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Review: Powdery Scab of Potato—Increased Knowledge of Pathogen Biology and Disease Epidemiology for Effective Disease Management

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Abstract The importance of the potato tuber disease powdery scab, caused by the zoosporic pathogen *Spongospora subterranea* f. sp. *subterranea*, has increased worldwide, and the disease is one of the most important problems facing potato production in some regions. This soilborne pathogen produces many resting spores which can remain dormant for long periods, are highly resistant to environmental stresses and can spread the disease on seed potatoes and in contaminated soil. The enigmatic nature of this organism exacerbates the development of effective powdery scab control methods. Substantial knowledge has been gained in the last decade on the biology of the pathogen and the epidemiology of the disease, but no single effective control measure is, or is likely to be, available. An integrated approach to powdery scab management is the aim, with host resistance as a substantial and sustainable component. Further research on the epidemiology of powdery scab and population genetics of the pathogen is urgently required. All stakeholders involved in the potato industry must become aware that solution of the powdery scab problem is likely to be a long-term goal. When resistant cultivars with all the other characteristics demanded for marketing high-quality potatoes are available, and when disease risk from the pathogen on seed and/or in soil can be accurately determined, then the mission to develop effective powdery scab control will become achievable.

Keywords Epidemiology · Integrated disease management · Population genetics · Potato · Resistance · *Spongospora subterranea* f. sp. *subterranea*

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Introduction

Research with obligate root pathogens of the *Plasmodiophoridae* (Cavalier-Smith 1993), here called 'plasmodiophorids', and in particular with *Spongospora*, demands a high degree of motivation. Laboratory trials often fail owing to complexity of the natural factors controlling dormancy, growth and multiplication of these organisms. According to Buczacki (1983), the researcher working with *Plasmodiophora brassicae* (which causes clubroot of *Brassica* spp.) is confronted with the following problem: "Whilst clubroot presents problems and frustrations to the crucifer grower, so *Plasmodiophora* presents problems and frustrations to the research worker. I believe that these two situations are not mere coincidence for this organism is so remarkably uncooperative in its response to many of the tests and procedures used with more conventional fungal pathogens that anyone wishing to study it and to establish control measures must devise new techniques at almost every turn."

Today, despite these difficulties, we have gained more insight into the biology of *Spongospora subterranea* f. sp. *subterranea* (*Sss*), the plasmodiophorid pathogen that causes the increasingly important disease powdery scab of potato. This review updates available information on the importance and epidemiology of powdery scab, and the biology of *Sss*, drawing conclusions from this information on appropriate strategies for management of this disease-causative pathogen.

Importance, Occurrence, Damage

Both *Sss* and *Spongospora subterranea* f. sp. *nasturtii* (*Ssn*), are unique, as important pathogenic organisms, on potato and watercress, respectively, and as being capable of vectoring important plant pathogenic viruses. *Potato mop-top virus* (PMTV) is transmitted under natural conditions by *Sss* and causes a range of superficial and internal symptoms on tubers making them unmarketable, especially for processing. This virus occurs in many of the major potato-producing regions of northern Europe, South America, China, Japan and Australia, and recently there has been an outbreak in northern USA and Canada. Tenorio et al. (2006) screened 21 potato cultivars and found no evidence for a positive correlation between their susceptibility to PMTV and the incidence of powdery scab on their tubers, a result later confirmed by Kirk (2007).

Powdery scab is a widespread disease in most of the temperate potato-producing areas of the world, but the disease also occurs in hot and dry climates where irrigation is applied (Wale 2000a). Numerous new 'first reports' of the disease have been published which show that powdery scab has probably been previously unrecognized or underestimated (Merz 1999), or is spreading to countries and regions where it has not previously occurred. Factors such as intensification of potato production, increasing use of susceptible cultivars (Wale 2000a), more frequent irrigation and discontinuation of mercury seed tuber treatments may all be contributing to greater disease incidence. Several countries have joined the *Spongospora* community since 1996. The first reports of the disease have come from Alaska (Carling 1996), Pakistan (Ahmad et al. 1996), Costa Rica (Montera-Astua et al. 2002), South Korea (Kim et al. 2003) and Malta (Porta-Puglia and

Milfsud 2006). A survey in the main potato-producing zones of Pakistan showed that contaminated soils were found in most of the locations examined (Iftikhar et al. 2003). The rising incidence of powdery scab in Brazil is of great concern as the disease was thought to be restricted to the centre-pivoted irrigation systems around São Paulo (de Nazareno and Boschetto 2002). Similarly, more widespread distribution of powdery scab than previously recognized was recently found in Argentina (Clausen et al. 2005). In the USA the disease further spread in 1997, reaching North Dakota, where environmental conditions were not previously considered to be favourable for powdery scab development (Draper et al. 1997). A few years later, Christ (2001) called the disease an emerging problem in the USA and presented results from field experiments on control. Surveys made in 2004 showed that powdery scab occurs commonly and seriously in Yunnan province of China (L. Xia, Yunnan Agricultural University, Kunming, personal communication). Israel is having increasing powdery scab problems (L. Tsror, personal communication) despite the warm, dry climate experienced there, as surveys have suggested that the disease might have been imported and spread through seed tubers (Tsror et al. 1999). Some early season potato production areas in Portugal are also confronted with the disease, e.g. around Vagos (C. Chatot and R. Oliveira, Germicopa, personal communication). In Albania, powdery scab was found to be one of the three most important potato diseases in the 1990s (Wennemann et al. 2002). In Germany, with a long history of powdery scab, there is an increasing problem with the disease (Stachewicz and Enzian 2002). Today, powdery scab is a serious quality issue in Swiss potato production. The pathogen has already become established in many soils (Merz et al. 2006). It is very likely that powdery scab problems will occur in other areas, especially in the Northern Hemisphere.

