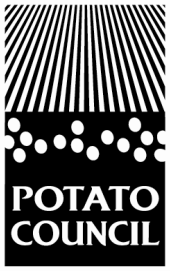

Research Review

Powdery Scab - Strains and Conducive Conditions

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A review of literature and other sources of information

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1 Industry Summary

Powdery scab has become a persistent problem for potato growers since the late 1980's. It has been recorded throughout GB since disease intelligence records began. However, whilst severe powdery scab can occur anywhere in GB, it is not perceived as a major issue in either the processing or table sectors of the ware market. There is a perception in the industry that the disease is more of a problem in northern Britain and that the seed industry is worst affected. Seed quality is critically examined when seed is purchased and powdery scab is high on a list of exclusion priorities for many domestic and export markets. Seed-borne inoculum is a major impediment to opening up new markets or expanding existing markets. The recent discovery that powdery scab may be carried on seed as latent infections adds another dimension to risk of disease development.

However, visually, latently infected or contaminated seed is only one source of inoculum. Recent results from a Potato Council- funded diagnostics project (R253) have indicated that soil-borne inoculum of powdery scab is widespread in GB, being detected by PCR soil diagnostics in 82% of potato fields tested. The longevity of resting spores of powdery scab, sporeballs, together with the increasing problem of groundkeepers, means that avoidance of the pathogen by long rotations is not effective. Soil testing is the only way in which soil contamination can be confidently predicted.

Life Cycle

In brief, the life-cycle of the pathogen (*Spongospora subterranea f. sp subterranea*) starts from germination of spores within a sporeball. This may occur in response to exudates from a susceptible host. The spores each release a swimming spore (primary zoospore) which swims in free moisture in the soil matrix to the host. If the swimming spore reaches the root, it infects the root hair or outer layer of roots and multiplies within the root cell, subsequently releasing further swimming spores (secondary zoospores). If favourable conditions exist, this multiplication may occur several times before tubers are formed. In this way inoculum can build up rapidly from low levels to high levels. Both primary and secondary swimming spores are able to infect tubers through unsuberised lenticels and develop into powdery scab lesions which contain sporeballs. If infection occurs through tuber eyes, secondary growth of the tuber may be stimulated and this secondary growth also infected to produce powdery scab lesions. Sometimes, infection of roots, stems or stolons leads to galls which also produce sporeballs. The period at tuber initiation is the most susceptible period for infection, although later infection is possible possibly as a result of lenticel proliferation in mature tubers or a delay in suberisation in lenticels due to low oxygen levels in wet soils.

Inoculum

Inoculum of powdery scab is the either the sporeball (an aggregation of thick-walled, tough, resting spores, comprising an average of 700 spores) or the swimming spore (zoospore) that each spore of the sporeball releases. Sporeballs of powdery scab have been shown to persist for long periods. Exactly, how long they can survive has not been fully determined, but experimentally and anecdotally, it is much longer than a typical rotation. In a Potato Council- funded project, sporeball survival over a few years was found to be much greater in cooler conditions (4^oC compared to 20^oC). The presence of volunteers in a field will prolong the duration of soil contamination.

Inoculum may be seed-borne or soil-borne and whatever the source sporeballs are able to cause infection and disease. Seed tubers may carry sporeballs within powdery scab lesions or may carry sporeballs symptomlessly where they have been picked up from adjacent infected tubers or contaminated machinery (e.g. on grading lines). In addition, recently, it has been found that tubers may be latently infected. That is where tubers are infected but symptoms are not expressed. Latent infections may be associated with conditions that are unfavourable for disease development, such as sub-optimal temperatures. In a recent Potato Council- funded project, 45% of 124 seed stocks sampled were found to have some level of latent infection.

The relative importance of seed- and soil-borne inoculum is not understood. In addition, there is no simple or clear relationship between level of inoculum and the incidence or severity of disease. Two studies have found a relationship between the level of infection on the roots and tuber disease severity but root infection is very difficult to measure visually. Thus it is concluded that the quantity of inoculum (i.e. sporeballs) play a minor role in determining the amount of disease that develops since, under favourable conditions, low levels of sporeballs can give rise to a high numbers of zoospores. The level of inoculum is only of real importance where conditions for infection are unfavourable. In this situation, disease may occur because of high number of sporeballs causing infection despite less than favourable conditions. In summary, powdery scab development is largely controlled by the occurrence of favourable conditions for the pathogen.

Only recently has it been possible to quantify inoculum accurately on seed or in soil. In a recent study, using a real-time PCR diagnostic test, of 122 soils tested, the highest concentration detected was 148 sporeballs/g soil. Whilst the methodology is different, researchers in other countries have found maximum inoculum levels of 105 sporeballs /g (Japan) and over 500 sporeballs /g (Switzerland).

Conducive Conditions

Soil Moisture

A high soil moisture content both encourages swimming spore release and facilitates movement to the host. It is generally accepted that swimming spores are unable to move through the soil without free water within the soil matrix (i.e. soil saturation). Many studies confirm the importance of free water in soil as a requirement for infection. The occurrence of wet soil conditions prior to tuber initiation, enabling inoculum multiplication, has been cited as important for high levels of powdery scab. Alternatively, prolonged wet soil conditions after tuber initiation can lead to high levels.

