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Advancements in *Spongospora subterranea*: Current Knowledge, Management Strategies, and Research Gaps

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Abstract

Powdery scab was first documented on locally sampled potatoes in Braunschweig, Germany. A hundred and eighty-one years later, the disease has spread globally to most potato-producing regions and is considered one of the most destructive potato diseases. Here, we review the knowledge of powdery scab and causative agent, *Spongospora subterranea* f. sp. *subterranea*, highlighting research progress made in the last 7 years. Much work has been done to increase our understanding of how zoospores respond to their environment (e.g. root exudates, Ca_2C signalling, and root metabolites) and the management of the disease by chemical and biological control agents. Recent research has utilised omics approaches — metabolomics, proteomics, and genomics — to gain a deeper understanding of the host–pathogen interaction in the powdery scab pathosystem. The management of powdery scab can be achieved using a combination of strategies that include (1) the planting of resistant potato varieties, (2) strategies that avoid disease (field selection and planting date), those that (3) reduce initial soil inoculum (crop rotation, organic soil amendments, and soil fumigation), and (4) in-crop approaches (soil chemical applications, biological control, proper field, fertility, crop, irrigation management, and crop sanitation). Lastly, we discuss research gaps for future research, including the disease's interaction with other potato diseases that may be impacting disease expression and opportunities to enable a greater understanding of the powdery scab pathosystem.

Keywords Disease management · Plasmodiophorid · Potato-pathogen interaction · Powdery scab · Root galling

Introduction

The obligate, parasitic plasmodiophorid, *Spongospora subterranea* (Wallroth) Lagerheim f. sp. *subterranea* (Sss), is the causal agent of powdery scab, a potato tuber disease of economic importance that impacts the global potato (*Solanum*

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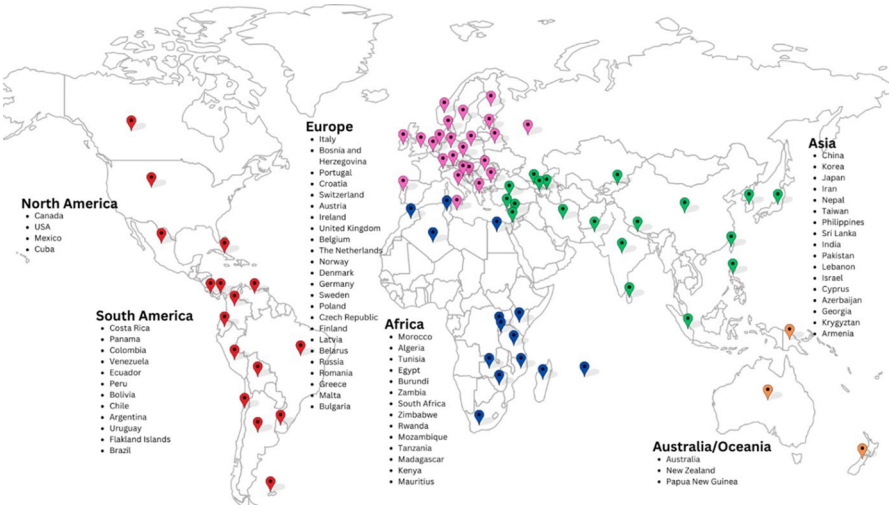

Fig. 1 The global distribution of *Spongospora subterranea* f. sp. *subterranea* as observed and detected on tomato or potato plants (CABI/EPPO 2012)

tuberosum L.) industry (Merz and Falloon 2009; Balendres et al. 2016b; Wilson 2016). This pathogen also infects potato roots, impacting root function and productivity, resulting in the expression of root galling (Shah et al. 2012; Thangavel et al. 2015). Additionally, Sss is the vector of potato mop-top virus (PMTV), which affects tuber quality and productivity (Carnegie et al. 2010). Powdery scab is the most well-known and devastating Sss-induced disease, with severe outbreaks leading to a substantial decrease in the quality and marketability of the tubers and subsequent profit loss in both the seed and fresh potato markets (Harrison et al. 1997; Tegg et al. 2016; Wilson 2016).

Powdery scab of potatoes was first documented on locally sampled potatoes in Braunschweig, Germany (Wallroth 1842). It had, however, already been observed by potato growers throughout Europe at the time and called by different common names in Germany until the causal agent was described (Merz 2008). Since then, Sss has been recorded globally in numerous countries where it was observed and detected on either tomato (*Solanum lycopersicum* L.) or potato (Fig. 1) plants (Balendres et al. 2016b). This pathogen most likely originated in the Andes region of South America, where the Solanaceous plant family, its main hosts, also stem from and then spread worldwide with the increase in global potato trade and cultivation (Harrison et al. 1997). Numerous studies have shown that Sss populations originating from South America exhibit greater genetic diversity than the global pathogen population, likely due to the pathogen's co-evolution with its host plants (Gau et al. 2013, 2015; Muzhinji and van der Waals 2019).

Potato is the third most important food crop for human consumption worldwide (Devaux et al. 2020). With the expansion and intensification of potato cultivation, Sss has spread to novel potato-growing regions, and the severity of Sss-induced disease outbreaks has increased (Jeger et al. 1996; Harrison et al.

1997; Merz 2008). Various factors of modern potato production have contributed to this global increase, including the replacement of dryland potato production with high-frequency irrigation, the cultivation of market-favoured Sss-susceptible potato cultivars, the failure of growers to implement Sss introduction prevention measures, and the overall lack of effective Sss disease management strategies, chemical and otherwise (Tuncer 2002; Merz 2008; Amponsah et al. 2021). The limited control options are due to the pathogen's unique biology (robust resting spores) and life cycle (polycyclic) as well as the past emphasis on ineffective control of the dormant life stage (Falloon 2008: Amponsah et al. 2021). Sss is mainly associated with more temperate potato-growing regions but has invaded areas with warmer climates due to the increased reliance on irrigation-based agriculture (Taylor et al. 1986; Adams et al. 1987; Wale 2000). Its detection within peat-based potting mixes in the USA is attributed to the natural infestation of peat bogs and indicates the pathogen's ability to infiltrate commercial seed production systems (Fulladolsa et al. 2020; Zeng et al. 2020; Alaryan et al. 2023). This claim is supported by an outbreak of powdery scab in a South African mini-tuber production facility, the suspected cause being contaminated coconut peat (Wright et al. 2012).

Several papers have synthesised knowledge of the biology of Sss (Harrison et al. 1997; Falloon 2008; Merz 2008; Merz and Falloon 2009; Balendres et al. 2016b; O'Brien and Milroy 2017; Amponsah et al. 2021). Harrison et al. (1997), Falloon (2008), and Merz and Falloon (2009) have provided excellent reviews on the history, epidemiology, and management of powdery scab and Sss. Balendres et al. (2016b) examined the literature related to the critical pre- and post-infection events in the *S. subterranea*-potato pathosystem and how the physical, biological, and chemical factors involved during these events may influence disease development and effective disease control deployment. O'Brien and Milroy (2017) argued for the development of a biocontrol strategy for powdery scab management. Finally, Amponsah et al. (2021) composed a comprehensive review identifying the potential weaknesses in the life cycle of phytomyxean species (including Sss) and how these life stages can be targeted in future management strategies. The last seven years have seen a significant increase in scholarly outputs on powdery scab and its pathogen, Sss. A great deal of work has been made in the omics field, where metabolomics, transcriptomics, proteomics, and genomics have been exploited to further our understanding of the biology of Sss, the host plant's response during infection, and Sss-host pathogen interaction. Some of the knowledge addressed questions raised in previous review papers (e.g. Falloon 2008, Merz and Falloon 2009, Balendres et al. 2016b). This new knowledge has led to novel approaches that either targeted the pathogen's life cycle or improved practices in the field that would lead to reduced inoculum pressure or better potato yield. It also provided insight into possible mechanisms to be exploited in potato resistance breeding programmes. Our review paper aims to synthesise the information produced in the last seven years and offer a contemporary perspective on the management of diseases caused by Sss. We further discuss gaps in our understanding of Sss and research opportunities that would contribute to further improving how we sustainably manage diseases caused by Sss.

Classification and Genetics of *Spongospora subterranea* f. sp. *subterranea*

Classification of *Spongospora subterranea*

This pathogen is an intracellular, obligate plant parasite (Braselton 1995) and requires living host plant tissue to grow, multiply, and complete its life cycle (Nitzan et al. 2007). It was initially referred to as *Spongospora solani* but was later renamed *Spongospora subterranea* (Wallroth) by Lagerheim (1891). *Spongospora subterranea* is grouped within the plasmodiophorids and classified as a phytomyxid (Neuhauser et al. 2014). Plasmodiophorids have been described by Braselton (1992, 1995), who considered them a monophyletic group because all the members have the trait of cruciform nuclear division. The members of this group are all obligate green-plant pathogens with multinucleate plasmodia and have the unique ability to produce free-swimming bi-flagellated zoospores and form resting spores (persistent survival structures) (Braselton 1995; Neuhauser et al. 2011). Plenty of major agricultural pests that cause devastating crop diseases belong to this group, including *Plasmodiophora brassicae* Woronin, which causes clubroot of brassica and canola crops (Neuhauser et al. 2011; Dixon 2014; Amponsah et al. 2021). These plasmodiophorid pathogens have a broad host range, and many are vectors of plant viruses (Amponsah et al. 2021). For example, *Phytomyxa betae* can transmit Beet necrotic yellow vein virus to sugar beet (Sarwar et al. 2020). Several different phylogenies have been allocated to plasmodiophorids in the past based on morphology or molecular attributes (Braselton 1995). Plasmodiophorids were initially grouped with the myxomycetes by Zopf (1885), then regarded as a type of protozoan, followed by true fungi, and then finally again considered protozoans and grouped as Plasmodiophorida (Order) in the family Plasmodiophoraceae (Braselton 1995). This group of organisms is classified as Phytomyxids and belongs to the Cercozoa phylum within the Rhizaria kingdom (Qu and Christ 2004). Neuhauser et al. (2014) concluded that phytomyxids are capable of cross-kingdom host shifts and that this group could be devastating to both terrestrial and marine-inhabiting species due to their ability to shift host speciation, their extensive dispersal, and complex diversity.

