Am. J. Pot Res (2008) 85:253–260
DOI 10.1007/s12230-008-9022-6

SYMPOSIUM PAPER

Control of Powdery Scab of Potato: Towards Integrated Disease Management

Richard E. Falloon

Published online: 25 April 2008

Abstract Powdery scab of potato, caused by the plasmodiophorid pathogen *Spongospora subterranea* f. sp. *subterranea*, is an increasingly important disease where potatoes are grown in cool/temperate regions. Powdery scab lesions on tubers downgrade their quality as seed, fresh vegetable or processing potatoes, and the disease can severely harm crop productivity. Aspects of the biology of *S. subterranea*, including long-term persistence in soil, high and rapid reproductive potential, and, possibly, ability to infect alternative hosts, pose considerable problems for development of effective control of powdery scab. Methods shown to reduce the incidence and severity of the disease are reviewed. These include field choice and crop rotation, pathogen detection, use of resistant cultivars, planting disease- and pathogen-free seed tubers, appropriate pesticide treatments for seed tubers and/or infested soil, adjustment of soil nutrient status, and use of suitable management practices during crop growth. No single method is likely to give complete control of powdery scab, particularly where *S. subterranea* inoculum levels are high on seed tubers or in soil. Effective disease management will therefore depend on implementation of several appropriate methods, using an integrated approach to powdery scab control. This requires understanding of the biology of *S. subterranea*, and comprehensive and conscientious adherence to appropriate disease control methods during most stages of the potato crop management cycle.

R. E. Falloon (✉)
New Zealand Institute for Crop & Food Research Limited,
Private Bag 4704,
Christchurch, New Zealand
e-mail: falloonr@crop.cri.nz

Keywords Crop rotation · Pathogen detection · Chemical control

Introduction

Powdery scab is an important disease of potatoes in many of the world's cool/temperate regions. This disease has increased in importance as the use of seed tuber pesticide treatments with broad spectrum activity has been discontinued, potato production has intensified, rotation intervals between potato crops have decreased, and irrigation has become increasingly used in potato production. Powdery scab is regarded as the primary problem facing potato production in many areas where intensive potato cropping is carried out. This disease is caused by the plasmodiophorid pathogen *Spongospora subterranea* f. sp. *subterranea*. The life cycle of this organism, as currently understood, has been outlined elsewhere (Harrison et al. 1997; Merz 2008). This pathogen thrives and powdery scab becomes severe particularly when cool, damp, soil conditions prevail.

Infection of potato tubers by *S. subterranea* results in development of surface lesions, which are the most obvious manifestation of the disease. These lesions drastically reduce tuber quality, particularly where potatoes are washed in preparation for supermarket sale. Lesions on tubers of processing potatoes are also undesirable because they require extra skin removal operations. Severely infected potatoes shrink and lose weight while in storage and may become rotten, because of respiration losses and/or ingress of tuber rotting micro-organisms through powdery scab lesions. Seed potatoes with powdery scab are commercially unacceptable for establishment of new crops because the disease can be transmitted on infected and infested seed potatoes, and seed certification systems usually include low tolerance levels for powdery scab incidence. Beside adverse effects on potato quality, recent research (Falloon et al. 2004; Lister et al. 2004) has indicated that infection of potato plants by *S. subterranea* reduces host growth through adverse effects on root function, and these effects are probably responsible for observed reductions in tuber yields where powdery scab is severe (Falloon et al. 1996). The pathogen is also important as the vector of potato mop-top virus, which causes "spraing", a significant production-limiting disease particularly in cool climatic zones (Jones and Harrison 1969). The reviews of Karling (1968) and Harrison et al. (1997) summarise knowledge on powdery scab and *S. subterranea* f. sp. *subterranea*.

Like many soilborne diseases, powdery scab of potato is difficult to control. This paper considers characteristics of *S. subterranea* that pose problems for growers attempting to produce high quality potatoes. A number of methods have been tested for control of the disease, and have been shown to be effective for reducing incidence and/or severity of powdery scab in potato crops. This paper reviews these methods, as they could be used by growers throughout the stages of potato crop management. Relationships of powdery scab control strategies to the biology of S. *subterranea* are also discussed.