In experiments investigating soil moisture, there is disagreement over the importance of constant versus fluctuating soil moisture conditions in powdery scab development. However, it is difficult to make clear comparisons because soil moisture levels have not always been measured and factors that may affect disease development (e.g. soil type, initial inoculum level) will have differed from experiment to experiment. Some studies have shown that constant high soil moisture has suppressed powdery scab development possibly due to low oxygen/high carbon dioxide levels rendering swimming spores inactive.

Temperature

The relationships between temperature and infection are much better understood than soil water relationships. The release of swimming spores is more rapid at warmer temperatures (15-25^{o}C) compared to cooler temperatures (3-10^{o}C) and root infection is very limited at low temperatures. Thus, at 9^{o}C infection is more limited than at 12^{o}C or 17^{o}C. The optimum temperature for root galling is around 17^{o}C. In contrast, the optimum temperature for tuber infection is around 12^{o}C.

Around this optimum, infection can occur from around 9°C to 17°C. Outside this range the extent of tuber infection has proved very limited.

Weather and Powdery Scab

It is clear from the studies on soil moisture and temperature summarised above that powdery scab is favoured by cool, wet conditions. In the UK, these occur in the north and west of the country predominantly. The occurrence and significance of powdery scab in the UK reported by industry confirms that northern Britain is most at risk, although in cool wet springs powdery scab can occur anywhere in the GB. In the British Potato Council Reference Crop project, funded between 1998 and 2000, the same stocks were planted in four locations and trials were carried out with and without irrigation. Seed infected with powdery scab (assessed visually) was planted in all three years. Whilst soil inoculum was not measured, in the two extreme sites (Cambridge and Dundee), tuber initiation temperatures at the two sites were c. 17.6°C and 14.2°C respectively. At Cambridge, very little powdery scab developed even in the irrigated plots. In the two years when rainfall was low at both sites at tuber initiation, high levels of powdery scab developed in the irrigated plots at Dundee. This suggests the lower temperatures at tuber initiation at Dundee were more conducive to infection.

Soil pH

Despite a reasonable number of studies, there is little evidence to suggest *S. subterranea* infection is influenced by pH within the normal range found in arable soils. In other countries, lowered pH associated with the addition of sulphur has reduced powdery scab (although the high levels of sulphur applied may have affected the pathogen) and increasing pH by use of lime or nitrochalk has indicated that the risk of powdery scab is increased (although the use of lime prior to planting a potato crop will affect incidence of common scab).

Soil Type

There is no clear evidence that powdery scab development is influenced by soil type. However, anecdotally and supported by some studies, lighter sandy soils are often reported to have the worst infection. There is no evidence of 'suppressive' or 'conducive' soil types although development of powdery scab in clay soils (e.g. in Essex) has been limited despite infected seed of susceptible varieties being planted. There is some evidence that powdery scab development in soils with high levels of zinc may be less.

Host Resistance

Trials have clearly demonstrated that changing from a susceptible variety to a more resistant one gives the most consistent reduction in incidence and severity of powdery scab in tubers of all control measures available. However, in GB, 75% of all varieties grown are susceptible or moderately susceptible to powdery scab. Published resistance ratings refer to tuber resistance but infection of roots and development of galls on roots, stems and stolons may still occur. Thus, whilst growing a (tuber) resistant variety will probably result in a lower incidence and severity of powdery scab on harvested tubers, effect on soil inoculum is not known. With some varieties, the occurrence of root galls may increase the level of soil inoculum. There are no published ratings on relative susceptibility in roots and it has been established that there is no correlation between root and tuber infection.

Some breeding programmes have identified sources of resistance to powdery scab. However, the lack of progress in breeding for powdery scab resistance is due to preferential selection of other traits by breeders or the potato industry.

Strains of Powdery Scab

In pathogens similar to *Spongospora subterranea*, such as *Plasmodiophora brassicae* (the causal agent of clubroot in brassicas) genetic strains and pathotypes (races) have been described. This has implications for breeding durable resistance to clubroot, where varieties are bred against specific pathotypes. No such pathotypes have been determined for *S. subterranea* (although some contend that they exist). For example, in a European wide study carried out over four years, relative resistance of a range of varieties proved consistent, suggesting in Europe at least a relatively uniform population of *S. subterranea* exists. Studies of genetic variation around the world by examining part of the DNA of *S. subterranea* have identified two 'ribotypes', types I and II. Work at SCRI has shown that powdery scab found in the European trial were all type II. This is in contrast to other researchers who contend that types I & II are associated with particular varieties in GB. Subsequent work by SCRI has demonstrated that whilst both types occur in GB (II is dominant) the type developing on a variety is simply related to the type occurring in that field.

If different pathotypes are found to exist within the powdery scab population, control would be even more difficult than at present. Firstly, variety resistance would differ depending on the predominant pathotype within a field and the resistance rating could not be relied on. The occurrence of different pathotypes would have affect the control measures applied. Assuming the pathotype were known, the degree of risk could be determined and greater (or less) effort would be required on control measures.

Resistance to powdery scab is probably conferred by mixtures of pathotype-specific genes along with combinations of several minor genes and this combination of different types of resistance genes may make determination of pathotypes difficult, if they exist. Variation in *S. subterranea* has not yet been evaluated and as a result any links between variation and pathotypes have not been defined. A substantial amount of technically complicated study would be required to investigate variation of the pathogen but this would have benefits in breeding resistant varieties for the future.

