern molecular techniques permitting accurate detection and identification of *Rhizoctonia solani* at anastomosis sub-group

levels in field soil and seed tubers allows to develop a decision-making system to support the growers in selecting seed materials and fields for planting potato crop. Assays such as RT-PCR, multiplex PCR, nested PCR, repetitive PCR, and LAMP are among the detection alternatives that endow rapid data analysis with specificity. As black scurf spreads through seed and soil-borne inoculums, the development of an integrated disease management (IDM) strategy that includes agronomic practices *i.e.* planting disease-free tubers, post-harvest drying and field disinfection, rotating to a non-host crop, and utilization of a recommended dose of registered chemicals can control the disease. However, continued application of chemicals has negative effects on human health and the environment as well as induces pathogen resistance. An eco-friendly sustainable approach for controlling *Rhizoctonia* disease in potatoes is using biological agents such as PGPRs, *Trichoderma* spp., *Gliocladium* spp., and hypovirulent *R. solani* strains. Planting black scurf-resistant cultivars is another economical, effective and eco-friendly approach to managing the disease. Further, the identification and validation of pathogenicity factors in *R. solani* and defense-related genes in host plants associated with molecular interaction between *R. solani* and the potato will be a reference for developing black scurf resistant varieties. Modern biotechnological approaches such as Host derived dsRNA mediated silencing and CRISPR/Cas9 mediated knockout/knockdown are additional approaches that may be included to achieve eco-friendly and efficient disease management over synthetic fungicides.

Various biosynthetic and chemically synthesized nanomaterials and inorganic compounds have been tested to explore their efficacy in nano-fungicide formulations for black scurf management. However, improved nano-formulations need to develop for their potency and stability, considering the safety of the environment and human health. When it comes to the transportation of seed tubers, the phytosanitary certificate should be issued following a careful examination of potato bags to limit the movement of inoculums. Additionally, information about disease epidemiology is required for integrated disease management (IDM) programs.

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