Spongospora subterranea f. sp. *subterranea* belongs to the genus *Spongospora.* Sss and *Spongospora subterranea* f. sp. *nasturtii* (Ssn), a pathogen of watercress, are considered important vegetable plant pathogens (Tomlinson 1958; Merz and Falloon 2009). These two were originally designated into two formae speciales (f. sp.) due to their similar biological features, such as the likeness of their sporosori (spore balls), which are a conglomeration of resting spores and are associated with the *Spongospora* genus (Tomlinson 1958). Qu and Christ (2004) reported that Sss and Ssn are two distinct species based on differences in their sporangial morphology, host specificity, and molecular properties. Both, however, react the same to monoclonal antibodies created against the sporosori of Sss, highlighting thus how closely related these organisms are (Merz et al. 2005).

Genetics

The obligate nature of Sss and its morphological and biological traits make it arduous to work with and is the primary reason for the lack of literature available on Sss in specific fields. Genetic studies on Sss are one area where research is scarce, especially compared to other important soil-borne pathogens. A few studies have been conducted to elucidate the genetic diversity, population biology, and structure of Sss populations globally (Bulman and Marshall 1998; Qu and Christ 2004, 2006; Gau et al. 2013, 2015; Muzhinji and van der Waals 2019). The South American (native) Sss populations exhibit higher genetic variation than other geographical populations but also between tuber and root tissue-derived isolates (Gau et al. 2013). The global Sss population (invasive) outside of South America is highly clonal in genetic structure, with no tissue type differentiation reported (Gau et al. 2015). The Sss populations have been classified into three distinct genetic groups (Type I, II, and III) based on diversity in the internal transcribed spacer (ITS) region observed between isolates from different regions (Bulman and Marshall 1998; Qu and Christ 2004; Osorio-Giraldo et al. 2012). Genetic diversity-focused research is necessary to identify which pathogen isolates to select and assess for potato cultivar resistance (Qu and Christ 2006). It has been suggested for decades that sexual recombination must occur somewhere in the Sss life cycle, with resting spore formation being the most likely process (Braselton 1995; Gau et al. 2015). Although conclusive proof has not yet been presented, Muzhinji and van der Waals (2019) may have indirectly confirmed this possibility. This study on the genetic diversity and biology of different Sss populations from several geographic regions in South Africa reported high gene flow, substantial genotypic diversity, and the presence of multiple shared multilocus genotypes (MLGs) within the country's pathogen population. These results infer that some hybridization/random mating (either sexual or asexual) occurs as the genetic diversity within this Sss population is comparable to other pathogens that exhibit sexual recombination (Muzhinji and van der Waals 2019; Pearce et al. 2019).

Previously, one of the most noteworthy genetics-related breakthroughs in Sss research was the complete sequencing of the Sss mitochondrial (mtDNA) genome (Gutiérrez Sánchez et al. 2014). This mtDNA sequence of Sss was the second complete mitochondrial genome sequence of any member of the phylum Cercozoan and the first one in the plasmodiophorids (Balendres et al. 2016b). This mtDNA sequence can be used to substantiate the phylogenetic relationships of the plasmodiophorids. Other significant breakthroughs include the publication of the RNA sequence (Schwelm et al. 2015) and cDNA sequence (Burki et al. 2010) of Sss and the location of comprehensive non-long-term repeat (non-LTR) retrotransposons (Bulman et al. 2011). A draft genome for Sss was subsequently published in 2018 (Ciaghi et al. 2018) but remains poorly annotated. Most recent Sss-based publications have focused on characterising and elucidating the specific underlying mechanisms involved during Sss host–pathogen interactions to better understand which factors determine the degree of cultivar susceptibility and intensity of potato immune response in reaction to Sss infection. These large-scale studies utilised the multi-omics (transcriptomics, proteomics, and metabolomics) approach to investigate host factors involved in Sss pathogenesis at various levels (gene expression pathways, RNA, protein, and secondary metabolites). This

includes the identification of specific root-exuded metabolites (Balendres et al. 2016a; Balotf et al. 2021a; Amponsah et al. 2023) as zoospore release stimulants and taxis attractants and which gene expression pathways and proteins have a regulatory function in the defence response towards Sss zoospore root attachment (Yu et al. 2022, 2023b) and root infection (Balotf et al. 2021b, 2022a, 2022b). These studies are the first to employ this approach to Sss and produced valuable databases for future research, potential novel management options, and potato Sss resistance breeding programmes.

Pathogen Morphology and Pathogenesis

Pathogen Life Cycle

The complete life cycle of *Spongospora subterranea* f. sp. *subterranea* is polycyclic, meaning it has two distinct phases (Braselton 1995; Harrison et al. 1997; Merz 2008). These are the asexual/zoosporangial (primary) phase and the sexual/sporogenic (secondary) phase (Fig. 2), with the inner circle representing the zoosporangial phase and the outer the sporogenic phase of the Sss life cycle (Merz 2008). The zoosporangial phase involves the production and release of secondary zoospores from several compartments within the fine-walled zoosporangia (Nitzan et al. 2007; Merz 2008). The sporogenic phase entails resting spore production and sporosori formation. The formation of new sporosori completes the Sss life cycle, whereas the zoosporangial phase does not produce new sporosori, so the life cycle is only partially complete (Qu and Christ 2006). Both phases start with the penetration of the host plant's tissue (root cells or tuber tissue) by a single bi-flagellated zoospore that forms a multinucleate sporogenic plasmodium (Merz 2008). The sporogenic phase is possibly initiated when two zoospores fuse to create a binucleate spore that penetrates and infects the host plant root cells. This structure then undergoes mitotic nuclear division to create the multinucleate plasmodium (Braselton 1995). This is followed by karyogamy and meiosis. The plasmodial cytoplasm is pinched off to form the resting spores (Balendres et al. 2016b). The ability of Sss to produce masses of secondary zoospores during the zoosporangial phase within one growing season allows for multiple cycles of infection and reinfection of the host plant, which can eventually result in the production of sporosori until environmental conditions are no longer favourable or the host is no longer susceptible (Nitzan et al. 2007). The complex and challenging nature of the Sss life cycle, which involves multiple phases and the ability to switch between them, makes it difficult to control. This explains why the diseases it causes can be detrimental to potato crop production. Some aspects of the Sss life cycle remain poorly understood, including the occurrence and timing of sexual recombination.

Pathogen Morphology

The motile primary and secondary zoospores of Sss are the pathogenic structures responsible for infection (Merz 1992). The zoosporangia-produced secondary zoospores and the resting spore-released primary zoospores are identical in their

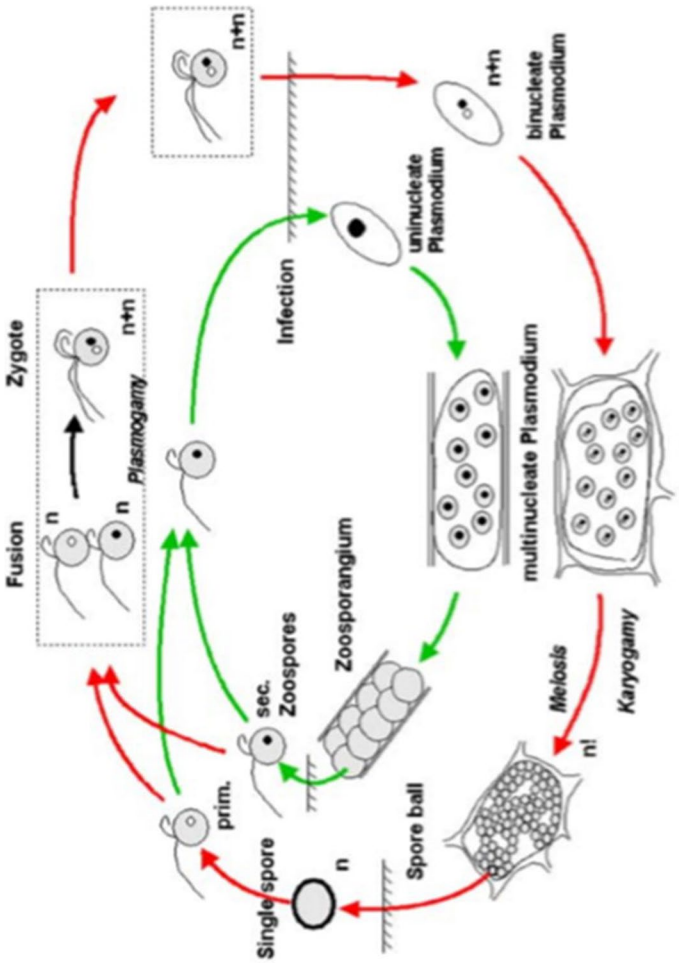

Fig. 2 The tentative life cycle of *Spongospora subterranea* f. sp. *subterranea*. The asexual/zoosporangial phase (inner circle) and the sexual/sporogenic phase (outer circle) are both depicted (Merz 2008). Image used with permission from Springer Nature (Merz 2008)

morphology and swimming pattern (Merz 1992). These zoospores are elliptical or round, averaging about 2.5 – 4.77 µm in diameter, and are bi-flagellated, with both flagella on the posterior end (heterokont flagella), one short (±4.35 µm) and another longer (±13.07 µm) (Ledingham 1934; Kole 1954). The three-walled resting spores (Lahert and Kavanagh 1985) close around one zoospore. Resting spores differ in size from a diameter of 4 µm to greater than 4.3 µm (Falloon et al. 2011).

As mentioned before, resting spores form masses to create sporosori (18 – 100 µm in diameter) (Jones 1978; Falloon et al. 2006), each of which can contain between 155 and 1526 resting spores (Falloon et al. 2011). The Sss pathogenic structures (zoosporangia and sporosori) found in host plant tissue vary in morphology (size and shape) between different plant species (Arcila et al. 2013). This variation depends on environmental conditions and the unique host–pathogen interactions (Arcila et al. 2013). Generally, Sss sporosori have a spongy or 'honeycomb' appearance with a range of different shapes (irregular, spherical, elliptical, or elongated) (Montero-Astua and Rivera 2005; Arcila et al. 2013). Sporosori size has been reported to differ between isolate sources (root gall or powdery scab lesion) (Villegas et al. 2008). The outer surface of the sporosori is covered in openings leading to internal channels, with the complexity of this channelling increasing with the size of the sporosori (Falloon et al. 2011). Moxham et al. (1983) mechanically isolated the cell walls of the spores of *P. brassicae*, analysed them for their composition, and found that it was predominantly made from proteins, then chitin, and some lipids and carbohydrates. The outer layer of these three-walled resting spores comprises mostly proteins and has a protective function over the inner chitin-composed layer (Moxham et al. 1983). It might be possible to use a biocontrol agent to break down the resting spores and inner zoospores (Moxham et al. 1983). The findings from these studies could perhaps also be applied to Sss resting spores due to their relatedness to *P. brassicae*.