Practical Steps for Current Production Methodology

Of the three sectors of production in the UK, table, processing and seed the greatest efforts to control powdery scab are required by the latter. Powdery scab can cause losses in the table and processing sectors but industry feedback suggests it is of a much lower priority than other diseases, pests or disorders. Nonetheless, the table and processing sectors need to be aware of risks within general production guidelines and reduce risks wherever possible. On the other hand, the seed sector, particularly in northern and western areas of the UK must pay greater attention to the disease since it can have a much greater impact. There are few differences in the measures that apply to each sector for control of powdery scab. However, there is a Specific Off-Label Approval for a soil fungicide treatment that is available for seed only crops.

Inoculum - assess level of powdery scab on seed and in soil

Identify if powdery scab is present on seed. This is achieved by visually examining a random sample of seed tubers. If powdery scab is present in a stock, tubers with low levels of infection will normally be found in a representative sample. If any powdery scab is observed, it is highly likely that symptomless tubers will be carrying sporeballs.

Determining whether soil contamination is present in a field is less easy. Knowledge of previous history of potato production in a field may help to determine whether soil is contaminated but this will depend on records being kept of disease occurrence in previous crops. But other factors should be borne in mind. These include:

- If soil conditions were unfavourable for infection when the last crop was grown, the crop may have escaped disease
- Some resistant varieties may develop root galls but not show tuber symptoms. The root galls will release sporeballs into the soil
- Volunteers surviving between crops can increase soil inoculum
- Sporeballs are long-lived and a long rotation is not enough to assume absence
- FYM or slurry from animals fed with infected potatoes can spread sporeballs onto uncontaminated land.

The most reliable way to determine risk from soil contamination is to determine the level of soil contamination. Soil tests to determine whether powdery scab is present in soil and at what level of contamination are in their infancy but now available from some organisations. However, the results of a soil test for powdery scab cannot be used to easily assess the risk of development of the disease since there is no simple relationship between level of soil contamination and powdery scab development on progeny tubers.

Conducive Conditions - reduce the risk of powdery scab developing in your field

The presence of free water in the soil matrix when soil temperatures are 'cool' creates the optimum conditions for infection by *S. subterranea*. Wherever possible these optimum conditions should be avoided.

- Select a free draining field
- Avoid over cultivating soil and creating too fine a tilth which results in slumping as this will increase the risk of prolonged soil saturation
- Avoid soil compaction either when cultivating soil or through vehicles wheels travelling through crops
- Avoid over irrigation leading to soil saturation.

Carry Out Specific Control Measures

Disease avoidance

By assessing the level of inoculum in soil (from knowledge of the field or a soil test) it is possible to select low risk fields or utilise the information to assign varieties with different resistance ratings to fields with different risks of powdery scab.

Where a risk of powdery scab exists and it is practical to do so, later planting may result in disease avoidance as soil temperatures are likely to be higher at tuber initiation.

Utilise variety resistance

Where a risk of powdery scab is identified, plant a moderately resistant or resistant varieties wherever possible.

Consider chemical control

If a soil analysis indicates the soil has greater than 6 mg/kg zinc, the risk of powdery scab is much lower. Where low soil zinc levels exist, applying zinc to soil may provide some limited control of powdery scab. However, trials have shown that this treatment works best where the disease pressure is lower. The maximum amount of zinc that can be applied annually is 15 kg elemental zinc per hectare. Ideally, it should be incorporated into soil before planting.

Following trials at SAC, there was sufficient evidence to show that a soil treatment with fluazinam (Shirlan, Alpha Fluazinam 50SC, Blizzard, Tizca, Volley) prior to planting resulted in a significant reduction of powdery scab, but not complete control. A Specific Off-Label Approval (SOLA) was

obtained for Shirlan as a treatment against soil-borne powdery scab. Subsequently, further SOLA's have been submitted for other fluazinam products. The SOLA permits use at a maximum dose of 3l/ha applied on a tractor mounted downward directed drench in 200 l/ha of water. It should be applied on ridged bed prior to destoning or bed-tilling. Seed-only crops may be treated and, if used, products containing fluazinam should not be applied to the haulm for blight control.

2 Introduction

Information on the Disease

Powdery scab of potato, caused by the plasmodiophorid pathogen *Spongospora subterranea* f sp. *subterranea* (also referred to as *S. subterranea, Sss*), can cause extensive losses in the British ware crop but is even more damaging to Scottish seed production (Wale, 2000). The disease is characterized by unsightly pustules covering the tuber surface and renders stocks unsuitable for the pre-pack market, and if the symptoms are very severe, unsuitable for processing due the necessity to remove excess amounts of skin.

Powdery scab has been recorded as a disease of potatoes in GB since records began: in England & Wales powdery scab outbreaks have occurred in all regions since disease intelligence records began in 1944. Serious outbreaks have been particularly related to the popularity of susceptible varieties and to wet seasons. The current rise in significance of powdery scab may be traced back to the rise in popularity of the susceptible cultivar Pentland Crown in the 1970's due to its high yield and uniform tubers. A series of seasons conducive to powdery scab resulted in infected seed being distributed widely to potato growing regions and these soils then became contaminated. Subsequent varieties were also susceptible and today, three quarters of varieties listed in the British Potato Variety Database (http://varieties.potato.org.uk) are susceptible or moderately susceptible to powdery scab.