Spongospora subterranea Biology

Spongospora subterranea is a plasmodiophorid (protozoan) plant pathogen. Organisms in this group are characterized by production of resting spores and zoospores. In *S. subterranea*, the resting spores are produced in sporosori (spore balls) in root and stolon (including tuber) tissues of host plants. Sporosori are conglomerations of individual resting spores. Although the life cycle of this organism is not completely defined, some generalizations can be deduced from morphological and pathological observations (Harrison et al. 1997).

Sporosori are released into the soil when roots decay, or are transmitted on infected or infested seed potatoes when they are planted. Resting spores release motile primary zoospores, and these encyst on the surfaces of host roots or stolons and infect epidermis cells of those tissues. The pathogen then enters a secondary cycle. Each successful infection by a zoospore develops as a plasmodium within a root or stolon epidermis cell, and then into a zoosporangium. Each zoosporangium produces several to many secondary zoospores, which are released from host cells, and each zoospore can infect a healthy host cell. This secondary cycle is likely to be repeated many times if conditions for host growth and zoospore production and infection are favourable. Heavily infected plants have roots and stolons that contain very many zoosporangia (>140 zoosporangia/mm^2 of root surface; Falloon et al. 2003), and root hairs can be very heavily infected with zoosporangia, so the secondary cycles of zoospore production, release and infection are likely to result in very substantial multiplication of the pathogen.

As host plants age, infected roots and stolons develop small galls (up to 3 mm diameter), which are initially creamy white but then mature to be dark brown. Similarly, infected tubers develop surface galls and blister-like lesions, which mature into typical powdery scab lesions. Mature root and stolon galls and tuber lesions each contain very many sporosori, which may be the result of sexual reproductive processes. Sporosori and resting spores are capable of long-term survival (several to many years) in soil.

Spongospora subterranea can infect a range of plants besides potato (Würzer 1964; Janke 1965; Andersen et al. 2002; Iftikhar and Ahmad 2005). Some of these, particularly other solanaceous plants, are common weeds in cropping fields where potatoes are grown. Reports of *S. subterranea* on other hosts have been observational, and cross inoculation studies, both from potato to alternative hosts and vice versa, have not been reported. Nevertheless, it is likely that alternative hosts provide means by which the pathogen can survive, and possibly multiply, during periods when potatoes are not grown.

Control Strategies for Powdery Scab

Strategies tested and advocated for control of powdery scab have concentrated on the resting spore stage of the pathogen cycle and on preventing zoospore infection of host root and stolon (tuber) tissues. These methods are likely to break the pathogen cycle at either or both of these stages. Methods for powdery scab control are considered here as they might be applied chronologically by a grower producing potatoes, from well before planting, through crop establishment and growth, to harvest and handling of product.

Crop Rotation and Field Choice

Spongospora subterranea is capable of surviving in soil for long periods (up to many years). A recent severe outbreak of powdery scab in New Zealand occurred in a field where potatoes had not been grown for 12 years, and anecdotal evidence in Scotland suggested that the pathogen survived in an area where heavily infected potatoes had been stored over 50 years previously but where potatoes had not been planted since. The pathogen survives in soil as resting spores and also probably through infection cycles on alternative hosts.

Long rotations are recommended between potato crops because these will reduce the likelihood of survival of *S. subterranea* from one potato crop to the next. It is important that interim growing seasons are free of hosts of the pathogen, so care should be taken to ensure that rotation crops are free of volunteer potato plants and weeds (particularly solanaceous species) that are likely to be alternative hosts. The period between potato crops should be at least 5 years, but longer periods are likely to be necessary to ensure that pathogen populations are reduced. Growers of high quality seed potatoes often aim to use fields in which potatoes have never been grown because powdery scab can be so detrimental to the commercial acceptability and economic value of their crops.

Grower observations and limited research suggest that some crop types in rotations may be better than others for reducing *S. subterranea* inoculum in soil. Growers have observed that growing potatoes in infested areas where vegetable brassicas have been grown results in less powdery scab than in areas where the rotation crops have been grass/clover pasture or cereals. Winter and Winiger (1983) reported that previous crops of winter or spring rape and thornapple reduced powdery scab on a subsequent potato crop. A field trial in New Zealand (Falloon et al. 1999) indicated that forage brassica crops in rotations could have the same effect. Limited experimental evidence (Falloon, unpublished data) suggests that soil incorporation of "biofumigant" brassica crops (plants with high tissue levels of glucosinolates) may reduce resting spore inoculum in soil infested by *S. subterranea*.