Initial Inoculum

Sporosori can be found in root galls, Sss-contaminated soil, and as a powdery mass inside the lesions on the surface of infected potato tubers (Harrison et al. 1997; Merz 2008). Sss is thus both soil- and seed-borne, and the disease can result from planting into contaminated soils/potting mixes and planting diseased or contaminated seed tubers (Tegg et al. 2016). The movement of infested seed and/or soil can introduce inoculum into new cropping sites that were previously pathogen-free. Tsror et al. (2020a) also demonstrated the aerial dispersal of Sss resting spores in contaminated dust to healthy fields/areas. Resting spores germinate and release zoospores, the primary source of inoculum in fields. The significance of the relationship between the initial level of soil inoculum and the final incidence or severity of Sss-related disease on the crop when soil environmental conditions are excluded is still contested (Merz 2008; van de Graaf et al. 2007; Shah et al. 2012). Some studies found no correlation due to the production of large amounts of secondary zoospores by repeated infection cycles in host plant root systems under optimal soil conditions, which then causes severe disease epidemics (de Boer 2000; van de Graaf et al. 2005). Others,

including Brierley et al. (2013), observed higher disease levels in soil with increased initial inoculum levels. Supporting this, within Australia, soil inoculum quantification is a key tool used by growers to predict Sss-related disease risk with threshold levels identified above 74 pg Sss DNA/g soil considered to be high risk for powdery scab outbreaks (Stagnitti 2015; Tegg and Wilson 2022). Nakayama et al. (2007) also reported an insignificant relationship between soil sporosori levels and powdery scab disease severity. However, they found that the infection level of tomato roots post-contaminated soil baiting positively correlated with observed disease intensity. Given the contradictory reports above, further evidence is required to accurately validate soil inoculum levels with Sss-related disease. The amount of initial inoculum in the soil is determined by several factors, including the residual soil inoculum from the previous growing season, the planting of infected seed tubers, the application of infested manure, the emergence of volunteer crops and alternate hosts, and the use of contaminated farming machinery (Merz 1989b; Iftikhar et al. 2007).

The multi-layered resting spores of Sss are an added defence mechanism against harsh and suboptimal environmental conditions that enables them to survive and stay viable for long periods in the soil (Kole 1954; Balendres et al. 2017; Amponsah et al. 2021). The ability of the inactive phase of this pathogen to withstand most chemical and physical stresses is why control strategies that target it are mainly ineffective. The period of resting spore viability, in the absence of a suitable host, has not yet been confirmed but is at least 5 years in the soil and possibly up to a few decades (de Boer 2000; Balendres et al. 2017).

Zoospore Release and Movement

When a resting spore germinates, a single uninucleate primary zoospore is released into the surrounding environment, and the Sss life cycle is initiated (Merz 1989b, 1992; Balendres et al. 2016b). The zoospore exists through an opening in the resting spore's cell wall (Falloon et al. 2011). The resting spores are stimulated to release primary zoospores by different environmental factors like adequate soil water, cooler soil temperatures, and other external stimuli like host and non-host root-secreted phytochemicals (root exudates) (Kole 1954; Merz 1989b, 1997; Balendres et al. 2016a, 2017, 2018). However, Balendres et al. (2017) verified that Sss resting spores could exhibit both stimuli-responsive and constitutive dormancy, with individual spores in a population able to stay viable and only germinating 2.4 years after being incubated in a conducive environment. This same study demonstrated that regardless of age (immature/mature), source (powdery scab lesions or root galls), or storage period (1 week – 5 years for powdery scab and 1 week – 1 year for root galls), a proportion of the resting spore population exhibits stimuli-responsive dormancy and will germinate in an external stimulating environment. Amponsah et al. (2023) also observed staggered zoospore release occurring over a few months of incubation. An analysis of the protein profile differences between dormant resting spores and those in the germination process has identified 20 proteins that change expression levels during germination (Balotf et al. 2021a). Proteins associated with the cell wall cytoskeleton are downregulated, indicating structural changes in the resting

spore walls before zoospore release. The staggered zoospore release is probably due to the resting spores in the centre of the 'spore ball' (sporosori) not being exposed to the stimulants at the same time or period as those on the outside (Amponsah et al. 2021). This could be a survival mechanism to ensure some zoospores reach a suitable host when released.

The availability of free-soil moisture is essential for zoospore release and movement toward the host plant roots (Kole 1954; Merz 1992). Cooler soil temperatures (9 – 17 °C) have been shown to promote the release of zoospores (Fornier 1997; van de Graaf et al. 2005, 2007; Shah et al. 2012). Yu et al. (2023a) reported a slightly higher optimal zoospore release temperature (20 °C) in a stimulating aqueous solution, with a speedy 2-day synchronised release and a steep decline afterwards. Earlier studies suggested the importance of root exudates, which was confirmed by the identification of specific compounds within potato root exudates that stimulate resting spore germination and zoospore attraction toward host plant tissue (Merz 1989b, 1992, 1997; Harrison et al. 1997; Balendres et al. 2016a, 2018; Lekota et al. 2020; Amponsah et al. 2023). Hoagland solution (a standard hydroponic nutrient solution) stimulates Sss zoospore release in the absence of a host (Merz 1997; Amponsah et al. 2023). A study on the individual components of this nutrient solution by Balendres et al. (2018) found that Fe (Ferric)-EDTA (ethylenediaminetetraacetic acid) stimulated zoospore release. Fe-EDTA in an inoculum solution resulted in more zoospores being released earlier, thus causing higher levels of tomato root infection. If favourable environmental conditions and external stimuli are available, Sss sporosori may germinate in the absence of a host plant, and subsequent soil inoculum levels may be decreased (Balendres et al. 2016a). This was proven by Balendres et al. (2018), where the application of both Hoagland's and Fe-EDTA led to reduced Sss soil inoculum levels. This could be exploited as a management tool.

The free-swimming Sss zoospores are only viable and active for a short period after release (Merz 1992; Harrison et al. 1997) and can only travel small distances to find a host. This implies that they need a reliable method to find a host or be released in large quantities to increase the chances of randomly locating a host. When Sss zoospores were released after exposure to a chemotactic response, they remained active and could infect the host plant roots for a couple hours (Merz 1997) to 1 day (Amponsah et al. 2023). The free-swimming zoospores' survival period depends on the surrounding environmental conditions. Root exudates were also suspected to be involved in the attraction of zoospores toward the host plant's root hairs through chemotaxis (Harrison et al. 1997; Merz 1997; Amponsah et al. 2023). Merz (1997) reported that zoospores encysted (attached to the host surface) on tomato bait plant roots, but it is unclear if the zoospores found the host roots through chemotaxis or by chance due to proximity to the host. Definitive evidence for potato root exudates having a chemotactic function for zoospores is discussed in this review. For the zoospores to detect chemicals secreted by their host, they must trigger specific signalling pathways. It is also possible that certain pathogens will only activate these pathways by recognising distinct compounds or proteins (Balendres et al. 2016b). The swimming pattern of some plant pathogens is impacted by the influx of ions like Ca^{2+}, which affects the movement of certain organisms' flagella and cilia (Donaldson and Deacon 1993; Wheeler et al. 2006). A recent study corroborated the importance of

Ca_2C signalling in Sss zoospore chemotaxis and subsequent disease development by demonstrating how Ca_2C signalling inhibition interfered in zoospore swimming patterns, movement, host attachment, and ultimately reduced root infection (Amponsah et al. 2022). The short-lived zoospore stage (post-release to pre-infection) is highly vulnerable and should be the primary target for control. Elucidating and interfering in the mechanisms regulating taxis, motility, swimming pattern, and attachment is the most viable option.

Infection and Pathogenesis

Host Recognition and Attachment

Most plasmodiophorid pathogens penetrate and infect cells of the host plant by utilising a unique mechanism and process (Braselton 1995). Before infection, the zoospores attach and become encysted to the host plant surface and form an adhesorium with 'Rohr' and 'Stachel' structures that help in the penetration of the host's epidermal cell wall (Keskin and Fuchs 1969; Braselton 1995). Interference in essential signalling pathways within the Sss zoospores can inhibit zoospore attachment to host roots (Amponsah et al. 2022). This is essential as preventing attachment to the root surface ultimately results in no infection and subsequent disease development (Yu et al. 2022). Multiple plant polymers have been shown to initiate the encystment of the pathogen to the plant's surface (Hardham and Suzaki 1986), and where specific plant cell wall proteins have been altered by enzymatic treatment, zoospore attachment is impeded (Yu et al. 2023b). Penetration of the plant tissue by Sss zoospores requires some host susceptibility and favourable soil environmental conditions (Merz et al. 2012; Shah et al. 2012), with the highest attachment intensity at 15 °C (Yu et al. 2023a). Resistance to infection by Sss is due mainly to a combination of factors such as the presence and abundance of the specific root surface and internal proteins that regulate pathways in the plant's defence response to Sss zoospore attachment and infection (Hernandez Maldonado et al. 2015; Balotf et al. 2022a; Yu et al. 2022, 2023b). Nucleic acid metabolism and enzyme activity within the pathogen are essential in Sss virulence and overcoming the host plant's immunity during infection and disease development (Balotf et al. 2021b). Bulman et al. (2011) demonstrated that Sss could initiate long-term potato cell callus cultures that contain sporosori. The question was raised on how newly divided cells are infected, as it is not through the typical method. The authors speculated that it might happen through amoeboid cell penetration or that infected cell division creates progeny that already includes parts of the pathogen's plasmodia.

Root Functionality Disruption by Zoosporangia Infection *Spongospora subterranea* f. sp. *subterranea* induces two diseases in susceptible host plant roots (Harrison et al. 1997), 'zoosporangia' root hair infection being one of them (Hernandez Maldonado et al. 2015). After the uninucleate plasmodium (zoospore) encysts, it penetrates the host plant's root hair cells to form a multinucleate plasmodium within the now-infected root tissue (Braselton 1992). This primary plasmodium is

a bag-like structure that expands and cleaves into several thin-walled zoosporangia, each with a nucleus (Kole 1954). The presence of zoosporangia in root hairs or cortical cells of the roots is regularly used to confirm infection by Sss in non-potato hosts (Jones and Harrison 1969, 1972; Andersen et al. 2002; Arcila et al. 2013; Simango et al. 2020; Tsror et al. 2020c). The zoosporangium matures within 5 days of infection (Merz 1989b). It comprises several compartments, each containing four to eight secondary zoospores, formed from subsequent nuclear divisions of the single original zoosporangium nucleus (Lahert and Kavanagh 1985). The secondary zoospores emerge from the zoosporangium through an opening in the zoosporangial wall (Merz 2008). They are then released into the soil, where they can penetrate the host plant's cortical root tissue to re-infect the same plant. They can also infect neighbouring plants to repeat the zoosporangial phase, possibly form sporosori-containing root galls, or infect potato tubers and cause powdery scab disease (Falloon 2008). Zoosporangial root infection occurs in species of various plant genera (Balendres et al. 2016b; Alaryan et al. 2023). It has been confirmed that the host plant roots are susceptible to Sss infection throughout the plant's life cycle and that the rate of root disease development is similar between species and the age of the tissue infected (Thangavel et al. 2015). However, zoospore root attachment is most severe on the youngest tissue (Yu et al. 2023a). Visual zoosporangial infection can be observed 15 – 45 days after inoculation (Thangavel et al. 2015).