Potato producers can suffer severe losses due to powdery scab. Seed potato lines with powdery scab may be completely rejected for establishment of new crops, or may require extra grading to remove infected tubers. As an example, in 2007 many Swiss seed farmers were confronted with heavily infected crops and losses of several hundred thousand euros were estimated (A. Kraehenbuehl, SEMAG, Switzerland, personal communication). Similarly, where potatoes are produced for high-quality fresh supermarket sale, particularly as washed product, extra grading is required to remove infected tubers to meet market standards. Where potatoes are produced for processing, powdery scab infection requires extra skin removal operations, producing more waste and less profit (Wale 2000a). Furthermore, recent research (Falloon et al. 2004, 2005; Lister et al. 2004) suggests that *Sss* can have harmful effects on host plant (and potentially crop) productivity. When compared with uninfected plants, those with *Sss*-infected roots used less water, had disrupted nutrient uptake and produced less dry matter, smaller shoots and fewer leaves.

Biology and Epidemiology

An extended review of various earlier findings on essential features of the life cycle of *Sss* was provided by Harrison et al. (1997). Recent advances in knowledge of the biology of the pathogen are providing basic information that is likely to assist development of new strategies for management of powdery scab.

Phylogeny

The enigmatic character of the plasmodiophorid pathogens is demonstrated by the many phylogenies suggested for this group by different authors over recent years. Some derived their phylogenies from reviews of historical treatments (e.g., Dylewsky 1990), others from morphology (e.g., Cavalier-Smith 1993; Braselton 1995) or, more recently, from molecular data (e.g., Bulman et al. 2001; Archibald and Keeling 2004; Bass et al. 2005). Although de Bary (1884) considered the group to be protozoans, they were regarded by many as true fungi for most of the time afterwards. Today the plasmodiophorids are again considered to be protozoans, within the order *Plasmodiophorida*, family *Plasmodiophoridae*, and include ten genera and 36 species (Huber et al. 2004). The rest of their classification remains unclear. The genus *Spongospora* has four recognized members. Two of them, *Sss* and *Ssn*, defined as *formae speciales* (Tomlinson 1958), are important pathogens of vegetables. It was recently proposed to separate these into two distinct species on the basis of sporangial morphology, host specificity and molecular data (Dick 2001; Down et al. 2002; Qu and Christ 2004). Originally Tomlinson's (1958) designation into two *formae speciales* was mainly based on the morphological similarity of their sporosori (also termed 'cystosori' or 'spore balls'), the conglomerations of resting spores characteristic of *Spongospora*. Merz et al. (2005b) found that sporosori of both *Sss* and *Ssn* showed the same reaction to monoclonal antibodies produced against *Sss* sporosori, suggesting that the two organisms are closely related.

Pathogen Variation

The availability of cultivars resistant to *Sss* will be a main part of future powdery scab management strategies. Breeders attempting to introduce disease resistance into new cultivars usually screen new lines against a range of pathogen isolates representing the known genetic diversity to select for the most durable resistance. However, little is known about the genetic variation of *Sss* or the role of sexual recombination in its life cycle. It is assumed that the sporosori are the product of sexual recombination (Braselton 1995), but this remains to be demonstrated.

The first substantial indication of pathogen variability in *Sss* was found by Wuerzer (1965). He characterized 17 collections of *Sss* from Europe and America into two groups according to the size of sporosori but found no evidence for biological significance of this grouping. Later Bulman and Marshall (1998) detected genetic variation (5.1% divergence) in DNA sequences of the ribosomal internal transcribed spacers (1 and 2) of *Sss* collections originating from different continents. Collections from Australasia and Europe (group type II) differed from one from Scotland, which was identical to two South American collections (group type I). The existence of these two internal transcribed spacer sequence groups was confirmed by Qu and Christ (2004). They also identified both groups in Scottish collections, but demonstrated that only sequence type II occurred in all Canadian and US collections. All their collections from the British Isles (Ireland, Scotland) were invariably associated with particular potato cultivars, which suggests a possible genotype × host relationship. A more detailed study was made with DNA

of 24 single sporosorus collections derived from locations in the USA and Canada and *Sss*-specific restriction fragment length polymorphism probes (Qu and Christ 2006a). Genetic variation was recorded among but not within geographic locations (fields). This suggests that field populations are clones and do not undergo sexual recombination. Consequently the sporosori from one location would also be genetically uniform, a theory not supported by actual knowledge (Braselton 1995). It is more likely that a sporosorus consists of many genotypes (single resting spores), and thus represents a 'population'. Transitional sporogenic plasmodia of *Sss* containing nuclei that undergo meiosis prior to cleavage as synaptonemal complexes have been observed in transections of infected potato cells (Braselton 1992). Hence, single resting spores are believed to be haploid (Nuismer and Otto 2004), but this and other cytological details, such as when and how nuclei that are capable of undergoing meiosis are formed (Braselton 1995), remain unclear. Analysis of the genetic nature of *Sss* populations is important for the development of successful and durable breeding strategies to develop resistant cultivars.