Beside considering previous cropping history when choosing fields for potato crops, soil type and condition should also be taken into account. Free-draining soils are less likely to encourage powdery scab development than soils with high water retention (see below). Growers have also observed that parts of fields where the soil is compacted by heavy machinery, such as headlands and previously used tracks, and low lying areas to which rainfall drains, can have more severe powdery scab than areas that are less compacted or water-logged. Using fields with free-draining soils and paying attention to efficient and deep cultivation before planting are likely to lessen the risk of powdery scab development.

The mechanisms of reduction in resting spore viability in soil during rotation periods are not adequately understood, but the level of initial soil infestation, as well as abiotic and biotic factors during crop rotations, are all likely to influence the effective period between potato crops that is required to avoid carryover of *S. subterranea* infestation. Increased understanding of these mechanisms would allow growers to use improved intercropping practices to reduce the likelihood of powdery scab outbreaks.

Pathogen Detection

Considerable advances have been made in recent years with detection of *S. subterranea* in soil. Microbiological culturing techniques cannot be used for this organism because it is an obligate biotroph. However, bioassays, antibody methods (Walsh et al. 1996; Merz et al. 2005a), and DNA techniques using polymerase chain reaction technology (Bulman and Marshall 1998; Bell et al. 1999; van der Graaf et al. 2003; Ward et al. 2004) have been used successfully to detect the pathogen on seed tubers and in soil. These methods aim to detect resting spores or sporosori of the pathogen. An immunochromatography system using antibody technology has recently been developed (Agristrip, BIOREBA AG) and shown to be useful for routine detection of resting spores on seed potatoes (Merz et al. 2005b). No method has been developed to the stage where routine assays to detect *S. subterranea* in soil can be carried out, however, because all of the methods so far examined require high levels of technical expertise for their operation and interpretation of results. Nevertheless, it is very likely that these methods, particularly those using antibody or DNA technology, will become increasingly available for practical use by growers.

Pathogen detection methods usually aim to identify *S. subterranea* resting spores (in sporosori) in soil or on contaminated seed potatoes. Effective pathogen detection will give growers tools to help establish the risk of developing powdery scab in particular fields, allowing them to make better-informed decisions on field choice before establishing potato crops. Efficient pathogen detection will also allow infested, possibly symptomless, seed potatoes to be identified, so these can be either rejected before they are used or appropriately treated before planting. This will help to ensure that the disease is not transmitted to new crops or to areas free of infestation.

Pre-Planting Field Management with Soil-Applied Chemicals

Chemicals in soil (soil elements and pesticides) affect expression of powdery scab. These are likely to affect resting spore and zoospore viability and the ability of zoospores to infect host root and stolon tissues. Manipulation of the soil environment in potato fields can be used for powdery scab management.

Soil nutrients Several studies have indicated that adjustment of the soil chemical content can reduce powdery scab expression in crops. Soil applications of sulfur (McCreary 1967) or salts of zinc (Wale 1987) have been shown to reduce the disease in the field. Boron as sodium tetraborate has been shown to reduce *S. subterranea* infection of laboratory- and glasshouse-grown host plants (Falloon et al. 2001). Raising the soil pH using various forms of lime has also been suggested as an approach to powdery scab control, but some reports indicate that these treatments can increase, rather than reduce, powdery scab (see Karling 1968; Harrison et al. 1997). Detailed laboratory studies suggest that *S. subterranea* is able to infect potato plants across a broad range of pHs (Kole 1954; Merz 1989; Falloon et al. 2005), so pH effects on the disease are likely to result from effects on soil chemical reactions rather than directly on the pathogen.

Recent field trials in Australia indicate that soil applications of high nitrogen fertilizers or organic amendments containing volatile fatty acids have promise for reducing powdery scab severity in soils with high levels of *S. subterranea* infestation (de Boer and Crump 2005; N Crump, personal communication). This research indicates that application of these materials has promise as a pre-planting treatment for reducing powdery scab incidence and severity.

Soil-Applied Pesticides A large number of pesticides have been tested as soil applications for controlling powdery scab, and several have been shown to reduce incidence and severity of the disease. Chemicals classified as fungicides, such as mercury- or copper-containing compounds, mancozeb, maneb, and quintozene (see Karling 1968) have been shown to reduce the disease in potatoes grown in infested soil. Recent studies have shown that fluazinam and flusulfamide are effective as soil applications for reducing powdery scab where soil is infested with *S. subterranea* (Falloon et al. 1996), and these chemicals are registered in New Zealand for this purpose. Soil fumigation with methyl bromide, or metam sodium applied in irrigation water (Nachmias and Krikun 1988), and soil-applied formaldehyde (see Karling 1968) have also been shown to reduce the disease.