Infection of tubers by *S. subterranea* occurs through unsuberised tissue, mainly through lenticels leading to the scab symptom, but sometimes infection of the eye can stimulate the tuber to swell in that area, forming an outgrowth or canker (Hims & Preece, 1975). Since the outgrowth is initially unsuberised it may also be infected through lenticels and be covered with scab lesions. As tubers age, lenticels become less susceptible to fungal infections due to increasing suberisation and the formation of a cork barrier below them (Adams, 1975a,b). Therefore the period at and shortly after tuber set has been identified as the most susceptible period for disease development. However, rainfall later in the growing season may still induce lenticel proliferation in mature tubers (Adams, 1975a,b) thus prolonging the period of susceptibility (Hims, 1976a; Diriwächter & Parbery, 1991). In addition, low oxygen levels in wet soils (Burton & Wiggington, 1970) have also been implicated in delayed suberisation of lenticels (Diriwächter & Parbery 1991), possibly prolonging the period of tuber susceptibility (Diriwächter & Parbery 1991; Harrison *et al.*, 1997).

Depending on conditions, tuber symptoms take 4-8 or more weeks to develop. Identification of initial tuber symptoms of powdery scab consisting of purple-brown pimples (1-2mm diameter), not dissimilar to a skin spot lesion, requires a trained eye. The pimples enlarge and the lesion grows proud of the tuber surface. At first, the raised lesion is white in colour but it soon darkens and the skin tissue covering the lesion bursts, exposing the powdery mass of spore balls (alternatively known as cystosori or sporosori) inside and resulting in the characteristic symptoms of the disease (Fig. 1). Powdery scab is sometimes difficult to distinguish from common scab (caused by *Streptomyces scabies* and other *Streptomyces spp.*) however, the presence of spore balls, which can be identified with the aid of a microscope provide a positive identification (Fig. 2).

Infection of the root or stolon can sometimes lead to development of a gall (Fig. 3). Infected tissue is stimulated to grow and sporeballs are formed inside the gall. These burst when mature and release the spore balls into the soil. Root or stolon galls can be easily overlooked in the field. There is evidence that varieties with resistance to tuber infection can be susceptible to root or stolon gall production (Eraslan & Turhan, 1989; Falloon *et al.*, 2003) and it is possible for a variety like this to be grown regularly causing an unseen build up of inoculum in the soil.

Spongospora subterranea is also the vector of potato mop-top virus (PMTV), one of the causes of spraing (Fig. 4). Although not specifically covered in this review it is useful to note that little is known about the interactions between the vector and virus, particularly in terms of conditions conducive to transmission of the virus and differential expression of symptoms of one or other of the diseases where infection by both organisms has occurred.

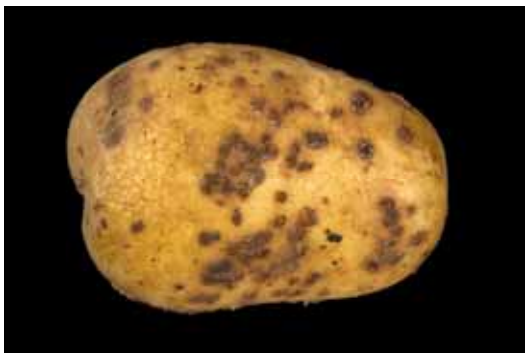

FIG. 1 CHARACTERISTIC LESIONS OF POWDERY SCAB ON CULTIVAR 'ESTIMA'.

FIG. 2. A TYPICAL POWDERY SCAB LESION

FIG. 3. ROOT GALLING SYMPTOMS ON POTATO

FIG. 4. SYMPTOMS OF SPRAING CAUSED BY PMTV IN CULTIVAR 'NICOLA'

The Pathogen

Spongospora subterranea f sp. *subterranea* belongs within the plasmodiophorids. The group was previously included in either the protoctists (Margulis *et al.*, 1989, Olive, 1975) or fungi (Sparrow, 1960; Waterhouse, 1972). Braselton (1995) reviewed problems associated with terminology and the presence of several genera within the plasmodiophorids and concluded that they should be considered as protozoans (at least for the time being). Bulman *et al.* (2001) endorsed this classification when they carried out a phylogenic analysis of members of the Plasmodiophorida and Phagomyxida. Key features of the plasmodiophorids are that they have zoospores with two anterior whiplash flagella, have multinucleated protoplasts (plasmodia), are obligate parasites (can only be cultivated on host plants) and have environmentally-resistant resting spores.

Spongospora subterranea f sp. *nasturtii* (*Ssn*) is the causative agent of crook root of watercress. *S. subterranea* f.sp. *subterranea* (*Sss*) and *Ssn* are indistinguishable in all ways apart from their host

range. In addition, they both are vectors of viruses: *Sss* is the vector of potato mop-top virus (PMTV), whilst *Ssn* transmits watercress chlorotic leaf spot virus and watercress yellow spot virus. *S. subterranea* (*Sss*) infects not only potato and tomato but also other both solanaceous and non-solanaceous plants (see the section on spore ball survival and germination, page 28). Other economically important and therefore relatively well researched members of the Plasmodiophoracea family are *Plasmodiophora brassicae*, the causative agent of clubroot of cabbage and other brassicaceous crops, and *Polymyxa graminis* and *Polymyxa betae*, which are the vectors of a number of pathogenic viruses of crops.