Pathogen Culturability

In 1979, Diriwächter et al. (1979) reported that they had maintained a culture of *Sss* in the form of amoebae on agar by regular transmission to fresh media. To prove the identity of the amoebae, soil was inoculated with agar containing amoebae and newly formed cysts and baited with tomato plants. After 50 days the tomato roots were examined and zoosporangia typical of *Sss* were found. Diriwächter et al. (1979) claimed that they had demonstrated a novel, simple and rapid viability test for sporosori, useful for tuber disinfection experiments. The biggest impact of their paper was that for the first time a plasmodiophorid pathogen, considered to be an obligate biotroph, was apparently culturable on artificial media, potentially making research with the organism a lot easier. The senior author started research using the methods of Diriwächter et al. (1979) in 1983. When it became evident that identification of the observed amoebae was impossible, he stopped these experiments. Later, Arnold et al. (1996) did experiments with *P. brassicae* similar to those of Diriwächter et al. (1979). The first generations of amoebae released by the resting spores on agar induced typical clubroot symptoms on cabbage and some showed positive hybridization with a *P. brassicae* DNA probe, but these abilities where lost after subculture of the amoebae. Harrison et al. (1997) observed amoebae on agar but were unable to fulfil Koch's postulates with them and concluded that they may have originated from contamination of *Sss* resting spores. It took 22 years until the myth of a saprophytic amoebal stage of a plasmodiophorid was finally 'demolished'. Qu et al. (2001) demonstrated clearly, using microscopy, bioassay and specific molecular primers, that the amoeba/cyst colonies isolated from surface-sterilized *Sss*-infected potato tubers and sporosori have a saprophytic phase but are contaminants and not *Sss*. An interesting alternative in vitro culture method for *Sss* has recently been introduced by Qu and Christ (2007). The system allows maintenance and proliferation of *Sss* on potato hairy roots and might be useful for studies on the pathogen's life cycle, its interaction with host plants or for mass production of contaminant-free sporosori.

Zoospore Morphology

Merz (1997) found no differences in morphology and swimming pattern between *Sss* primary zoospores (those released from sporosori) and secondary zoospores (those released from zoosporangia in host roots). He used a pulse inoculation method with tomato bait plants (Merz 1993), and prepared the sporosori for electron microscopy after 1-, 2- or 5-h baiting periods. As only few developing and no mature zoospores could be seen in numerous observed single spores, he suggested that zoospore formation and release may occur quickly, e.g., within 15 min. The encysted primary zoospores on bait plant root surfaces showed the 'Stachels', typical and unique plasmodiophorid host penetration structures, along with adhesoria when stained with an optical brightener, strong indications that the infection process for *Sss* was the same as for other plasmodiophorids.

Primary Zoospore Release

The pulse inoculation method (Merz 1997) was used because spontaneous release of primary zoospores occurs very arbitrarily (Fornier 1997). The same observation was reported by Harrison et al. (1997). They stated that there remained much to be learned about factors controlling germination of resting spores. The conclusion reached by White (1954), that sporosori need stimuli to release their zoospores, was the initial hypothesis for the thesis of Merz (1989a). A 5-h incubation of sporosori together with roots of tomato plants was sufficient to increase the intensity of root infection of subsequent tomato bait plants, but the same effect was also obtained with wheat plants (Merz 1993). Similar results were presented by Fornier (1997). Some sporosori may spontaneously release zoospores, while others may need external stimuli to break the dormancy, as MacFarlane (1952) postulated for *P. brassicae*. Merz (1993) and Harrison et al. (1997) found no evidence for the hypothesis that resting spores might have a dormant period during which they mature, immediately after their formation (Gilbert 1929 cited in Harrison et al. 1997).

Another aspect of primary zoospore release is under investigation by Falloon et al. (2006). Previously, it was assumed that an *Sss* sporosorus was one inoculum unit when estimating inoculum concentration. But sporosori consist of numerous single resting spores, each a potential infection unit, and this should be considered for inoculum standardization or correlation of soil inoculum with risk of powdery scab. Falloon et al. (2007) enumerated resting spores in a large sample of sporosori, using light, confocal and electron microscopy and image analysis software, and derived a general formula to estimate resting spore numbers. Their results indicate that sporosori each contain approximately 700 resting spores (range 160–1,530), and that numbers of resting spores in sporosori can be accurately calculated from simple measurements of sporosorus dimensions.

Host Range

Hosts other than potato (*Solanum tuberosum*) may assist *Sss* to survive, especially when sporosori are formed. Early work showed that many members of several plant families are hosts of the zoosporangial stage of the pathogen (Harrison et al. 1997).