Soil application of pesticide chemicals for powdery scab control is likely to be expensive, and may not be environmentally acceptable. Furthermore, experimental assessments have shown that most chemical soil treatments do not completely eliminate the disease, particularly where soil infestation levels of *S. subterranea* are high. For example, the most effective soil treatments tested by Falloon et al. (1996) reduced powdery scab incidence in harvested tubers from 90% (untreated soil) to 71%. Nevertheless, where crops are at risk from soilborne inoculum, or where high value crops are being grown (e.g. for seed potato production), pesticide or fumigant application to the soil may be justified either before or during the planting operations. Improved techniques for targeted, low rate, pesticide applications (rather than broadcast treatments), similar to those recently developed for control of clubroot of vegetable brassicas (Donald et al. 2001) could have a place in these situations.

Cultivar Choice

It has long been recognized that different lines of potato germplasm and different potato cultivars react differently to *S. subterranea*. The successful utilization of plant resistance to powdery scab is likely to be a key component of sustainable management of this disease. Growers should obtain information on the reaction to the disease of the cultivars they plan to plant before they establish their crops. If powdery scab is likely to be important, they should use cultivars that are resistant to the disease.

No potato lines have been identified that are immune to infection by *S. subterranea*, so crops of resistant cultivars are likely to support pathogen multiplication and survival, and maintain soil infestation. Furthermore, there is some evidence of pathogenic variation in *S. subterranea* (see Falloon et al. 2003), and the molecular study of Bulman and Marshall (1998) has also demonstrated that the pathogen is variable. This variability suggests that different pathotypes of *S. subterranea* may exist, and that cultivars identified as resistant to powdery scab may become susceptible to different pathotypes. For these reasons, using disease resistance for management of powdery scab is unlikely to provide complete control of the disease, particularly in situations of severe disease pressure.

Mechanisms and Genetics of Resistance Although the mechanisms of resistance are not fully understood, Falloon et al. (2003) demonstrated that resistant cultivars generally have fewer *S. subterranea* zoosporangia in their roots and fewer root galls than susceptible cultivars. This indicates that host resistance is expressed at the sites of zoospore penetration of root and stolon cells. Exceptions were noted, however. One cultivar with a short growth cycle had heavily infected roots but little infection on tubers. Some cultivars (e.g. 'Russet Burbank') are moderately resistant to tuber (stolon) infection, but are known to develop severe galling on their roots. These results suggest that different mechanisms of resistance may operate for roots and stolons (tubers), and for different potato varieties.

The genetics of resistance are likely to be complex becuase the spectrum of resistance across a large number of cultivars is a continuum from highly resistant to highly susceptible (Falloon et al. 2003). This indicates that resistance is of the 'quantitative' type, probably based on the additive effects of several resistance genes, each with relatively small effects (Parlevliet 1989; Bradshaw 1994).

Powdery Scab Resistance Breeding and Cultivar Characterization Potato breeding in New Zealand (Genet et al. 2005) continues to incorporate powdery scab resistance into new breeding lines, and to develop these for release as new cultivars. This programme uses conventional and marker-assisted methods to identify resistance and develop a better understanding of the inheritance of resistance. As well, a long-term project is identifying the reactions to powdery scab of commercially available cultivars. To date, the reactions of 132 cultivars to the disease have been determined in field trials (Genet et al. 2007). These studies will result in new powdery scab-resistant cultivars, but are also providing growers with information that allows them to select cultivars that are less likely to develop the disease. Some examples of cultivars with different reactions to powdery scab are (Genet et al. 2007): very resistant, 'Gladiator', 'Red Rascal', 'Norkotah', Moonlight; moderately resistant, 'Russet Burbank', 'Ranger Russet', 'Nooksac', 'Sebago', 'Dakota Red' and 'Katahdin'; moderately susceptible, 'Atlantic', 'Shepody' and 'Frontier Russet'; and very susceptible, 'Kennebec', 'Rosa', 'Agria' and 'Asterix'.