Life Cycle

A brief version of the life cycle of *S. subterranea*, taken from the detailed description of Harrison *et al.* (1987) follows:

There are two major phases in the life cycle of the Genus *Spongospora*, each initiated by host cell infection through single uninucleate plasmodium:
In the sporogenic (spore-producing) phase, sporogenic plasmodia are located within infected plant tissue, either in tuber lesions or root, shoot or stolon galls. Following nuclear divisions within the plasmodium, thick-walled resting spores are produced, each being around 3.5-4.5 µm diameter (Jones, 1978). These spores clump together and form spore balls. Falloon *et al.* (2007) determined the number of resting spores in spore balls to be on average 700, but the number varied according to the size of the spore ball. The resting spores may then persist in the soil, where they are able to survive in a dormant state for a number of years, or on tubers. Under suitable conditions, as outlined below, the spores germinate and release a single biflagellate primary zoospore which can then infect the host plant. The mechanisms of host infection are not well understood, but within the infected plant the pathogen causes abnormal growth of the infected cells in tubers and in roots and stolons leading to lesions and galls filled with a powdery mass of spore balls.

In the sporangial phase, within a thin-walled sporangial plasmodium, secondary zoospores develop in the host's cells. The secondary zoospores, also biflagellate, can exit the host and initiate another infection cycle. For further information on the plasmodiophorids also see http://oak.cats.ohiou.edu/~braselto/plasmos/.

The biphasic nature of the life cycle ensures that the pathogen is both persistent, with the production of resting spores, but also capable of very rapid multiplication through the formation of secondary zoospores if conditions are suitable. This means that infection is not consistently related to initial inoculum levels, but rather to secondary infection by zoospores if conditions are conducive to their formation. This, in combination with the fact that *Sss* is an obligate parasite, makes it particularly difficult to study.

Geographical Occurrence

The first European description of powdery scab symptoms dates back to 1842 (Wallroth, 1842, referred to in Harrison *et al.*, 1997). In the later half of the twentieth century more countries began to recognize the existence and indeed the problems caused by powdery scab. Kole (1954), for instance, pointed out that the disease was of increasing importance in Holland. More recently, powdery scab has become economically important in parts of Europe, including the U.K (Hide, 1981; Wale, 2000), Switzerland (Winter & Winiger, 1983; Blum and Merz, 1993; Merz, 2000), the Netherlands (van de Haar, 2000) and Turkey (Eraslan & Turhan, 1989). In addition, there are reports of the disease in most potato growing regions of the world, for example; in Peru (Torres *et al.*, 1995) in South America, in North America (Christ, 2001), in India (Bhattacharyya *et al.*, 1985),

Pakistan (Ahmad *et al.*, 1996) and Korea (Kim *et al.*, 2003) in Asia, in Australia (de Boer, 2000) and New Zealand (Braithwaite *et al.*, 1994) in Australasia, and in Israel (Tsror *et al.*, 1993).

Whilst the disease is prevalent in most temperate potato producing areas, it is not limited to cool-wet climates, but can also be problematic even in warm dry countries. This is usually attributed to the use of irrigation (Wale, 2000), which not only provides the necessary water but may also cool the topsoil quite considerably, particularly when bore water is used as the irrigation source. There are reports of heavy infections in sandy soils in semi-arid zones with the use of centre pivot irrigation in Australia (de Boer, 2000).

Disease Management

There are no totally effective control methods currently available for powdery scab. However, a number of chemical treatments have been found to provide limited control of the disease. For example, in field trials, treatment with zinc gave some control of powdery scab (Burgess *et al.*, 1992; Burnett & Wale, 1993). Evidence from controlled conditions and field trials carried out as part of BPC funded research 807/211 (2002) investigating control options for powdery scab, found fluazinam treatments to be more effective against soil-borne inoculum of *S. subterranea* than zinc. Fluazinam treatments were more effective on severity rather than incidence of disease, and where the principle source of inoculum was soil-borne rather than seed-borne. A Specific Off-label Approval (SOLA) has been secured for the application of fluazinam in seed-only potato crops. The SOLA permits use at a maximum dose of 1.5 kg a.i./ha applied on a tractor mounted downward directed drench in 200 l/ha of water. It should be applied on ridged bed prior to destoning or bed-tilling to ensure that it is thoroughly incorporated into soil.

As part of the same project non-chemical means of control were also assessed and the application of prawn shell waste to the soil in pots before planting was shown to reduce powdery scab but was not effective against root galling (Lees *et al*., unpublished data). In addition, *Brassica juncea* was found to be the most effective biofumigant crop tested and application of freeze dried powder of this species to the soil before planting may significantly reduce powdery scab incidence and severity.