The best hosts are members of the *Solanaceae* and *Chenopodiaceae*, but sporosori were only found in *Solanaceae*. Fornier (1997) found only zoosporangia in tomato and potato plants but not in non-solanaceous plants. When 16 plant species commercially cropped in Pakistan were examined after cultivation in contaminated soil, only eight showed zoosporangial root infection, with maize as the most intensely infected (Iftikhar 2001). No *Sss* root galls were seen on any of the crops, including solanaceous plants such as tobacco, *Datura stramonium* and tomato. Seventeen weeds common in Danish potato fields were tested as potential hosts for *Sss* and PMTV by Andersen et al. (2002) and 13 of them yielded zoosporangia. Recently Qu and Christ (2006b) reported the observation of sporosori on tomato and on two previously unreported hosts, yellow mustard and oat. Ten of 14 crop species and six of 12 weed species were zoosporangial hosts. These results suggest that *Sss* has a wide host range in its zoosporangial phase, but only a few hosts allow the pathogen to complete its life cycle by producing sporosori. The control of these alternative hosts has to be incorporated in an overall powdery scab management strategy.

Environmental Factors

Several environmental factors control host infection by *Sss*. It is widely accepted that powdery scab thrives in cool, wet and heavy soils (Lawrence and McKenzie 1986).

Temperature

Several studies have considered effects of temperature on infection of potato by *Sss*, and this knowledge could be applied to avoid growing potato crops in periods when soil conditions favour development of powdery scab. In pot trials, van de Graaf et al. (2005) found high infection and disease levels of tubers at 9, 12 and 17 °C, but symptoms were most severe at 12 °C. In contrast, root galling was only severe at 17 °C and did not occur at 9 °C although the roots were infected, as revealed by DNA detection methods (van de Graaf et al. 2007). A study by Fornier (1997) demonstrated that greater numbers of zoospores were released when sporosori where incubated at 15 and 25 °C, compared with 5 and 10 °C, but root infection of tomato plants was inhibited at 30 °C. Claxton et al. (1995) reported more diseased watercress roots at 10 °C than at 5, 15 or 20 °C, with the lowest number at 20 °C, when they inoculated soil with *Ssn* sporosori. Both Fornier (1997) and Claxton et al. (1995) observed a longer duration of relatively high concentrations of swimming zoospores in sporosorus suspensions at lower than at higher temperatures, explained by Claxton et al. (1995) as resulting from prolonged survival rather than continual zoospore release. In an experiment in which potato plants were grown in inoculated sand under controlled conditions, de Boer (2000a) showed that the incidence and severity of powdery scab on progeny tubers was greatest at 12.5 °C, intermediate at 15 °C, and low at 17.5 and 20 °C, and no disease occurred at 10 °C. The results of these various studies indicate that *Sss* zoospore release varies with temperature (5–25 °C) but that zoospore activity and potato tuber infection are probably favoured by cool temperatures (12–13 °C) and root galling by higher temperatures (around 17 °C).

Soil Water Content

Soil water is essential for the swimming zoospores of *Sss* to reach host tissue. Consequently, a recommended powdery scab control measure is to withhold irrigation (de Boer 2000a) or avoid overwatering during tuber initiation (Wale 2000b). Constant dampness of the soil resulted in more disease on tubers than did a fluctuating moisture regime in the pot trials reported by van de Graaf et al. (2005), but there were some problems with the fluctuating treatment. Zink et al. (2004), however, suggested that conditions in the host root zone are always likely to be adequate to foster extensive disease even when water management for potato cropping is ideal. When irrigation becomes more frequent, soil temperatures at the root zone decrease to a range highly favourable for infection, especially when cold water is used. This probably explains the occurrence of powdery scab in hot, dry countries such as Israel (Nachmias and Krikun 1988) where potato crops are grown in winter or at high altitude and/or where sometimes excessive irrigation is applied (Wale 2000a). The senior author (unpublished data) found in a preliminary field experiment that a period of dry–wet–dry soil conditions over 25 days between the 60th and 85th day after planting, with an average soil temperature of about 13 °C, induced tuber infection.

Soil Type

Avoiding poorly drained or compacted soils and creation of impermeable layers through cultivation are general recommended practices to limit powdery scab development (Wale 2000b). Although heavy soils with high water retention capacities are thought to encourage the disease (Prentice et al. 2007), several reports point out that sandy soils seem to be the worst. In Australia, there has been a rapid expansion of potato production into alkaline or acidic sandy soils in semi-arid regions with centre-pivot irrigation. In these areas powdery scab has become a very serious problem in winter-planted crops, mainly because of the high-frequency irrigation regimes that are applied (every 1–2 days) (de Boer 2000a). According to van de Haar (2000), powdery scab was found on potatoes grown in several different types of soil in the Netherlands, but the disease was more severe in crops grown on sandy or organic soils. The few Danish farmers who encounter severe powdery scab grow potatoes in coarse black sandy soils having high humus content (Nielsen and Nicolaisen 2000). In the Cappadocia region, where 43% of the Turkish potato crop is produced and powdery scab is a problem, the main soil type is sandy or sandy loam (Tuncer 2002). Despite the relatively low number of root galls seen at 12 °C in the pot experiments of van de Graaf et al. (2007), the incidence and severity of root galling was less when the plants were grown in clay soil, compared with sand or loam. The difference between the soils was also found for tuber infection and symptom development (van der Graaf et al. 2005).