Root hair infection can inhibit root functionality by reducing the uptake of water and nutrients from the soil by infected root hairs (Gilchrist et al. 2011; Shah et al. 2012; Falloon et al. 2016). A study by Falloon et al. (2016) reported that water uptake was reduced by 53% in an Sss susceptible potato cultivar compared to a more resistant cultivar, where root functionality was reduced by only 21% after root infection. It has been reported that outbreaks of this disease from repeated infection cycling could cause severe root infections that can significantly reduce the plant growth rate (haulm length, foliar, and root dry mass) and final tuber yield of the infected potato crop (Genet et al. 2005; Gilchrist et al. 2011; Falloon et al. 2016). Delaying root infection by various treatments can reduce the Sss levels in root tissue and, subsequently, the final disease severity at harvest (Thangavel et al. 2015).

Root Gall Formation Root gall formation, or root hyperplasia, is induced by Sss infection of the roots or stolons of some host plant species (Braselton 1995; Qu and Christ 2006; Hernandez Maldonado et al. 2013; Johnson and Cummings 2015). It was assumed that root galls develop due to rapid sporosori production within infected root cells and thus indicate the completion of the sporogenic phase of the pathogen's life cycle, as is the case with *P. brassicae* resting spores (Falloon 2008; Kageyama and Asano 2009). Root galls do not always contain visible or viable sporosori (Qu and Christ 2006). The viable sporosori are white when immature but eventually turn brown (Falloon et al. 2016). Root gall formation can be observed 45 – 75 days after inoculation (Thangavel et al. 2015). When the plant material decomposes, the Sss sporosori are released into the soil and contribute to the Sss

soil inoculum load. Several studies have reported that root galls disrupt root functionality and reduce the growth and yield of the infected host plants (Gilchrist et al. 2011; Shah et al. 2012; Hernandez Maldonado et al. 2015). Johnson and Cummings (2015), however, found that the root gall formation did not significantly impact the tuber yield (number and weight of tubers) of infected plants. The authors suggested that other factors (cultivars used, environmental conditions, etc.) in previous studies could have affected yield and not the level of gall formation.

Powdery Scab on Potato Tubers Powdery scab is the most devastating disease caused by Sss (Falloon et al. 1996; Harrison et al. 1997; Falloon 2008; Nitzan et al. 2010), which is recognised by the formation of distinct raised lesions on the skin of infected potato tubers. These yellowish-brown lesions appear scab-like with a brown powdery mass of sporosori in the centre that gives the disease its name (Falloon et al. 1996; Harrison et al. 1997). The initial symptoms of this disease are purple-brown pimple-like bumps on the skin of the infected potato tubers (Harrison et al. 1997). These small swellings can eventually enlarge to 10 mm in diameter and split open when they reach maturity to release sporosori into the surrounding environment (Melhus 1913; Lawrence and McKenzie 1981; Genet et al. 2005). These prominent lesions are generally circular (Hughes 1980; van de Graaf et al. 2007) and develop around 60 days after inoculation (Thangavel et al. 2015). Powdery scab lesions can be misidentified as those of common scab, a potato tuber disease caused predominantly by *Streptomyces scabies* Thaxter (Balendres et al. 2016b). Microscopy is often needed to differentiate between the two diseases. Unlike the potato plant roots, the tubers are only susceptible to Sss infection during the early periods of tuber growth and elongation, which is a couple of weeks after tuber initiation (Hughes 1980; van de Graaf et al. 2007; Thangavel et al. 2015).

The scabs are primarily cosmetic and superficial and can be removed through hand peeling but are not preferred by the consumer, reducing marketability. High levels of potato tuber infection by Sss can result in severe powdery scab disease epidemics that lead to a significant reduction in tuber quality (Harrison et al. 1997); for example, deep scabs on processing potatoes may need double peeling, increasing processing time and wastage. In Australia, the annual losses due to powdery scab in the processing potato sector alone are estimated to be over AUD$ 13.4 million (Wilson 2016). For seed potato growers, powdery scab-infected seed potatoes can be rejected within low tolerance, stringent seed certification, and quality control programmes, leading to economic loss (Falloon 2008). Potato tubers that are prewashed before going to market also require additional grading and separation of diseased tubers to pass the necessary standards that are acceptable for the fresh market or processing (Falloon 2008). The lesions are also weakened areas with an increased gas exchange that causes weight loss in cold storage and acts as an opening for secondary infections by other plant pathogens (Merz 2008; Tegg et al. 2016). This has been demonstrated in a study where a higher incidence of several common potato tuber diseases such as black dot (*Colletotrichum coccodes* Wallr.*)*, Fusarium dry rot (*Fusarium* spp.), late blight (*Phytophthora infestans* Mont.), and pink rot (*Phytophthora erythroseptica* Pethyb.) has been recorded on tubers with visible powdery scab

lesions (Johnson and Cummings 2015). The interaction of Sss-related diseases with other potato diseases is worthy of further investigation as many studies tend to focus on a single pathogen; however, in the field, multiple pathogens co-exist and interact with each other, impacting disease expression.

Potato Mop-Top Virus (PMTV) *Spongospora subterranea* f. sp. *subterranea* is the vector of potato mop-top virus (PMTV), a serious viral disease of potato plants (Jones and Harrison 1972; Carnegie et al. 2010). PMTV occurs in many potato-growing regions, with new and recent detections also highlighting the significance and challenge of this virus (Xu and Gray 2020; Frampton et al. 2022). This virus is disseminated by Sss-infected seed tubers or through Sss zoospores in contaminated soil (Carnegie et al. 2010) causing superficial and occasional internal injury, making infected tubers less marketable (Merz and Falloon 2009). The virus results in slightly raised rings or stripes on the infected tuber's surface and reddish-brown necrotic arcs or lines (spraing) in the internal tissue of the susceptible tubers (Calvert and Harrison 1966; Harrison and Jones 1971). Some of the PMTV-induced foliar symptoms on potato plants are yellow spots and V-shaped chlorotic marks on the progeny leaves, distorted small leaves followed by blotching, and possibly severe plant stunting (Carnegie et al. 2010). This virus can be controlled through several cultural practices, including Sss control measures.

Environmental Factors Affecting Sss Pathogenesis

The germination of Sss resting spores, survival and motility of its zoospores, and its pathogenesis depend on the presence of a favourable soil environment, which involves various factors.

Soil Temperature

Spongospora subterranea f. sp. *subterranea* zoospore release can be initiated over a wide temperature range (5 – 25 °C) in soil and aqueous solutions (Fornier 1997). However, the ideal temperature for zoospore release occurs at 20 °C in an aqueous Hoagland solution (Yu et al. 2023a). Sss pathogenesis is generally restricted to cooler temperatures, with zoospore root attachment most abundant at 15 °C (Yu et al. 2023a). The optimal range for Sss zoospores to initiate repeated root infection cycles in one potato growing season is 11 – 18 °C; potato tuber infection occurs from 9 to 17 °C but is most severe at 12 °C; and root gall formation happens at a wide temperature range (11 – 25 °C) but is optimal at 17 °C (Kole 1954; Hughes 1980; de Boer 2000; van de Graaf et al. 2005, 2007; Shah et al. 2012). Soil temperature has a little effect on the viability of the resting spores (Amponsah et al. 2021). The exact temperatures optimal for the development of Sss-related diseases differ between studies with confounding factors, including soil type and the cultivar of the specific crop evaluated as the most likely reasons (van de Graaf et al. 2007).

Potato growers could exploit the data gathered from these studies to make more informed decisions regarding Sss disease avoidance and management (de Boer 2000; Tsror et al. 2020b; Tsror et al. 2021). Kirkham (1986) reported that planting potato crops earlier, with cooler soil temperatures, resulted in increased powdery scab severity compared to later planted crops. The spread of Sss to regions with unfavourable environmental conditions is due to the increasingly frequent application of irrigation in modern potato production systems (Nachmias and Krikun 1988), which creates an optimal soil environment for disease development by reducing the temperature surrounding the plant's root system. This is especially important if irrigation water is cold and can explain why powdery scab is prevalent in countries like Australia, Israel, and South Africa (Nachmias and Krikun 1988; de Boer 2000; van der Waals 2015), where the climate is hot and dry.

Soil Moisture

The importance of adequate free-soil water for Sss disease development has been emphasised throughout this review because it stimulates the release of zoospores from the resting spores and assists in their movement toward susceptible host plant tissue (Merz 1992; Baldwin et al. 2008; Merz and Falloon 2009). As a result, more rainfall, frequent irrigation, and intense rain events are linked to the worsening of Sss disease severity and powdery scab outbreaks (Kirkham 1986; Adams et al. 1987). If the timing of these high soil moisture events corresponds with early tuber initiation and development (1 week pre-tuber set (TS) to 4 weeks after), a critical period of tuber susceptibility to Sss diseases, then powdery scab may be severe (Taylor et al. 1986; Adams et al. 1987). Hence, water management and limiting irrigation are important during this early tuber development phase (de Boer 2000; Wale 2000).

As mentioned, an increase in soil moisture has the added consequence of reducing the soil temperature around the host plant's root systems, thus increasing the suitability of the soil environment and susceptibility of tubers to Sss (Adams et al. 1987; Wale 2000). Increased soil water content also means more soil pore spaces are filled, reducing the soil oxygen levels (Harrison et al. 1997), which can slow tuber development and growth, resulting in an extended period of increased susceptibility of the tuber tissue to infection by Sss (Diriwächter and Parbery 1991). Thus, poorly drained (Tuncer 2002; van de Graaf et al. 2005) and waterlogged soils (Hughes 1980) are often reported to have higher incidences of severe powdery scab outbreaks.