Non-chemical treatments involving hot water or steam have also been shown to give some control of powdery scab. Warm water seed tuber treatments were assessed specifically for control of black leg, but the effect on powdery scab was also tested by Mackay & Shipton, (1983) who found good control with a 10 min treatment at 55 °C two months before planting. However, there were signs that the treatment caused some damage to the seed tubers. Afek and Orenstein (2002) found that steam treated tubers had significantly reduced levels of *Sss* contamination levels compared with untreated controls and found no evidence of damage to the treated seed.

In addition to direct control measures as indicated above, there are some indirect control measures which can result in reductions in powdery scab and by large these are a result of manipulating the factors (e.g. water) that are critical for infection and symptom development.

For example, irrigation increases powdery scab especially during tuber initiation (6-8 weeks after planting and 2-3 weeks after 50% emergence). Taylor *et al.* (1986) showed that starting irrigation only at tuber initiation or interrupting it from 1 week before tuber initiation until 3 weeks after reduced powdery scab significantly. However, common scab is currently controlled with irrigation at precisely this time and so there are conflicting interests.

A good crop rotation practice helps in not increasing powdery scab levels, but there are several reports that even after more than ten years cropping period without potatoes there was a severe attack at harvest time.

Control Measures: Summary Points

- **Disease avoidance, using healthy seed and soils which are not infested, is the most desirable control option**

However this option is not always available, therefore other control measures must be considered:

- **For seed only producers, fluazinam provides some control of powdery scab, particularly in limiting the severity of disease rather than incidence and where soil-borne rather than seed-borne inoculum is the primary source**
- **Hot water seed treatments may provide some control over powdery scab**
- **Withholding irrigation during the period of tuber set may limit powdery scab development, but this practice conflicts with control of common scab**
- **Growing disease resistant cultivars (see section below)**
- **Avoid any action that prevents free drainage of soil e.g. over cultivation of soil, creating compaction etc**

Host Resistance

Of all the methods assessed for reducing the incidence and severity of powdery scab it is widely recognised that host resistance is the most effective and sustainable approach, when used in combination with other disease management practices in an integrated way. For example, in BPC funded project 807/211 (2002) disease resistance was found to be the most effective method of controlling powdery scab: changing from a susceptible variety to a more resistant one gave the most consistent reduction in incidence and severity of powdery scab of all control measures evaluated.

It is has been demonstrated that resistance to powdery scab exists in some cultivars, in the UK (Gans, *et al.*, 1987) and worldwide (Christ, 1987; Genet *et al.*, 1996). However, despite the availability of disease resistant cultivars, genetic resistance to *S. subterranea* currently plays a minor role in disease control as cultivars are usually selected by growers for characteristics other than their ability to resist powdery scab (Harrison *et al.*, 1997). Jellis *et al.* (1987a) screened cultivars widely grown in the UK and found few had high levels of resistance. Similarly, (Falloon *et al.*, 2003) found that cultivars ranged from very susceptible to resistant, but as all developed zoosporangia and root galls, none possessed immunity.

Difficulties in establishing consistent susceptibility rankings have been reported due to a number of factors; differential performance in pot and field experiments (Gans & Vaughan, 2000); the emergence of between-year differences (Torres *et al,*. 1995; Gans & Vaughan, 2000; Lees, 2000) linked to weather conditions and the patchy distribution of the pathogen in soil (Lees, 2000) or genotype x environment interactions (Gans & Vaughan 2000). The relative susceptibility of cultivars has also been shown to vary with geographical location (Torres *et al.*, 1995; Bus, 2000; Schwärzel *et al.*, 2002; Merz *et al.*,. 2004) and has been attributed to various factors such as differences in soil type (Bus, 2000), climate (Schwärzel *et al,*. 2002) and the possible existence of different *S. subterranea* isolates (Torres *et al,*. 1995; Merz *et al.*, 2004). There is no scientifically tested evidence as to the influence of any of these factors on reported differences in host resistance. Recent trials conducted across Europe showed that there was good consistency of resistance ratings between trials (Merz et al, unpublished data), but the consistency of influencing factors such as weather conditions and differences in *Sss* populations was not, or could not, be tested, Current trials across several sites worldwide aim to investigate in more detail the relationship between environmental conditions, infection and symptom development. The GB component of the work is being carried out at SAC and SCRI with Potato Council funding.

Furthermore, it is known that the susceptibility of individual cultivars to root and tuber infection is not always closely correlated (Melhus *et al,*. 1916; Hughes, 1980; Eraslan & Turhan, 1989; Falloon *et al,*. 2003), particularly with regards to the relationship between root and tuber infection and root galling (Falloon *et al,*. 2003; Merz *et al.*, 2004; van de Graaf *et al.*, 2007). The use of certain cultivars with high tuber resistance may therefore still maintain populations of *S. subterranea* in the soil (de Boer, 2000; Falloon *et al,*. 2003). Where potatoes have been grown previously the relative resistance of previous cultivars had little effect on the subsequent incidence of disease (Burgess & Wale, 1996).

A number of studies have illustrated the use of disease resistant cultivars as a control option. Cultivar resistance was found to be an important factor influencing the severity of powdery scab (Burgess & Wale, 1994, 1996) and work carried out as part of the recently completely Potato Council- funded projects R249 and R253 also found clear differences in powdery scab levels on progeny tubers in relation to cultivar resistance rating.