Pathogen-Free Seed

Crop establishment with pathogen-free seed tubers is highly recommended because it is accepted that *S. subterranea* on seed tubers is the most likely means of transmitting the pathogen to areas previously free of infestation. It is important that seed lines are free both of powdery scab infection and from contamination from resting spore inoculum. Official seed certification schemes have low tolerance for powdery scab infection. Removal of infected tubers from infected lines before certification is likely to allow symptomless carriage of resting spores on tubers, however. Obtaining seed potatoes from reputable sources, stringent implementation of appropriate seed certification standards, and careful pre-planting inspection of seed potatoes will help ensure that potato crops are established with planting material that is free of *S. subterranea* infestation. Recently developed sensitive detection methods (see above) may also be useful for identifying infested seed potato lines.

Seed Tuber Treatments Chemical treatment of seed tubers has been advocated as a method for preventing transmission of powdery scab. In New Zealand, many growers of seed potatoes dip their seed tubers in formaldehyde before planting to kill *S. subterranea* resting spores. A seed tuber dip (5 min) in 0.5% formaldehyde (1.25 l of formalin solution per 100 l water) is commonly used. Tubers treated with formaldehyde should not have active sprouts, and treated tubers should either be dried before storage or planted immediately after treatment because formaldehyde can be very damaging to tuber sprouts and adversely affect plant emergence.

The pesticide flusulfamide has label registration in New Zealand as a seed tuber treatment for control of powdery scab. A number of other seed tuber treatments have been shown to reduce transmission of the disease, including heat, dichlorophen-sodium, mancozeb, propineb, sulfur, and compounds of copper, mercury or zinc (Karling 1968; Braithwaite et al. 1994; Falloon et al. 1996; Harrison et al. 1997).

Seed tuber treatments are rarely completely effective for controlling powdery scab. For example, Falloon et al. (1996) reported that the most effective treatments they tested, when applied to seed tubers infected with powdery scab, reduced incidence of the disease on progeny tubers to 5% compared with 25% from untreated seed tubers.

Post-Planting Crop Management

Cool, damp soil conditions are known to enhance incidence and severity of powdery scab in potato crops. These factors are likely to affect resting spore and zoospore viability and the ability of zoospores to infect host root and stolon tissues. The optimum temperatures for infection are about 12–15°C, and zoospores are likely to require free moisture in the soil for movement to infection sites (see Harrison et al. 1997). Therefore, manipulation of the soil environment in potato fields during crop growth can reduce the likelihood of the disease developing on potato tubers.

Irrigation management Appropriate use of irrigation may lessen the likelihood of powdery scab development (Taylor and Flett 1981; Taylor et al. 1986). Withholding irrigation during the early stages of crop growth, when soils are cool, may reduce the release of zoospores from resting spores and lessen the ability of zoospores to infect host plants.

Planting Date Late planting of crops, to avoid cold soils and reduce the likelihood of infection (Kirkham 1986) may help to ensure that soil temperatures are above optimum for *S. subterranea* infection during the early stages of crop growth. If growers have the choice, planting later in spring will reduce the likelihood of severe powdery scab outbreaks.

Biological Control

Recent research (Neilsen and Larsen 2004) has indicated that biological control agents, particularly *Trichoderma* spp., have potential for reducing activity of *S. subterranea*, presumably through effects on either resting spore viability or zoospore activity and infectivity. The efficacy of practical biological control of powdery scab in the field has yet to be demonstrated, however.

Hygiene

Maintenance of good hygiene in operations relating to harvesting, grading, storage and handling of seed potatoes is generally recommended as an approach to reducing the likelihood of transmitting *S. subterranea*. Harvesting seed potato crops in conditions (dry soil) that minimize soil contamination may help to reduce transmission of the pathogen from infested fields. Removal of contaminating soil and debris on grading equipment and in potato stores and seed tuber containers will remove sporosori and resting spores of the pathogen, reducing the potential for contamination of seed tubers. Routine treatment of grading and storage equipment with appropriate disinfectant chemicals (e.g. products containing formaldehyde, chlorine or hydrogen peroxide) is recommended (R de Boer, personal communication). In Scotland, soil and dust are regularly removed from seed potato stores using commercial vacuum cleaners as part of managing seed tuber-borne pathogens (including *S. subterranean*; S Wale, personal communication).