However, there are some inconsistencies in the data; a study by de Boer (1991) yielded insignificant results when comparing Sss disease development and severity between well and poorly-drained soils. Van de Graaf et al. (2005) reported that planting in loamy soil at different soil moisture regimes had no noticeable effect on the rate of potato tuber infection or Sss disease severity. These authors did, however, observe more Sss-related diseases at constant soil moisture in pot trials compared to at fluctuating moisture regimes, but this could also have been due to other factors. These conflicting results contribute to the ongoing dispute and research gap

regarding whether constant soil moisture or fluctuating wetness levels are more important in Sss disease development. With the uptake and increased usage of soil moisture probes and the collection of useful real-time data, relationships between soil moisture and Sss disease development may be more accurately determined in the future.

Soil pH

Conflicting information exists regarding the role of soil pH in Sss disease development (Hughes 1980; de Boer 2000; van de Graaf et al. 2005; Wright et al. 2021). Some studies suggest that the disease worsens with an increase in pH, whilst others indicate that applying lime can reduce severity (Harrison et al. 1997). The contradiction may arise due to other soil properties being affected by pH changes or inaccurate detection methods (Harrison et al. 1997). Lowering pH (usually through sulphur application) has been shown to decrease powdery scab incidence and severity (Hughes 1980; Wright et al. 2021). However, Sss can infect potatoes at a wide pH range (Hughes 1980; Wright et al. 2021), with pH not affecting the rate of zoospore release, motility, or chemotaxis between the pH values of 5.3 and 8.5 (van der Graaf et al. 2005; Amponsah et al. 2023). Merz (1989b) observed pH to have an insignificant effect on root infection intensity. Soil pH has the most pronounced impact on disease development during early tuber initiation (van de Graaf et al. 2005). Indirectly, soil pH could impact pathogenesis by altering other soil properties, like improving soil drainage, which makes the environment less favourable to zoospore movement (Merz 2008; Amponsah et al. 2021). None of the studies directly links soil pH to Sss infection.

Soil Type

Potato growers are often advised to avoid poorly draining, easily compacting, and excessively water-retaining soils (Wale 2000; Sinton et al. 2022). However, there exist contradictions in the literature sources on the influence of soil type on Sss-related diseases. Certain studies suggest that soil type may not significantly affect the incidence and severity of powdery scab on potatoes (van de Graaf et al. 2005). Heavier soils, with higher clay content and greater water retention capacity, have been shown to stimulate Sss pathogenesis (Prentice et al. 2007), but the most severe Sss disease is not always observed in this soil type. According to van de Graaf et al. (2007), potato plants grown in clay soils exhibited the lowest amount of root gall formation compared to sandy or loam soil. Similar results were observed for the rate of tuber infection and powdery scab disease development (van de Graaf et al. 2005). Powdery scab epidemics in fields or growing regions with high levels of sandy soils have also been reported elsewhere (Tuncer 2002; Prentice et al. 2007; Merz 2008). The frequent irrigation application (almost daily) required to cultivate potatoes in predominantly sandy soils is the most probable reason for the high incidence of powdery scab being recorded in fields with this soil type (de Boer 2000).

Studies assessing the effect of organic matter content on powdery scab development also offer conflicting results. Higher disease incidence has been reported in soils with low organic matter content (Wallenhammar 1996) than with higher levels. Other trials assessing Sss and *P. brassicae* diseases have documented the opposite results (Merz and Falloon 2009; Dixon 2014). This could be due to higher organic matter enhancing the soil micro-organism diversity and nutrient availability whilst improving soil texture. Some cultivated soils are naturally suppressive to various soil-borne diseases (Weller et al. 2002; Mazzola 2007; Wright et al. 2021), which are attributed to the specific physicochemical properties of the soil or its microbial composition that reduces pathogen survival, spread, infection, and reproduction via various direct and indirect methods (Weller et al. 2002). Wright et al. (2021) reported that some soil samples collected from different geographical regions in New Zealand exhibited natural microbe-mediated suppression of powdery scab. This was potentially a form of specific suppression (select microbial communities responsible) as the suppression was transferable (Wright et al. 2021). Further research is needed on the factors that make some soils naturally suppressive to Sss. This could allow for more informed decision-making regarding selecting fields with specific soil types for potato cultivation or amending the soil to promote specific microbial communities antagonistic to Sss (Mazzola 2007).

Host Range

Establishing the host range of Sss is crucial to fully understand this pathogen's epidemiology, pathogenesis, and management measures. Incorporating alternative hosts of Sss in a crop rotation system could increase Sss inoculum levels in the soil if root galls and sporosori are formed on or within the roots of these hosts (Clark et al. 2018; Alaryan et al. 2023). Therefore, the host status of crops frequently rotated with potatoes should be determined to avoid the build-up of Sss inoculum and subsequently increase the disease severity in the follow-up potato crop.

The hosts of Sss can be classified into several groups based on the pathogenic structures observed in their roots (Arcila et al. 2013). These groups are non-hosts, trap crops, Type I and Type II hosts (Arcila et al. 2013). Non-host plants are not susceptible to infection by Sss with no pathogenic structures in their root tissue. Trap crops are only zoosporangial phase hosts, as they exhibit only zoosporangia in their roots when observed by microscopy. These plants prevent the completion of the pathogen's lifecycle as sporosori are not produced (Harrison et al. 1997; Arcila et al. 2013). Type I hosts exhibit only sporosori when examined, and Type II hosts show both zoosporangia and sporosori. The classification of plant species based on their host status can be determined by performing biological assays, examining the roots of the plants by microscopy techniques, and then analysing the root samples using molecular-based techniques to confirm infection and prevent the overestimation of the Sss host range (van de Graaf et al. 2003; Tsror et al. 2020c).

Numerous studies have concluded that Sss has a wide host range, infecting members belonging to at least 26 different plant families (Jones and Harrison 1972; Andersen et al. 2002; Qu and Christ 2006; Nitzan et al. 2009; Shah et al. 2010;

Arcila et al. 2013; Clark et al. 2018; Simango et al. 2020; Tsror et al. 2020c; Alaryan et al. 2023). Although this pathogen was initially thought to primarily infect Solanaceous plant species (Nitzan et al. 2009; Shah et al. 2010), sporosori development and root gall formation have been recorded within the roots of many non-solanaceous species like oats (*Avena sativa* L.) and yellow mustard (*Brassica campestris* L.) (Qu and Christ 2006; Simango et al. 2020). Arcila et al. (2013) suggested that several alternative hosts, including tamarillo (*Cyphomandra betacea* Cav.) and Kikuyu grass (*Pennisetum clandestinum* Chiov.), do not form root galls even though sporosori develop inside infected root hairs. A diverse range of weed species and commercial crops have been identified as Sss alternative hosts, including maize (*Zea mays* L.), onion (*Allium cepa* L.), tomato, and wheat (*Triticum aestivum* L.) (Andersen et al. 2002; Qu and Christ 2006; Arcila et al. 2013; Tsror et al. 2020c). The discovery that several weed species, commonly found in potato cropping systems and volunteer rotation or potato crops, serve as Sss alternative hosts highlights another potential source of inoculum accumulation in the field soils (Shah et al. 2010; Clark et al. 2018). This emphasises the importance of selecting the appropriate rotation crop species and implementing effective field sanitation practices, such as volunteer crop removal and weed management during and between potato growing seasons (Tsror et al. 2020c). The impact of planting Sss alternative hosts, particularly True hosts (Type I and II), on disease severity in subsequent potato crops and the potential utilisation of trap crops as management tools require additional investigation. Some alternative hosts of Sss may not produce sporosori in large enough amounts, if they do at all, to substantially contribute to the soil inoculum load and affect disease severity in the follow-up potato crop (Alaryan et al. 2023). The exact mechanisms that prevent Sss infection in non-host species or restrict Sss development to only the zoosporangial stage should be investigated. This information could be valuable for Sss management if incorporated into future potato or rotation crop breeding programmes.

Root Exudates

Root exudates were suspected of facilitating the breaking of Sss resting spore dormancy, as demonstrated with other soil-borne pathogens (Harrison et al. 1997; Merz 2008; Rashid et al. 2013). Any external factor that affects zoospore release also impacts Sss disease development and could be exploited in Sss management (Balendres et al. 2016a, 2018; Amponsah et al. 2021). Merz (1989b, 1992, 1997) observed the responses of Sss zoospores to the host plant roots and proposed that certain phytochemicals may stimulate the release of Sss zoospores from the resting spores. Merz (1993) observed root infection when bait plants were added to a sporosorus suspension. Balendres et al. (2016a) illustrated that potato root exudates stimulated Sss resting spore germination, with more zoospores released earlier in the presence of the host plant than in the control. The study also identified 24 specific low-molecular-weight compounds from different chemical groups within the potato root exudates as possible stimulants for Sss resting spore germination and zoospore release (Balendres et al. 2016a).

Spongospora subterranea f. sp. *subterranea* resting spore populations exhibit staggered dormancy and contain dormant and non-dormant resting spores (Balendres et al. 2017; Amponsah et al. 2023). The non-dormant spores require only favourable environmental conditions for germination, whilst dormant ones need extra external stimuli, like specific compounds within the exudates, to germinate. The root exudates stimulating Sss zoospores are most likely not host-specific, as seen with other plant pathogens (Nelson 1990; Suzuki et al. 1992; Friberg et al. 2005), as non-host plants also secrete chemical compounds that were found to stimulate Sss resting spore germination (Balendres et al. 2016a). This attraction towards commonly manufactured metabolites could account for the broad host range of Sss (Amponsah et al. 2021). Chemotaxis was thought, and subsequently validated, to be involved in the chemical luring and thus the movement of Sss zoospores towards the origin (plant roots) of the secreted exudates (Fornier et al. 1996; Merz 1997; Balendres et al. 2018). Amponsah et al. (2023) demonstrated that different components of potato root exudates are either taxis inhibitory or attractant for Sss zoospores. The abundance and balance of these compounds were found to reflect the susceptibility of a potato cultivar to Sss infection (Lekota et al. 2020; Amponsah et al. 2023). The chemotaxis of Sss zoospores could be altered through the exogenous application of treatments containing these metabolites (Amponsah et al. 2023).

Detection and Quantification of Sss

The reliable detection and quantification of *Spongospora subterranea* is challenging due to its obligate biotrophic nature, which impedes detection using conventional microbial culturing methods (Falloon 2008). Nevertheless, various techniques have been developed to effectively identify Sss on potato tubers, in soil, and within infected plant material. These methods are crucial for establishing effective disease risk assessment programmes (McCartney et al. 2003).