A breeding programme in New Zealand has resulted in the highly resistant cultivar "Gladiator" (Genet *et al.*, 1995) and research at SCRI has shown that clones of long-day-adapted *Solanum tuberosum* group *phureja* are a genetic source of resistance for powdery scab as well as other potato diseases. It is important for breeding programmes to assess durability and consistency of cultivar resistance to any differences in *S. subterranea* virulence, which as yet remain largely uncharacterized. As stated earlier, despite the obvious benefits of host resistance, many of the currently grown cultivars are susceptible.

This is a result of other selectable traits such as quality and late blight and PCN resistance being prioritized. The availability of cultivars that combine the characteristics that make them commercially acceptable, in combination with resistance to powdery scab is central to the long-term aim of controlling the disease.

Host Resistance: Summary Points

- **Host resistance, in combination with other control measures is the most effective method of powdery scab control available**
- **There are sources of resistance to powdery scab in cultivars and germplasm that could be utilized in breeding programmes**
- **The lack of progress in breeding for disease resistance is due to preferential selection of other traits by the breeders/potato industry**
- **In the future screening for resistance should take into account both tuber and root resistance and the existence of *Sss* populations.**

3. Conducive Conditions

Not surprisingly, the majority of work investigating *S. subterranea* has focused on factors affecting disease symptom development, as this is by far the easiest manifestation of infection to measure, and is of the most importance to the potato industry. However, to fully understand how disease development is affected by various conditions we must also understand what conditions are conducive for root and tuber infection.

Soil Moisture

Laboratory experiments investigating zoospore release from resting spores into water or an aqueous solution are relatively easy to undertake, but both Harrison *et al.* (1997) and Fornier (1997) found it to be quite unpredictable. Studying zoospore release in soils is more difficult and there is little information to be found. Killham (1996) notes that protozoa in soil are adversely affected in drying soil because they need continuous water films in which to move and graze on other soil microbes. In a similar way, it is likely that the movement of zoospores of *S. subterranea* will be curtailed in soil not much drier than field capacity i.e. there will be insufficient water-filled pores in which they can swim. Killham (1996) also notes that drying soil to an extent that limits the locomotion of protozoa, will cause them to encyst and that these protozoal cysts are then extremely resistant to water stress.

While zoospores are motile, the distance they can move through the soil, using their flagella to swim, is limited. Based on experience with other organisms Harrison *et al.* (1997) suggest that the range of motile zoospores is likely to no more than a few centimetres, even when following a possible chemical signal in the water.

It is broadly accepted therefore, that high soil water content encourages zoospore release and that soil in which most pore spaces are filled with water facilitates movement of zoospores towards the host, and subsequent infection and disease development.

Therefore, in general, very low levels of soil moisture or very high constant levels of soil moisture limit disease development.

The timing and duration of periods of elevated soil moisture appears to be important but the flexible nature of *S. subterranea* life cycle permits infection and disease development under a multitude of conditions. Jellis *et al.* (1987 b) found that dry conditions during tuber initiation could prevent existing root infection progressing to tuber infection. It has been widely reported that powdery scab incidence and severity can be substantially reduced by delaying irrigation until tuber set or several weeks post tuber set (Taylor & Flett, 1981; de Boer *et al.*, 1985;, Adams *et al.*, 1987; Burnett, 1991). In addition, Taylor *et al.* (1986) reported that withholding irrigation from the week before tuber initiation was of particular importance in reducing powdery scab, and Ramsey (1918) found that rainfall during the first half of the growing season was particularly important for powdery scab development. Hims (1976a) reported that high levels of disease could result from short periods of high soil moisture post tuber-initiation if soils had been moist prior to tuber initiation, or alternatively, if they were subsequently maintained at field capacity for 20-40 days having been dry prior to tuber initiation. This finding is supported by the observations of a number of authors who reported that disease may still result from wet conditions later in the growing season (Forsund, 1971; Hims, 1976a, 1976b; Adams, 1975a; Parker, 1984b; Christ & Weidner 1988; Diriwächter & Parbery 1991).

There is some disagreement concerning the importance of constant versus fluctuating soil moisture conditions: van de Graaf *et al.* (2005) found incidence and severity of tuber infection were significantly higher when plants were grown under constant damp conditions rather than under fluctuating wet and dry conditions and Adams *et al.* (1987) found continuous irrigation to be more conducive to disease development than fluctuations in soil moisture. However, Hims (1976a) concluded that several periods of 2-3 days of rainfall sufficient to raise topsoil to field capacity, separated by 8-10 days of dry weather during the growing season, were particularly favourable to disease development. Burnett (1991) also concluded that fluctuating conditions were more conducive to powdery scab infection of tubers than constant wetness. Experience in commercial field production has suggested that powdery scab is worst in light sandy fields where water drains quickly and periods of wet and dry soil conditions are more frequent. Anecdotally, during the wet summer of 1985, growers in NE Scotland reported less powdery scab developing on farms where soil inoculum was known to be high in those fields that remained water-logged throughout the season rather than those where drainage was free.

Harrison *et al.* (1997) concluded that more work is needed on the temporal distribution of precipitation and its interaction with other factors in relation to powdery scab development. Standardized field trials are underway in the UK at SCRI and SAC Aberdeen (Potato Council-funded project R411) and in a number of other countries, with the aim of better understanding how variations in the timing and level of rainfall affect powdery scab development in conjunction with a number of factors such as timing of tuber initiation, temperature and soil types.