Integrated Management of Powdery Scab

Like most soilborne pathogens and the diseases they cause, *S. subterranea* and powdery scab are difficult to control. The combination of the pathogen's capacity to survive for very long periods as resting spores, and its potential to multiply as zoospores and resistant resting spores means this disease poses severe threats for potato growers. Increasing intensity of production, where irrigation is used to optimize crop productivity and where increased specialization of production requires short rotation cycles between potato crops, has probably resulted in the increased importance of this disease, and concomitantly an increased need for effective powdery scab management. Another factor that has increased the importance of the disease may be the withdrawal of broad spectrum chemical seed tuber treatments, which were previously widely used and effective for preventing transmission of *S. subterranea*.

None of the control methods available to potato growers alone is likely to give complete control of powdery scab. Research on individual control methods, while demonstrating feasibility for reducing disease levels through effective treatments, almost universally presents results where control is incomplete. Growers must therefore use as many of the individual powdery scab control methods as are practically possible in their potato production operations. Optimum field choice, soil treatment at pre-planting or planting stages, selection of resistant cultivars, seed tuber treatment, post-planting crop management, harvesting strategies and post-harvest hygiene should all be components of overall powdery scab management. Implementation of effective control is particularly important in production of seed potatoes so that the pathogen is not transmitted to vegetable and processing production operations. Using as many of these methods as possible in an integrated powdery scab management strategy (Burgess and Wale 1994) is likely to be the most successful approach to sustainable control of this disease.

Effective and sustainable integrated management of powdery scab will depend on the application of appropriate control methods by growers across the rotation cycles on their farms and throughout the processes involved with individual potato crops. Furthermore, powdery scab control requires integration across the different components of the potato industry, particularly between those involved with production, processing and marketing of seed potatoes and growers of fresh vegetable and processing crops. This integration is increasingly under the control of large potato marketing and processing enterprises, so these organisations will also play important roles in managing powdery scab.

Expanding knowledge of soil factors affecting survival of *S. subterranea* and development of powdery scab, and application of new methods for detecting the pathogen in soil to determine risk from the disease before crop establishment, are likely to provide improvements in control of this disease. Further development of potato cultivars that have high levels of powdery scab resistance, both during vegetative growth (root infection) and tuber development (stolon and tuber infection), is also likely to be a key component for improved powdery scab control. These developments, and their practical application by potato growers, will continue the progress towards effective management of powdery scab, a disease that has increasingly posed problems for intensive potato production.

Acknowledgements This paper has been prepared as part of research funded by the New Zealand Foundation for Research, Science and Technology. Financial assistance for attendance at the 88th Annual Meeting of the Potato Association of America was provided by a grant from the USDA-ARS Potato Program under the leadership of Dr Barbara Christ. Dr Ueli Merz gave helpful suggestions on the manuscript of this paper.

References

Andersen, B.A.B., M. Nicolaisen, and S.L. Nielsen. 2002. Alternative hosts for potato mop-top virus, genus Pomovirus and its vector *Spongospora subterranea* f. sp. *subterranea*. *Potato Research* 45: 37–43.

Bell, K.S., J. Roberts, S. Verrall, D.W. Cullen, N.A. Williams, J.G. Harrison, I.K. Toth, D.E.L. Cooke, J.M. Duncan, and J.R. Claxon. 1999. Detection and quantification of *Spongospora subterranea* f. sp. *subterranea* in soils and on tubers using specific PCR primers. *European Journal of Plant Pathology* 105: 905–915.

Bradshaw, J.E. 1994. Quantitative genetics theory for tetrasomic inheritance. In *Potato genetics*, eds. J. E. Bradshaw, , and G. R. Mackay, 71–99. Wallingford, UK: CAB International.

Braithwaite, M., R.E. Falloon, R.A. Genet, A.R. Wallace, J.D. Fletcher, and W.F. Braam. 1994. Control of powdery scab of potatoes with chemical seed tuber treatments. *New Zealand Journal of Crop and Horticultural Science* 22: 121–128.

Bulman, S.R., and J.W. Marshall. 1998. Detection of *Spongospora subterranea* in potato lesions using the polymerase chain reaction (PCR). *Plant Pathology* 47: 759–766.

Burgess, P.J., and S.J. Wale. 1994. Development of an integrated control strategy for powdery scab of potatoes. Brighton Crop Protection Conf. Pests and Diseases, 1994. Vol 1. British Crop Protection Council, pp. 301–306.

de Boer, R.F., and N.S. Crump. 2005. Powdery scab (*Spongospora subterranea*) of potatoes—research in Australia. Abstracts of papers presented at the 88th Annual Meeting of the Potato Association of America, Scottsbluff, NE, USA, August 8–12, 2005. *American Journal of Potato Research* 82: 64–65.