Environmental Factors and Disease Risk Assessment

In an integrative approach, mainly based on temperature, amount and frequency of rainfall and soil type, Stachewicz and Enzian (2001) identified regions in Germany

with high, medium or low risk for the disease by overlaying specific climate and soil maps. This is a relatively straightforward approach for a country to begin developing integrated disease management based on disease risk.

Disease Avoidance and Direct Control

The primary aim of a short-term powdery scab control strategy is to avoid soil contamination from *Sss* by planting clean seed into uncontaminated soil. This is because direct control of the soilborne pathogen is difficult.

Seed Tuber Infection

Infected seed is mostly responsible for short- and long-distance disease spread. In Switzerland, the tolerance limit for powdery scab on seed tubers is not more than 1% of tubers with more than five lesions (Anonymous 1989), and analogical tolerance levels are used in other countries where seed potato certification systems are used. This level of severity is equivalent of an average tuber surface infection of about 1%. This level may be too high to prevent spread of the disease, but there is no information about the level of seed tuber infection necessary to induce powdery scab epidemics. Even symptomless seed tubers originating from an infested field are reported to cause infection of the progeny (Theron 1999). However, a practicable tolerance limit is essential if seed certification authorities are required to prevent high levels of infection on seed tubers. The considerable variation among national powdery scab tolerance levels (Wale 2000a) shows the need for international coordination to create a standard.

The traditional visual inspection of normally unwashed seed tubers risks misidentification of scab symptoms, as common scab lesions (caused by *Streptomyces* spp.) are sometimes difficult to distinguish from powdery scab lesions (Merz 2000). Tubers with suspicious symptoms should be washed and further inspected under good light conditions and the visual diagnostic skills of the inspectors must be refreshed regularly. Finally, visually unidentifiable symptoms can be tested with a rapid on-site test for *Sss*, based on lateral flow immunochromatography (AgriStrip, Bioreba, Switzerland; Merz et al. 2006). This allows accurate identification of *Sss* within 5 min. Molecular methods based on PCR (Bulman and Marshall 1998) can also be used for highly sensitive laboratory-based *Sss* detection. Bell et al. (1999) used primers similar to those reported by Bulman and Marshall (1998), and detected amplification from peel and washings of apparently healthy tubers. Using real-time PCR, van de Graaf et al. (2005) found that symptomless infection was common for tubers harvested from their pot trials, especially under conditions suboptimal for powdery scab development. De Haan and van den Bovenkamp (2005) used the same DNA quantification method to clarify the nature of severe and suspicious symptoms on tubers of 103 Dutch potato samples, compared with microscopic examination. ELISA was a good complementary test, with sensitivity for detecting sporosori comparable to that achieved with real-time PCR. One of their conclusions was that some photographs in Dutch disease guides and on posters probably did not show the effect of *Sss* but showed symptoms caused by *Streptomyces* spp. Qu et al. (2006)

tested six 'asymptomatic' tuber samples originating from Ireland and the USA using PCR and all tested positive for *Sss*. As mentioned above, there is no information about the epidemiological importance of symptomless but infected seed tubers.

A novel method was proposed by Merz (2000) to examine samples of 20–30 tubers for the presence of *Sss*. The tubers were placed in a kitchen peeling machine operated for a few seconds, and subsamples of the washing water were tested for *Sss* by ELISA. In an experiment, the detection limit was two tubers with one lesion each in a sample including 18 healthy tubers. Once standardized, such a system could be useful where high-throughput sample testing is required.

Seed Tuber Treatments

No chemical with the efficacy equivalent to mercury-containing compounds has been found since these products were banned as seed tuber treatments in the 1980s. A promising chemical for this purpose is fluazinam, which gave best but not total control when applied to infected seed tubers 1 day before planting into uncontaminated soil (Falloon et al. 1996). New Zealand was first to register fluazinam for tuber treatment against *Sss*, although this use has since been withdrawn because of phytotoxicity problems. In Switzerland the chemical failed in field trials to reduce powdery scab and was not promoted further (E. Hess, Syngenta Agro, Switzerland, personal communication). The trial fields may have been heavily contaminated with *Sss*. De Boer (2000a) applied fluazinam to seed tubers and planted them into soil with a history of powdery scab, but found no effect on powdery scab incidence or severity in progeny tubers. Flusulfamide (1–2 g a.i. in 2 l water per Mg seed tubers, as Nebijin™, Mitsui Chemicals, Tokyo, Japan), a fungicide with a control spectrum similar to that of fluazinam, is also registered in New Zealand for seed tuber treatment against powdery scab (Falloon 2008). Both chemicals were originally introduced in Japan for control of clubroot. The application of zinc oxide to seed tubers was a common practice in Scotland and is effective when the disease pressure is low (Wale 2000b). The same chemical had no effect on disease incidence in the trials of Falloon et al. (1996). Several other chemicals are reported to reduce transmission of the disease to some extent (Falloon 2008). An alternative method has been successfully tested by Afek and Orenstein (2002). Steam produced by a diesel-powered steamer was applied to tubers for 10 s, through a nozzle system fitted to a conveyor belt. The treatment had the same control effect on the progeny as organic mercury. As seed tuber treatments are rarely completely effective for powdery scab control (Falloon 2008), they are only likely to be economically justifiable where tuber infection levels are not more than moderate, and where the soil is not infested with *Sss*.