Morphological Identification

The pathogenic structures of Sss (bi-flagellated zoospores, zoosporangia, resting spores, and sporosori) are distinguishable in infected host plant root tissue through light or transmission electron microscopy (TEM) (Merz 1992; Falloon et al. 2011; Arcila et al. 2013; Tsror et al. 2020c). The distinct shape of Sss zoospores, characterised by two different-sized flagella (Merz 1992) and a unique swimming pattern, serves as a diagnostic tool (Amponsah et al. 2022). The disadvantage of utilising this method is that it requires the time of a skilled diagnostician to ensure an accurate and reliable diagnosis, as often infected tissues can include other structures from other pathogens and the plant material itself that resemble Sss structures (Hernandez Maldonado et al. 2013). Supporting morphological identification with other diagnostic tools provides improved clarity in Sss identification.

Tomato Bait Bioassay

The tomato seedling bioassay can detect a minimum of 100 Sss spore balls/g of soil, enabling confirmation of soil contamination and the quantification of soil inoculum levels (Merz 1989b; Walsh et al. 1996; Alaryan et al. 2023). The approach strictly identifies viable Sss inoculum (Merz and Falloon 2009) and is best combined with polymerase chain reaction (PCR) for confirmation (Nakayama et al. 2007). However, the downside is the possibility of repeated infection cycles in the root system of the plant used as bait (Merz 1989b; Wallace et al. 1995; Merz and Falloon 2009). This can be prevented by exposing the bait plant roots to the inoculum source for only a short period (24 h) and assessing the roots before repeated infection cycling can occur (Nakayama et al. 2007).

Immunological-Based Techniques

Immunological-based methods for disease detection rely on the detection of antibodies of certain antigens associated with a specific pathogen (McCartney et al. 2003). For Sss, the enzyme-linked immunosorbent assay (ELISA) (Harrison et al. 1993, Walsh et al. 1996, Merz et al. 2005) and the Sss Agristrip® test (Merz et al. 2005) have been proven effective in detecting specific levels of spore balls (100 spore balls/g soil) (Walsh et al. 1996). On the other hand, the Agri-Strip test kit is commercially available and based on a lateral flow immunoassay and has the benefit of rapid on-site testing and evaluation of potato tubers for confirmation of Sss infection/contamination during standard inspections (Merz and Falloon 2009; Bouchek-Mechiche et al. 2011). It is user-friendly and has high enough specificity (as few as one to ten sporosori/ml solution) that misdiagnoses are rare (Bouchek-Mechiche et al. 2011). Seed potato certification schemes and grading programmes often only grade tubers for visible powdery scab lesions (Tegg et al. 2016), which is not enough to prevent accidental Sss introductions and successive diseased progeny tubers. An effective disease detection method is thus required and crucial for the confirmation of suspected powdery scab lesions and for the detection of contaminated seed potatoes to prevent the spread of Sss to uncontaminated fields (Falloon 2008; Hernandez Maldonado et al. 2015).

Molecular-Based Techniques

Conventional Polymerase Chain Reaction (PCR)

Species-specific primers for Sss have significantly increased the sensitivity and accuracy of detection. PCR can detect as few as one to ten spore balls/g of soil (Bell et al. 1999). This technique has been used for Sss detection on potato tubers, in water, soil, and infected host plant material (Bulman and Marshall 1998; Bell et al. 1999; van de Graaf et al. 2003). DNA sample contamination with PCR inhibitors (phenolic compounds and natural soil humic acids) can interfere with this method,

especially when Sss levels are low in the sample (Bulman and Marshall 1998). Furthermore, conventional PCR only amplifies; it does not quantify the Sss DNA and also demands skilled labour, access to laboratory facilities and tools, and adherence to stringent protocols.

Real-Time PCR Real-time PCR (RT-PCR) or quantitative PCR (qPCR) amplifies and quantifies the DNA of the targeted organism and has been utilised for the detection of different Sss pathogenic structures in a variety of sample types (van de Graaf et al. 2003; Ward et al. 2004; Wright et al. 2012; Brierley et al. 2013; Mallik et al. 2019; Simango et al. 2020). qPCR surpasses PCR in sensitivity, detecting Sss at lower concentrations, even asymptomatic tuber contamination (McCartney et al. 2003; van de Graaf et al. 2003). Additionally, qPCR offers faster results, greater resilience to sample contaminants, and requires less training. This emphasises its essential role in Sss control strategies, facilitating the implementation of risk assessment and control measures (McCartney et al. 2003; van de Graaf et al. 2003).

Isothermal Amplification Method The most recent addition to the diagnostic tools used to detect Sss is the RT-recombinase polymerase amplification or RT-RPA. This PCR-based approach can detect at least 100 *S. subterranea* sporosori/g of soil in at least 10 min (DeShields et al. 2019). Another isothermal detection method, loop-mediated isothermal amplification (LAMP), has also been developed and was found to have higher sensitivity (at least 2 pg of the pathogen's DNA) in detecting *S. subterranea* (Jiang et al. 2023). These two new tools and techniques offer more reliability, speed, and sensitivity in Sss detection (DeShields et al. 2019; Jiang et al. 2023).

Management of *Spongospora subterranea* f. sp. *subterranea* Diseases

No single method is currently available for successfully managing Sss diseases; instead, an integrated approach utilising multiple strategies is recommended for sustainable control (Falloon 2008). The different management strategies available are aimed at targeting the pathogen resting spores, preventing, or delaying the zoospores from reaching and infecting the roots or tubers of the host plants (Falloon 2008; Amponsah et al. 2021). A combination of host resistance, disease avoidance, pre-plant soil treatments, and in-crop management strategies should be considered.

Host Resistance

The cultivation of potato cultivars that show high resistance or tolerance to Sss tuber and root infection is regarded as one of the most important and sustainable tools for disease management (Iftikhar et al. 2007; Falloon 2008; Merz and Falloon 2009; van der Waals 2015). Whilst there are currently no commercial cultivars that are immune to infection, cropping of more resistant cultivars will decrease the impact of Sss-related diseases and reduce pathogen inoculum accumulation in fields over successive growing seasons (Merz et al. 2004; Merz et al. 2012; van der Waals 2015).

Market demand for fresh market or processing tuber qualities can, however, limit the choice of more resistant cultivars (Harrison et al. 1997; van der Waals 2015; Wilson 2016).

Traditionally, resistance assessment has focused on reduced expression of tuber lesions (Harrison et al. 1997). However, in more recent times, the understanding of the impact of root infection on crop yields and the build-up of soil inoculum has led to additional assays specifically for root infection (Merz et al. 2004; Shah et al. 2012; Falloon et al. 2016; Yu et al. 2022). Importantly, it has been shown that the expression of resistance to root infection, root galling, and to tuber lesions is not always linked (Falloon et al. 2016). Thus, an assessment at all phases of disease expression is required to fully understand cultivar susceptibility. For example, the cultivar 'Swift' shows resistance to powdery scab in the field but is quite susceptible to root galling in the glasshouse (Falloon et al. 2003). Similarly, cv. 'Russet Burbank' shows good resistance to tuber disease but has moderate susceptibility to root infection and galling (Boyd 1951; van de Graaf et al. 2007; Falloon et al. 2016; Yu et al. 2023a).

Cultivar resistance assessment for tuber or root galling disease requires extensive field or glasshouse challenge trials with ratings developed based on visual assessment of the extent of the disease (Kirkham 1986; de Boer 1991; Torres et al. 1995; Falloon et al. 2003; Merz et al. 2004; Nitzan et al. 2010; Hernandez Maldonado et al. 2013, 2015; van der Waals 2015; Bittara et al. 2016; Falloon et al. 2016; Tsror et al. 2021). These assays provide valuable data on cultivar susceptibility but are also resource intensive and must manage the confounding impacts of varying environmental conditions and erratic distribution of soil inoculum to obtain robust results (Falloon et al. 2003; Nitzan et al. 2008; Hernandez Maldonado et al. 2013). To obtain data on the susceptibility of cultivars to root infection, however, a laboratory-based assessment is required as it is impossible to assess infection using a simple visual assessment. Merz et al. (2004) described a laboratory bioassay that observed the relative abundance of zoosporangia within root hairs from tissue-cultured plantlets incubated with sporosori inoculum with results within weeks. Yu et al. (2023a) developed an even more rapid assay for root infection that can assess relative zoospore binding to root segments within 48 h. Since root infection drives cyclic inoculum build-up within roots and, subsequently, tubers (Thangavel et al. 2015), and the infection environment within in vitro assays can be closely controlled, these assays of early pathogen: host interaction have added importance.

Cultivar comparisons from many trials have suggested that resistance to Sss disease in roots and tubers is polygenic, based on multiple different resistance genes (Falloon et al. 2003; Genet et al. 2005; Nitzan et al. 2010; Yu et al. 2023a). Conventional breeding for resistance is complex, providing significant challenges to breeders to accumulate resistance genes whilst maintaining critical agronomic and quality factors essential for market demands. This perhaps explains the lack of commercial cultivars with high levels of resistance. Genetic engineering, gene editing, or somaclonal selection, where variants of elite cultivars with improved disease can be generated whilst avoiding sexual genetic exchange, can assist in this (Evans and Sharp 1986; Hameed et al. 2018; Del Mar Martinez Prada et al. 2021); however, a detailed knowledge of effective resistance genes is required for the first two approaches

which has largely been absent for Sss. Some potential sources of resistance to root galling can be found in the germplasm collection of the Northwest Tri-State potato breeding programme (a collaborative work of the USDA/ARS, Oregon State University, Washington State University, and University of Idaho (Nitzan et al. 2008). Potato wild species germplasm collections can also be explored for possible resistance to diseases caused by *Spongospora subterranea* f. sp. *subterranea*. These world collections include, but are not limited to, the International Potato Centre (CIP, Lima, Peru), the Dutch-German Potato Collection (CGN, Wageningen, The Netherlands), the Commonwealth Potato Collection (CPC, Dundee, Scotland), and the US Potato Genebank (NRSP-6, Sturgeon Bay, USA) (Bradshaw et al. 2006). Tuber skin physiology likely plays a part in resistance to tuber lesions, with russet-skinned cultivars generally showing greater resistance to tuber disease than smooth-skinned cultivars (Nitzan et al. 2007). Furthermore, somaclonal variants with enhanced powdery scab resistance have been shown to have a thicker tuber periderm and increased levels of periderm suberin (Tegg et al. 2012; Thangavel et al. 2014, 2016).