Donald, E.C., I.J. Porter, and R.A. Lancaster. 2001. Band application of fluazinam (Shirlan) into soil to control clubroot of vegetable brassica crops. *Australian Journal of Experimental Agriculture* 41: 1223–1226.

Falloon, R.E., A.R. Wallace, M. Braithwaite, R.A. Genet, H.M. Nott, J.D. Fletcher, and W.F. Braam. 1996. Assessment of seed tuber, in-furrow and foliar chemical treatments for control of powdery scab (*Spongospora subterranea* f. sp. *subterranea*) of potato. *New Zealand Journal of Crop and Horticultural Science* 24: 341–353.

Falloon, R.E., R.A. Genet, A.R. Wallace, and H.M. Nott. 1999. Integrated management of powdery scab of potato; a 3-year field evaluation of disease resistance, chemical and cultural controls. In *Proceedings of the 1st Australasian Soilborne Diseases Symposium*, ed. R.C. Magarey, 179–181. Brisbane: Bureau of Sugar Experiment Stations.

Falloon, R.E., U. Merz, D. Curtin, and R.C. Butler. 2001. Boron affects *Spongospora subterranea* infection of host roots; laboratory and glasshouse results. In *Proceedings of the 2nd Australasian Soilborne Diseases Symposium*, ed. I.J. Porter et al., 101–102. Lorne, Victoria, 5–8 March 2001.

Falloon, R.E., R.A. Genet, A.R. Wallace, and R.C. Butler. 2003. Susceptibility of potato (*Solanum tuberosum*) cultivars to powdery scab (caused by *Spongospora subterranea* f. sp. *subterranea*), and relationships between tuber and root infection. *Australasian Plant Pathology* 32: 377–385.

Falloon, R.E., D. Curtin, R.A. Lister, and R.C. Butler. 2004. The obligate pathogen *Spongospora subterranea* affects host (*Solanum tuberosum*) root function. In *Proceedings of the 3rd Australasian Soilborne Diseases Symposium*, eds. KM Ophel-Keller and BH Hall, 30–31. Adelaide: South Australian Research and Development Institute.

Falloon, R.E., D. Curtin, R.A. Lister, and R.C. Butler. 2005. Different soil pHs have little effect on *Spongospora subterranea* infection of potato roots. Abstracts of papers presented at the 88th Annual Meeting of the Potato Association of America, Scottsbluff, NE, USA, August 8–12, 2004. *American Journal of Potato Research* 82: 68–69.

Genet, R.A., R.E. Falloon, W.F. Braam, A.R. Wallace, J.M.E. Jacobs, and S.J. Baldwin. 2005. Resistance to powdery scab (*Spongospora subterranea*). Proceedings of the 16th Triennial Conference of the European Association of Potato Research, Bilbao, Spain, July 15–22, 2005, p. 738.

Genet, R.A., W.F. Braam, A.R. Wallace and R.E Falloon. 2007. Susceptibility of potato cultivars and germplasm lines to powdery scab in New Zealand. www.spongospora.ethz.ch/EUWorkshop07/index.htm, Programme with abstracts, Thursday.

Harrison, J.G., R.J. Searle, and N.A. Williams. 1997. Powdery scab disease of potato—a review. *Plant Patholology* 46: 1–25.

Iftikhar, S., and I. Ahmad. 2005. Alternative hosts of *Spongospora subterranea* f. sp. *subterranea*, the causal organism of powdery scab of potato. Abstracts of papers presented at the 88th Annual Meeting of the Potato Association of America, Scottsbluff, NE, USA, August 8–12, 2004. *American Journal of Potato Research* 82: 74–75.

Janke, C. 1965. Untersuchungen über den Wirtspflanzenkreis von *Spongospora subterranea* Wallr. Johns. *Nachrichtenblatt für den Deutschen Pflanzenschutzdienst Berlin* 19: 1–4.

Jones, R.A.C., and B.D. Harrison. 1969. The behaviour of potato mop-top virus in soil, and evidence for its transmission by *Spongospora subterranea* (Wallr.) Lagerh. *Annals of Applied Biology* 63: 1–17.

Karling, J.S. 1968. The Plasmodiophorales, 2nd edition. New York, USA: Hafner Publishing Co. p. 256.