Disease Spread Through Contaminated Manure

Pethybridge (1911) reported a crop badly affected by powdery scab when clean seed was planted into soil treated with manure of pigs fed with unboiled, infected potatoes. He suggested that the manure obtained from pigs fed with diseased potatoes could be a source of infection. Recent experiments (U. Merz, A. Keiser, P.-Y. Jaquiéry and T. Oberhänsli, unpublished data) with goat and cow manure

indicated that *Sss* resting spores can survive digestion and are still infective. Thus, the common practice of feeding ruminants with powdery scab infected tubers removed by grading operations, then spreading animal effluent on fields, is likely to widely disseminate *Sss* inoculum to effluent-treated areas.

Soil Inoculum Detection and Quantification

There is urgent need for tools to rapidly and reliably detect and quantify soil inoculum of *Sss*. Soil detection is an essential requirement for progress in epidemiological studies and for developing disease risk assessment as part of effective powdery scab management.

Several different approaches have been made. A bioassay with tomato bait plants in nutrient solution, introduced by Merz (1989b) and modified later, allowed detection down to 100 sporosori/g soil (Walsh et al. 1996). To reduce labour and avoid the need for expertise in recognizing zoosporangia in the bait plant roots, an ELISA was developed using a polyclonal antiserum with the same detection limit of 100 sporosori/g soil (Walsh et al. 1996). Discrimination with ELISA was better for concentrations > 2,000 sporosori/g soil, whereas the bioassay showed better discrimination at lower inoculum levels. This difference can be explained by the opportunity for the pathogen to multiply in the bait plant roots. An improvement in specificity with less background signal was achieved with a monoclonal antiserum against *Sss* sporosori (Merz et al. 2005b). This is now routinely used for semi-quantitative soil inoculum assessment in Switzerland.

The development of oligonucleotide sequences as specific primers for *Sss* was a further progression for increasing the sensitivity of soil detection of the pathogen compared with immunology. Bell et al. (1999) detected as few as one to ten sporosori/g soil applying an adapted DNA extraction method. The biggest problem to overcome was with humic acids which interfered with the PCR. The same sensitivity results were obtained by van de Graaf et al. (2003) with a similar extraction method but a different set of primers and quantitative PCR. Qu et al. (2006) designed their own *Sss* primers and were able to amplify a product from one sporosorus/g soil after a special purification of their DNA extracts. In a preliminary survey of naturally infested soil samples, they could estimate sporosorus concentrations with a competitive PCR assay by comparing the data with a standard curve generated from soil samples inoculated with known numbers of sporosori.

In contrast to ELISA and PCR, the bioassay of Merz (1989b) detects living and virulent resting spores of *Sss*. Thus, a bioassay with PCR (preferably quantitative) for detection of root infection (Bouchek-Mechiche et al. 2000; Nakayama et al. 2007) could be the optimal approach for detection of viable pathogen inoculum.

Soil Inoculum and Disease Risk

Several attempts have been made to find relationships between soil inoculum and tuber infection, to allow development of disease risk assessment. Nakayama et al. (2007) used competitive PCR to quantify *Sss* in soil and roots of tomato bait plants. They found a poor relationship when they compared tuber infection with contamination of soil samples taken from the same field. Prediction was impossible

with low contamination levels; only fields with high levels of sporosorus contamination (≥ 100 sporosori/g soil) gave high tuber infection grades. Infection potential derived from the roots of tomato plants after baiting soil samples was a more reliable predictor of later tuber infection. A positive correlation was obtained between the infection potential and tuber attack. Van de Graaf et al. (2005, 2007) studied the effect of soil inoculum level on disease occurrence on tubers and roots in pot experiments. No differences were detected among the inoculum concentrations tested (5, 15 and 50 sporosori/g soil), as each concentration gave similar tuber and root infection severity. These results can be explained by the likely release of large numbers of secondary zoospores from zoosporangia in infected roots during growth of host plants (several months), giving large multiplication of infection units. Qu et al. (2006) quantified sporosori in a range of field soils and found some indication for a correlation between initial inoculum and the subsequent powdery scab incidence. They estimated > 10,000 sporosori/g in the soil where the highest disease incidence was found. In contrast to this high number, the estimated sporosorus density of the four fields with the highest crop disease incidence tested by Nakayama et al. (2007) varied from 0.1 to 105 per gram of soil. Merz (1993) compared root infection in a bioassay, baiting a series of inoculated soils together with naturally infested field soils, and concluded that a highly infested field soil contains > 500 sporosori/g. These data show that it will be difficult to determine a single reliable threshold for soils with high risk, let alone to define several values for different risk levels. Many other factors, particularly those in the soil environment, are likely to have greater influence on powdery scab development than initial soil inoculum.