The complexity of resistance and difficulty working with the Sss pathogen has meant knowledge of specific Sss disease defence mechanisms and resistance genes remains poorly understood. Lekota et al. (2020) showed that when infected by Sss, several defence-related genes in root tissue were upregulated at higher levels in the tolerant versus the susceptible cultivars. Transcriptomic and proteomic analyses of potato roots have associated genes and proteins with enhanced resistance in potatoes against Sss disease, specifically highlighting a role for glutathione and lignin metabolism in cultivar resistance (Balotf et al. 2021a, 2021b, 2022a, 2022b; Yu et al. 2022). In a targeted proteomic study using trypsin shaving of potato roots, Yu et al. (2023b) identified putative root surface proteins that may also have roles in zoospore root attachment.

As the role of host root exudates as resting spore germination stimulants (Balendres et al. 2016a) and zoospore chemotactic attractants or inhibitors (Amponsah et al. 2023) has been established, a comparison of root exudate metabolomes of potato cultivars has shown that known attractants are present in greater abundance, and inhibitors in reduced concentrations in susceptible cultivars compared to resistant cultivars (Lekota et al. 2020; Barsalote-Wei 2023). These studies suggest that the degree of susceptibility of a specific potato cultivar to Sss is associated with the balance of zoospore attractant and inhibitory compounds in root exudates, an abundance of defence-associated metabolites, the presence of putative root pathogen receptors, and by the level of upregulation of important defence-related genes.

Strategies to Avoid Disease

Selection of Fields With Low Inocula

Avoiding initial contamination of the field and crops by the pathogen is often referred to as disease escape (Agrios 2005). This includes selecting non-contaminated fields and planting healthy seed potato tubers (Harrison et al. 1997). The planting history of a field or location should be considered before cultivating

potatoes in that field (Wale 2000; Falloon 2008). The potential field should preferably not previously have been cultivated with potatoes (de Boer 2000; Nitzan et al. 2007) or not have a history of major disease outbreaks. Pre-plant pathogen soil testing should be considered where such tests are available (such as the Predict-PT scheme offered in Australia, Hay et al. 2016; Wright et al. 2022) and only fields with low inoculum used, especially for seed crop production where lower disease tolerance is accepted. Pathogen levels below 2pg Sss DNA/g soil are recommended for growing certified seed in Australia (A. Leo, Simplot Australia Pty Ltd., personal communication). The pathogen status of any nearby potato fields should also be assessed, as it has been shown that Sss inoculum can be disseminated in wind-borne contaminated dust (Tsror et al. 2020a).

Selection of Fields With Low Disease Conducive Characteristics In addition to the pathogen content of a field, the soil type and properties, including moisture-holding capacity, pH, and drainage, should be determined (van de Graaf et al. 2007). Specific soil properties that promote Sss disease development have already been discussed, and thus selecting fields with free drainage that avoid the accumulation of excess soil water, for example, can be beneficial. Technologies, including landscape pattern (EM38- clay type, soil depth, etc.) identification, can aid in determining the potato fields or sections thereof that may be more susceptible to Sss diseases (Whelan and Mulcahy 2017). Some soil types naturally suppressive to Sss disease development have also been identified due to inhibitory soil biology and/or chemistry and thus provide opportunities to avoid disease (Wright et al. 2021).

Alteration of Planting Date By planting potato tubers at the correct time, growers can reduce the incidence and severity of powdery scab at harvest (de Boer 2000; Falloon 2008; Tsror et al. 2021). The planting date should be selected based on the predicted soil temperature during tuber initiation (de Boer 2000), with higher soil temperatures during this period being desired (Tsror et al. 2021). By either delaying or hastening the planting, pathogen-favourable conditions can be escaped during the susceptible period (Tsror et al. 2021). It is important to note, however, that root infection has a higher soil temperature tolerance than tuber infection, and thus lack of tuber symptoms under warmer soil conditions does not necessarily mean a lack of disease impact (van de Graaf et al. 2005).

Ensure Seed Tubers Have Low Pathogen Inocula Infected potato seed tubers are a major driver of Sss disease within subsequent crops and are sources of contamination of previously pathogen-free fields (Jeger et al. 1996; Falloon 2008). Growers should always plant crops with the best quality seed available. Certified seed tubers with low tolerance levels for visible disease should be used where possible (Jeger et al. 1996; de Boer 2000; Bouchek-Mechiche et al. 2011; Tegg et al. 2016). It is important to note that visibly disease-free seed tubers can still carry pathogen inoculum, especially if sourced from seed crops that have had symptomatic tubers graded out (Tegg et al. 2016). Asymptomatic tubers graded from a heavily infected seed line (20 – 40% powdery scab incidence) contain significantly higher pathogen

levels (and associated disease risk) than asymptomatic tubers graded from a less infected (5 – 7% powdery scab incidence) seed line (Tegg et al. 2016). Using appropriate registered seed treatments to disinfect tubers after grading (Falloon 2008) and to provide some protection for early emerging roots is a useful practice to further ensure seed health.

Strategies to Reduce Soil Inoculum Prior to Planting

Crop Rotation

Crop rotation is important to limit the build-up of soil-borne pathogen inoculum levels and effectively reduce the ability of the pathogen to survive in the field from one growing season to another (Nitzan et al. 2007; Larkin 2008; Wright et al. 2015). Pathogens adapted to a particular host will proliferate during the cropping of that host but then generally decline in subsequent years in the absence of the host through competition with other soil microbiota. The effectiveness of crop rotation for Sss disease control is limited (de Boer 2000; Wale 2000; Sparrow et al. 2015; Wright et al. 2015). This is primarily due to the durability and longevity of Sss sporosori within cropping soils exacerbated by shorter rotation periods (de Boer 2000). Longer crop rotation intervals with more tolerant potato cultivars and Sss non-hosts are recommended for reducing powdery scab (Arcila et al. 2013; Sparrow et al. 2015). Potato growers are advised to enact a crop rotation programme for at least 3 to 5 years (Nitzan et al. 2007; Shah et al. 2010), but even this period between potato crops might not be sufficient to reduce the level of Sss inoculum below the high powdery scab disease risk threshold (Sparrow et al. 2015; Stagnitti 2015).

Understanding the presence and effectiveness of alternative hosts for pathogens is also important when devising a suitable rotation. Sss has a moderately wide host range (Qu and Christ 2006; Arcila et al. 2013; Simango et al. 2020; Tsror et al. 2020c), although few non-solanaceous alternative hosts produce abundant resting spores and thus perpetuate soil inoculum. Additionally, the species identified as hosts in greenhouse trials may not be infected or at lower rates in the field due to less conducive conditions (Clark et al. 2018; Tsror et al. 2020c). Different varieties of a specific crop could differ in their susceptibility to root infection and pathogen proliferation (Alaryan et al. 2023). Unharvested ‘volunteer’ potatoes left in fields from prior potato crops can act as pathogen reservoirs within rotations, and their removal should be prioritised to ensure effective rotation periods.

Organic Soil Amendments Incorporating cover or green manure crops within a rotation has many beneficial advantages. These include improving soil structure, moisture retention, nutrition, and biological health by increasing the soil organic matter levels (Mazzola 2007; Larkin 2008). The choice of cover crop may impact benefits, as some are hosts of Sss and can complete the pathogen life cycle, resulting in inoculum accumulation (Alaryan et al. 2023).

Biofumigant cover crops have specifically been promoted to assist in soil pest and disease management (Matthiessen and Kirkegaard 2006; Larkin and Lynch 2018). In addition to soil amendment with organic matter, these specialised crops produce volatile sulphur compounds that are toxic to soil microorganisms upon incorporating macerated plant materials into the soil (Matthiessen and Kirkegaard 2006). In a trial on Sss-contaminated fields, canola, rapeseed, and Indian mustard (*Brassica juncea* L.) crops were grown with a reported decrease in Sss disease of between 15 and 40%, with Indian mustard shown to provide the greatest efficacy (Larkin and Griffin 2007). Larkin and Lynch (2018) found that selected brassica (mustard blend) and non-brassica (perennial ryegrass) crop rotations reduced powdery scab disease. The individual role of the biofumigant activity versus organic amendment in such studies is unclear and may be impacted by soil type, but benefits for disease control can be achieved (Larkin and Lynch 2018). Plenty of brassica crops (e.g. 'Caliente' mustard) are however Sss hosts and can potentially increase pathogen soil inoculum levels, but perhaps not at rates that will offset the numerous benefits that cultivating brassica cover crops provides (Alaryan et al. 2023).

Understanding the possible host status of cover crops used for potato rotations is important. Those Type I or Type II alternative hosts of Sss are discouraged because of the risk of accumulation of Sss sporosori in the soil with subsequent infection cycles (Arcila et al. 2013; Simango et al. 2020; Tsror et al. 2020c). In contrast, the use of Sss host plants in which the entire pathogen lifecycle is not supported or termination of the cover crop before sporosori induction has the potential to decrease Sss inoculum levels in the soil through encouraging germination of resting spores (Merz 1989a). Such, trap crops like leafy daikon (*Raphanus sativus*) and jimsonweed (*Datura stramonium*) have been shown to reduce the severity of soil-borne diseases on crops when planted in highly contaminated fields before the susceptible crop (Murakamia et al. 2000).

In a similar manner, recent studies have suggested that the direct addition of organic materials that mimic root exudates could be beneficial for inoculum management through premature stimulation of synchronised resting spore germination, releasing short-lived zoospores that perish in the absence of a suitable host plant (Balendres et al. 2016a; Amponsah et al. 2021). Treatment of Sss-contaminated cropping soils months prior to planting potato could lower inoculum levels below severe risk thresholds. No commercial products are currently available; however, similar approaches have been successfully used to manage other soil-borne diseases, such as onion white rot (Davis et al. 2007), and further investigations are warranted.

Soil Fumigation Soil fumigants can be applied to cropping soils before planting to reduce pathogen inoculum and have been shown under some circumstances to reduce Sss disease (Nachmias and Krikun 1988; Simango and van der Waals 2017; Tsror et al. 2019, 2020a). However, in other studies, whilst fumigant treatment reduced pathogen inoculum levels, it did not reduce subsequent disease, perhaps due to their impact on beneficial soil microbiota (Bittara et al. 2017). Many potato-growing regions worldwide do not have access to these chemicals due to environmental and human safety concerns, and where they are still utilised, there is an increasing

movement to source environmentally sustainable alternative options (Hills et al. 2020; Powell et al. 2020).