Kirkham, R.P. 1986. Screening for resistance to powdery scab. *Australian Journal of Experimental Agriculture* 26: 245–247.

Kole, A.P. 1954. A contribution to the knowledge of *Spongospora subterranea* (Wallr.) Lagerh., the cause of powdery scab of potatoes. *Tijdschr Plziekt* 60: 1–65.

Lister, R.A., R.E. Falloon, D. Curtin, and R.C. Butler. 2004. *Spongospora subterranea* reduces host (*Solanum tuberosum*) growth. In *Proceedings of the 3rd Australasian Soilborne Diseases Symposium*, eds. KM Ophel-Keller and BH Hall, 135–136. Adelaide: South Australian Research and Development Institute.

McCreary, C.W.R. 1967. The effect of sulphur application to the soil in the control of some tuber diseases. Proceedings of the 4th British Insecticide and Fungicide Conference, pp. 303–308.

Merz, U. 1989. Infectivity, inoculum density and germination of *Spongospora subterranea* resting spores. *Bulletin OEPP* 19: 123–127.

Merz, U. 2008. Powdery scab of potato—occurrence, life cycle and epidemiology. *American Journal of Potato Research* (in press).

Merz, U., J.A. Walsh, K. Bouchek-Mechiche, T. Oberhaensil, and W. Bitterlin. 2005a. Improved immunological detection of Spongospora subterranea. *European Journal of Plant Pathology* 111: 371–379.

Merz, U., P.-Y. Jaquiéry, A. Keiser, T. Oberhaensli, and J.A. Walsh. 2005b. Powdery scab—tools for an integrated control approach. Proceedings of the 16th Triennial Conference of the European Association of Potato Research, Bilbao, Spain, July 15–22, 2005, pp. 129–131.

Nachmias, A., and J. Krikun. 1988. Etiology and control of powdery scab of potato in a semi-arid region of Israel. *Phytoparasitica* 16: 33–38.

Neilsen, S.L., and J. Larsen. 2004. Two *Trichoderma harzianum*-based biological control agents reduce tomato root infection with *Spongospora subterranea* (Wallr.) Lagerh., f. sp. *subterranea*, the vector of potato mop-top virus. *Zeitsch Pflanzenkrankheit Pflanzenschutz* 111: 145–150.

Parlevliet, J.E. 1989. Identification and evaluation of quantitative resistance. In *Plant disease epidemiology. Vol 2. Genetics, resistance and management*, eds. K. J. Leonard, , and W. E. Fry, 215–248. London, UK: McGraw-Hill Publishing.

Taylor, P.A., and S.P. Flett. 1981. Effect of irrigation on powdery scab of potatoes. *Australasian Plant Pathology* 10: 55–56.

Taylor, P.A., S.P. Flett, R.F. de Boer, and D. Marshall. 1986. Effects of irrigation regimes on powdery scab disease and yield of potatoes. *Australian Journal of Experimental Agriculture* 26: 745–750.

van der Graaf, P., A.K. Lees, D.W. Cullen, and J.M. Duncan. 2003. Detection and quantification of *Spongospora subterranea* in soil, water and plant tissue samples using real-time PCR. *European Journal of Plant Pathology* 109: 589–597.

Walsh, J.A., U. Merz, and J.G. Harrison. 1996. Serological detection of spore balls of *Spongospora subterranea* and quantification in soil. *Plant Patholology* 45: 884–895.

Wale, S.J. 1987. Powdery scab—are there any easy solutions? *Potato World* 4: 8–9.

Ward, L.I., P.A. Beales, A.V. Barnes, and C.R. Lane. 2004. A real-time PCR assay based method for routine diagnosis of *Spongospora subterranea* on potato tubers. *Journal of Phytopathology* 152: 633–638.

Winter, W., and F.A. Winiger. 1983. Einfluss verscheidener Fangpflanzen sowie von Kalk und Kalstickstoff auf die Bodenverseuchung mit *Spongospora subterranea*, dem Erreger des Pulverschorfes. *Mitt Schw Landw* 31: 190–206.

Würzer, B. 1964. Ergänzende Untersuchungen über den Pulverschorf der Kartoffel und dessen Erreger *Spongospora subterranea* (Wallr.) Lagerh. Dissertation, Landwirtschaftlichen Hochschule Hohenheim, Band 34, Verlag Ulmer Stuttgart, 104 pp.