Planting healthy seed into contaminated soil did not prevent tuber infection (Merz et al. 2005a) when the environmental conditions were favourable. Soil samples taken at planting and harvest time at the same positions in a field and tested with ELISA gave an increasingly positive result during the season. Even at positions where the ELISA tests gave negative or slightly positive results, tuber infection levels were often high, and these results are similar to those of Nakayama et al. (2007). Variation of the ELISA data derived from 96 soil samples evenly distributed over the field (0.5 ha; grid mesh size 10 m × 5 m) confirmed other reports that soil contamination is unevenly distributed. Thus, the method of soil sampling across a field needs careful consideration if soil contamination is to be accurately determined. In Switzerland, the routinely used sampling procedure now used is to take ten soil samples of about 100 g each along each diagonal of a field and test the samples separately for *Sss* inoculum (Merz et al. 2006).

Treatments of Contaminated Soil

In cases where potatoes must be grown in contaminated soil, it may be economically justifiable to apply chemicals for powdery scab control. An example would be for seed tuber production of a high-value cultivar. A more environmentally safe treatment would be the use of biofumigation, and there may be potential for biocontrol of the disease.

Chemicals

Similar to their effectiveness in seed disinfection, fluazinam and flusulfamide have been shown to be effective in reducing powdery scab in infested soil, and these chemicals are registered in New Zealand for this purpose (Falloon 2008). The recommendation for fluazinam is to apply 2 kg a.i. in 500 l water/ha (Gem®, 50% SC, Agronica, New Zealand) to cultivated ground before planting and to incorporate the chemical into the soil to a depth of 15 cm using a rotary hoe (Anonymous 2007). In the UK there is a specific off-label approval for the use of fluazinam (Shirlan®) as soil treatment in seed production with a maximum dose of 3 l/ha (Hilton et al. 2007). For flusulfamide, the recommendation is to similarly apply the chemical at 0.9–1.8 kg a.i. in 300–400 l water/ha (Nebijin® 5 SC; Young 2008). Recently, the fungicide cyazofamid, used to control late blight (*Phytophthora infestans*), proved to be particularly effective to control *Sss* on roots and tubers (Thomson et al. 2006). The soil application of stable bleaching powder reduced powdery scab incidence and severity in field trials conducted in the seed-producing region of Kaghan Valley of Pakistan (Hamidullah et al. 2002). Greater disease reduction was achieved when the seed tubers were also treated with a boric acid solution. Boron (as sodium tetraborate) can also reduce root infection of tomato plants, when applied to nutrient solution, or galling of potato plants in pot experiments at rates below phytotoxicity (Falloon et al. 2001). Nevertheless, soil application of chemicals to control powdery scab is likely to be very costly, and may be environmentally unacceptable, and in any case is unlikely to give complete control of the disease (Falloon et al. 1996).

Soil Organic Amendments

Brassica crops as green manures have been shown to reduce soilborne pathogens, an effect attributed to the production of volatile sulfur compounds toxic to soil microbes. The possibility of controlling powdery scab with *Brassica* crops was originally suggested by Winter and Winiger (1983). Falloon et al. (1999) reported a field trial where different 'cover crops' were grown in soil heavily infested with *Sss*. They recorded trends for reduced powdery scab infection in subsequently planted potatoes after 3 years of wheat and especially *Brassica* crops, but not after 3 years of ryegrass/clover pasture. In an on-farm biofumigation field trial, Indian mustard, rapeseed and canola reduced powdery scab in the subsequent potato crop by 15–40% (Larkin and Griffin 2007), with Indian mustard as the most effective biofumigation crop.

Biological Control

Nielsen and Larsen (2004) have shown in glasshouse pot experiments that *Trichoderma harzinum* based commercial biocontrol products reduced tomato plant root infections by *Sss* when the products were mixed with sporosori in soil. This suggests there is potential for these agents to be used for powdery scab control, possibly as seed tuber treatments.

Host Resistance

The availability of resistant potato cultivars with other characteristics required for commercial acceptability is essential for long-term and efficient control of powdery scab. Screening for resistance to the disease, commonly conducted in field trials with naturally infested soils, has invariably shown that there are substantial differences in susceptibility to tuber infection between the cultivars and lines tested (Torres et al. 1995; Fornier 1997; Lees 2000; Gans and Vaughan 2000; Bus 2000; Iftikhar 2001; Schwärzel 2002; Falloon et al. 2003; Genet et al. 2007). As *Sss* also attacks potato roots and stolons, and sporosori produced in root galls contribute to a large part of the soil inoculum, susceptibility to root infection should be assessed as well. Cultivars with low tuber susceptibility but high root susceptibility are likely to be a particular risk factor in potato production (Schwärzel 2002), because they will maintain and increase *Sss* inoculum levels in fields.