In Crop Strategies to Reduce Disease

Application of Fungicides or Other Chemicals at Planting or During Crop Growth

Progressive withdrawal of toxic soil chemicals and limited investment in developing and registering new chemistries have restricted the availability of fungicides for Sss diseases. There are currently no highly effective chemical treatments for disease control, with available materials often having limited efficacy due to the robustness of the pathogen resting spores, uneven distribution of inoculum, and soil properties (Braithwaite et al. 1994). Registered fungicides applied to the soil before or during the growing season can, however, provide some protection against disease through inhibition of resting spore germination or killing of zoospores prior to root or tuber infection (Falloon et al. 1996; de Boer 2000; Falloon et al. 2008; Thangavel et al. 2015; Simango and van der Waals 2017; Tsror et al. 2020a). Whilst treatments may not prevent infection, a delay in the onset of cyclic root infection can still result in a substantial reduction in root and tuber disease (Thangavel et al. 2015). Soil treatments with certain compounds containing zinc, sulphur, or boron have also been suggested to provide some management of Sss disease (Kirkham 1986; Wale 2000; Falloon et al. 2010; Simango and van der Waals 2017).

A novel approach for in-crop management involves the addition of non-fungicidal organic amendments that mimic root exudates responsible for the attraction or inhibition of zoospore taxis (Balendres et al. 2016b, 2017; Amponsah et al. 2023). Recent studies have suggested that this approach can reduce disease incidence (Amponsah et al. 2021). This strategy is not limited to chemoattractants but any compound that can potentially interfere with or alter the pre-infection Sss biology (resting spore germination, zoospore movement, swimming patterns, attachment, and encystment) and life cycle, thus delaying or preventing infection (Amponsah et al. 2021, 2022).

Biological Suppression of Disease There is very limited research on the use of biological control to manage Sss compared with other plant pathogens, and the available results are inconsistent and often contradictory (O'Brien and Milroy 2017). Biological agents have the potential to affect zoospore activity and their ability to infect the host plant, as well as resting spore viability (Nielsen and Larsen 2004). Targeted treatments at planting, as seed or in-furrow applications, could be beneficial, and we see increasing investment from agrichemical companies in biological suppressants. Several *Trichoderma* species have shown efficacy in the control of the related pathogen, *Plasmodiophora brassicae* (Cheah et al. 2000; Kim et al. 2002), and Nielsen and Larsen (2004) determined the efficacy of several different commercially available *Trichoderma harzianum* biocontrol products against Sss in pot trials. Simango and van der Waals (2017) also found that *Trichoderma asperellum* notably reduced zoosporangia root infection. Nakayama and Sayama (2013) conducted a

study with *Aspergillus versicolour* applied to Sss-infected potato tubers that significantly inhibited the Sss tuber disease. *Bacillus subtilis* has also effectively reduced Sss root infection (Simango and van der Waals 2017).

Rhizosphere bacterial and mycorrhizal inoculants also have great potential to assist in disease management, often with the added benefit of increasing plant productivity (Xavier and Boyetchko 2004; Aliye et al. 2008; Gómez Expósito et al. 2017). For example, Barsalote-Wei (2023) isolated a rhizosphere bacterium that selectively degrades root exudate compounds that act as chemotactic attractants for Sss zoospores. When established within the potato rhizosphere, the bacterium inhibited root and tuber disease and boosted root growth and tuber yield.

New biological control agents against this pathogen may be acquired by identifying and isolating the microbial communities responsible for microbe-mediated suppression of Sss observed in some naturally suppressive cultivated soils (Mazzola 2007; Wright et al. 2021).

Soil and Crop Management Strategies — Irrigation and Soil Moisture Management When preparing and working fields, growers should prevent water retention and waterlogging whilst improving water drainage to reduce disease incidence on potato tubers (Hughes 1980). Overworking fields can form a fine tilth that increases water retention (Wale 2000). Frequent heavy machinery use or farm traffic on wet soils can induce soil compaction and should be avoided, as these will encourage water retention (Wale 2000; Sinton et al. 2022). Compacted or poorly structured soils will also decrease microbial activity associated with disease repression. Compacted soils may be remediated by deep tillage.

Consideration of the irrigation programme used immediately before and during tuber set can be important for the incidence and severity of powdery scab on potato tubers (Taylor et al. 1986; Tuncer 2002; van de Graaf et al. 2007; Shah et al. 2014). One study reported a 75% decrease in disease severity when irrigation was withheld for a month at the susceptible tuber set period of potato crop growth (Taylor et al. 1986). However, limiting soil water during this period can harm tuber quality and yield (Shock et al. 1992). Growers could seek to apply less water through irrigation during this period than what is required by the soil moisture deficit (Wale 2000; Tuncer 2002). Crop monitoring tools, like real-time moisture probes, can aid in determining the soil moisture level, which can then be used to alter the irrigation programme and management practices (Whelan and Mulcahy 2017).

Soil Fertility and Temperature Plant stress will exacerbate disease risk, thus, ensuring appropriate pH, macro-, and micro-nutrient balance is essential. Nitrogenous fertilisers have been suggested to affect disease. Tuncer (2002) and Shah et al. (2014) reported that higher soil nitrogen levels increased powdery scab, but other studies reported a reduction in powdery scab severity in contaminated soils after the application of high nitrogen-content fertilisers or organic soil amendments due

to an increase in volatile fatty acids in the soil (de Boer and Crump 2005). The type of nitrogen fertiliser applied can be important. Urea fertiliser has been reported to reduce powdery scab in the field (Shah et al. 2014), whilst ammonium nitrate decreases root gall formation and nitrate nitrogen has minimal effect on root gall severity. Applying a fertiliser (calcium ammonium nitrate) that contained both ammonium and nitrate increased the incidence and severity of powdery scab and the level of pathogen DNA in the soil (Shah et al. 2014). Manipulating soil nutrients, like applying high levels of zinc and manganese, offered only moderate control of Sss-induced root galling (Falloon et al. 2010).

Direct application of organic fertilisers such as manure can provide similar benefits to green manure in enriching soil organic matter and improving soil health (Bonilla et al. 2012). However, care on the source of materials may be required. Merz and Falloon (2009) cited a study by Pethybridge (1911) where severe powdery scab infection was observed on tubers from plants grown in a field fertilised with manure from pigs fed powdery scab-diseased tubers. Similar anecdotal observations have been noted in potato crops following dairy pastures where infested potato waste was fed to stock. It has been speculated that Sss resting spores can survive the digestive tract of animals and remain viable.

Soil temperatures will influence disease. However, the management of soil temperature is difficult. Withholding irrigation may increase soil temperature during critical infection periods and alter the planting date. Raising soil temperatures by 1.8 – 4.2 °C during tuber set has also been successfully achieved in some circumstances through soil mulching (Tsror et al. 2020b).

Crop Hygiene Considerations Maintaining good hygiene practices throughout the crop production process, such as disinfecting farming and grading equipment after use in confirmed or suspected Sss-contaminated fields, decreases the risk of Sss introduction into healthy potato fields (van de Graaf et al. 2005; Falloon 2008). Removing potential Sss resting spore contaminants like soil and plant debris from storage and tuber surfaces can significantly reduce the risk of transmitting Sss resting spores (de Boer 2000; Wale 2000; Falloon 2008; Wright et al. 2012).

Conclusion

This review provides a contemporary perspective on Sss diseases and their management with a particular focus on recent material since the last significant review of Sss was completed in 2016 (see ‘Introduction’). It also highlights key research gaps, which are summarised in Table 1. These gaps represent some of the opportunities that will enable a greater understanding of this pathogen and disease, which may provide further opportunities to manage this recalcitrant soil-borne disease.

Table 1 Knowledge gaps that may aid understanding of Sss and associated diseases

Knowledge or research gap	Opportunity
Development of a fully annotated Sss genome	To better understand host/pathogen interactions and identify possible pathogen effectors and host resistance, greater investment in sequencing and annotation of the Sss genome is warranted
Does Sss undergo sexual recombination?	A basic question, but one that will assist in assessing the likelihood of further development of pathogen diversity
There is a limited understanding of the interactions of the pathogen with soil microbiota, including other potato pathogens	Evidence of suppressive soils exists, but the microbiology of suppression is not understood. Similarly, rhizobacteria and mycorrhizae are known to assist in disease suppression Furthermore, co-occurrence or lack thereof of other potato diseases suggests possible synergistic or antagonistic interactions, which are critical to understand for an integrated management strategy to be implemented. Elucidation of the impact of soil and rhizosphere microbiota, including other pathogens, on pathogen persistence and infection and the mechanisms involved, is warranted
How do agronomic practices, including pesticide treatments, affect Sss disease?	Agronomic treatments, including nutrition management and fungicide treatments for control of other potato pathogens, will impact the soil microbiome and may have a positive or negative effect on Sss disease. A better understanding of these treatments' impacts and the interaction mechanisms will allow more effective integrated disease management approaches
The dynamics of soil environmental conditions throughout the cropping cycle that are essential for the disease are poorly understood	It is known that disease is favoured by cool, wet soil conditions, but what role does soil moisture and temperature fluctuation play in disease? How does the soil environment interact with the susceptibility of the host plant? Elucidating key environmental conditions that trigger disease may enable growers to prevent such favourable disease conducive conditions and allow for more timely and effective in-season management. Real-time monitoring of in-ground environmental parameters (e.g. soil moisture and temperature) may provide predictive models of likely root and tuber infection and possible immediate remediation (control) responses
Limited availability of effective chemical controls	Consider pathogen weaknesses in its lifecycle and develop/target treatments that interfere with zoospore viability, release, taxis, etc. Also, consider materials that augment host resistance
Limited development of commercial varieties with high-level disease resistance	Targeted breeding, including the development of effective molecular markers, incorporating new resistance targets (e.g. root encystment factors, altered root exudation metabolic profiles, new resistance genes) would increase growers' opportunities to sustainably manage this disease

Table 1 (continued)

Knowledge or research gap	Opportunity
What are the host or environmental triggers that stimulate root gall formation?	Understanding the physiological and genetic drivers of root gall formation may assist in breeding strategies to reduce or eliminate gall formation and thus decrease their contribution to soil inoculum
What is the significance of Sss host status in non-potato crop species on Sss diseases?	By investigating the impact of Sss host status in different rotation crop species on soil pathogen inoculum and disease severity in subsequent potato crops, potato growers can make more well-informed decisions regarding selecting rotation crops. Verifying 'trap crops' as effective, potential management for soil inoculum, and suitability in an integrated control programme will allow for additional control options. Furthermore, understanding the impact of the density of volunteer (unharvested) potatoes within the rotation on the maintenance of soil inoculum is warranted

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Declarations

Conflict of Interest The authors declare no competing interests.

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