Several different standard keys have been developed to assist assessment of powdery scab severity on potato tubers. To produce reliable and comparable screening data representing the resistance level of a cultivar, it was agreed and highly recommended at the First European Powdery Scab Workshop to use a standardized visual severity scoring scale (Gans 2000; http://www.spongospora.ethz.ch/LaFretaz/scoringtable.htm), similar to that developed by Falloon et al. (1995). A root gall severity scoring scale has also been proposed (http://www.spongospora.ethz.ch/LaFretaz/scoringtablegalls.htm).

Powdery scab has not been considered in potato breeding programmes until relatively recently. Plant breeders in New Zealand released their first powdery scab resistant cultivar (Gladiator) in 1995 from an ongoing programme (Genet et al. 1995). This cultivar results from a cross between breeding lines, one with resistance to *Potato virus X*, *Phytophthora infestans*, *Globodera rostochiensis* and *Streptomyces scabies* and the other with cyst nematode resistance derived from the wild tuber-bearing *Solanum vernei*. Since then, cv. Gladiator has performed well in field trials at different international locations (Iftikhar 2001; Schwärzel 2002). Falloon et al. (2003) suggest that the resistance in potato to powdery scab is of the quantitative type, because the spectrum of resistance across a large number of cultivars is a continuum from highly resistant to highly susceptible. Torres et al. (1995) screened numerous potato accessions over 6 years at different locations in Peru. Some of them were recorded as resistant over years and in different locations, while others were recorded as both resistant and susceptible. A possible explanation was the existence of *Sss* pathotypes. This again emphasizes the need for better understanding of the genetic nature of the pathogen, as successful disease resistance breeding relies on detailed knowledge of the genetic background of pathogen populations.

Field trials are costly, laborious and time-consuming. Even more important, their success (establishment of infection) depends heavily on cool, damp soil conditions during the first half of the cultivation period. To reduce the need for extended field evaluations, Merz et al. (2004) proposed a laboratory-based micro-bioassay with the potential to screen and select for resistant material at an early stage in breeding programmes. Experiments have shown that resistant cultivars have fewer zoosporangia in their roots than susceptible ones, confirming the more detailed results of pot experiments reported by Falloon et al. (2003). They assessed zoosporangial root

infection and root galling of potato cultivars with a *Sss* susceptibility range from low to high, and found a generally strong relationship between numbers of zoosporangia in roots and numbers of galls on root systems as well as between tuber field resistance and zoosporangial root infection. They concluded that glasshouse evaluation of relative susceptibility of cultivars to *Sss* generally indicated the field response to powdery scab.

Conclusions and Outlook

The soilborne pathogen *Sss* is an efficient plant pathogen, with its ability to produce very large numbers of infection units which can remain dormant for long periods (up to many years) until a suitable host is planted. The three-layered resting spore wall of *Sss* gives the pathogen resistance to stress factors, and makes direct control of powdery scab very difficult. The disease is transmitted on seed tubers wherever infested seed tubers are transported. We have to accept that there is no single completely effective control method available for the disease. Even cultivars classified as very resistant to powdery scab show low levels of infection on roots and tubers (Falloon et al. 2003). Therefore, the best approach to powdery scab control is to incorporate several components into an integrated disease management strategy (de Boer 2002b). These components include:

- *Avoidance and field choice.* Seed tubers should be free of powdery scab to prevent infestation of virgin soils. This requires implementation of effective and internationally standardized certification rules. Contaminated soils or compacted soils with reduced drainage should be avoided. This is especially important for crops producing basic (high-quality) seed potatoes.
- *Treatments of seed tubers and soil*. In those cases where the use of infected seed or contaminated soil is inevitable, chemicals, biofumigation, trap crops or biocontrol may help to reduce the initial inoculum.
- *Crop management practices.* Several measures reduce disease risk. The most important are appropriate irrigation regimes, soil preparation and planting time, crop rotation, control of weed and volunteer potato plants, and appropriate hygiene practices, e.g., disinfection of grading areas and not feeding infected potatoes to cattle.
- *Cultivar resistance.* The availability and choice of resistant cultivars with good quality is crucial. Many of the cultivars recently introduced are susceptible or moderately susceptible to *Sss* (Merz et al. 2006; Prentice et al. 2007).

Although substantial knowledge has been gained of the powdery scab pathogen and its relationship to hosts, and tools have been developed for the implementation of integrated disease management strategies, there are still many gaps in current knowledge of this disease and the causative pathogen. Future research should focus on epidemiology and population genetics of the pathogen. International potato breeders need to either adopt powdery scab resistance as an important goal or enhance efforts to develop resistant cultivars. Potato growers should accept that effective powdery scab control is likely to be a long-term goal, and their advisers must give them as much relevant information as is available. Concepts of integrated

strategies have been introduced (Burgess and Wale 1994; Genet at al. 2005; Merz et al. 2006; Falloon 2008). A comprehensive and useful guide for farmers is disseminated by the British Potato Council (Prentice et al. 2007).

When all stakeholders involved in the potato business become aware that solution of powdery scab problems is likely to be a long-term goal, when a range of resistant cultivars are available and when powdery scab risk can be accurately predicted for seed tuber lines and for fields, then the mission to find effective control of this important disease will become accomplishable.

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