Soil Moisture: Summary Points

- **Little is know about the effect of soil moisture on the germination and subsequent infection of potato by *S. subterranea*, most work has concentrated on factors affecting disease development**
- **In general, low levels of soil moisture or very high constant levels of soil moisture limit disease development**
- **The timing and duration of periods of elevated soil moisture appears to be important but the flexible nature of *S. subterranea* life cycle permits infection and disease development under a multitude of conditions**
- **More work is needed on the interaction between precipitation/irrigation and other factors in relation to powdery scab development**

Temperature

Claxton *et al.* (1995) studying the effects of temperature on zoospore release from infected *Ssn* roots, found that zoospores were released more rapidly at higher temperatures, with few being released at 5°C. However, subsequent encystment and disease were lower at the warmer temperature (20°C) than at lower temperatures (15, 10 and 5°C). Fornier (1997) also found that *Sss* zoospore release was more rapid at warmer temperatures (15 and 25°C) than at cooler temperatures (3 and 10°C).

In infection studies Kole (1954) found that moderate to severe infection of root hairs of bait plants developed rapidly at 14-20ºC, with infection of new bait plants persisting over relatively long periods. At 22-25ºC zoosporangia occurred occasionally, but in general root hairs of bait plants remained uninfected and infection was less severe and took longer to occur at 11-13ºC. Harrison *et al.* (1997) reported that zoospores can still swim vigorously at close to 0ºC, suggesting that infection is still possible at temperatures well below 11ºC. However, van de Graaf *et al.* (2007) reported that the percentage of plants with infected roots increased with temperature when plants were incubated at 9, 12 and 17ºC. Temperature had a greater effect on root than tuber infection, as root infection was very limited at low temperatures, whilst tuber infection occurred at all temperatures but was most severe at 12 ºC. Ramsey (1918) found no evidence of tuber infection in plants cultivated at c. 70 or 80ºF (21.1ºC and 26.7ºC), regardless of soil moisture status, whilst tuber infection was evident in plants cultivated at 60ºF (15.6ºC) with moist soil. van de Graaf *et al.* (2007) found that whilst limited root infection occurred at 9 ºC, no root galling was evident at this temperature, whilst it did occur at 12 ºC and all plants developed root galls at 17 ºC. They found that the optimum temperature for root galling was therefore higher than that for tuber infection/powdery scab development.

Experimental studies including those of Hims (1976a) found that soil temperatures of 12-13°C were, amongst other factors, conducive to attacks of powdery scab. This is supported by the work of de Boer *et al.* (1985), who compared disease levels in progeny tubers from plants cultivated at 10, 12.5, 15, 17.5 and 20ºC. They found no evidence of disease in tubers grown at 10ºC, whilst the highest level of disease incidence and severity was at 12.5ºC. Work carried out in Australia by Hughes (1980) found no evidence of disease in roots or tubers when grown at warm ambient temperatures but severe infection was detected when plants were grown at 14-17ºC. van de Graaf *et al.* 2005, found that at tuber maturity, whilst there was no significant difference between temperature treatments in the percentage of plants with infected tubers, disease severity was significantly higher at 12ºC than at 9 or 17ºC.

A number of studies have shown that powdery scab symptoms are more prevalent as a result of cool conditions (Hims, 1976a; Ramsey, 1918; Hughes,1980; Christ & Weidner 1988). Other researchers have reported disease development to be limited in areas/seasons where temperatures are high (Hughes, 1980; Adams *et al.,* 1987). There are also reports of powdery scab being restricted to higher (cooler) altitudes in Turkey (Eraslan & Turhan, 1989) and Costa Rica (Montero-Astúa *et al,*. 2004).

Temperature: Summary Points

- **Zoospore release is more rapid at warmer temperatures (15 and 25 ºC) compared to cooler temperatures (3 and 10 ºC)**
- **Infection of root hairs develops rapidly at 14-20 ºC and infection of new plants can persist over relatively long periods**
- **The optimum temperature for tuber infection/powdery scab development is around 12 ºC**
- **The optimum temperature for root galling is around 17 ºC**

Therefore, processes necessary for disease development generally favour relatively cool temperatures, but all the necessary processes may still occur at temperatures up to 20ºC

Seasonal Variation - weather

Harrison *et al.* (1997) note that variation in disease incidence from year to year is likely to be linked to the variability of temperature and rainfall which can affect the rate of crop development, and thus the period of susceptibility to the disease and the development of conducive conditions in the soil. Agronomic practices such as delayed planting and tuber chitting affect the timing of tuber development and whether or not tuber susceptibility coincides with periods when conditions are conducive to plant infection and disease development.

A number of studies report yearly/seasonal and geographical variation in the incidence and severity of powdery scab due to differences in temperature and rainfall. Within the UK, Hims (1976a) reported that a study of meteorological records from 1917-1971 revealed that powdery scab was more severe in the North, Midlands and Wales (with relatively cool wet summers) than the South East, South West and East of England (slightly warmer and drier). This appeared to be due to a combination of the temporal distribution and amount of rainfall and lower soil temperatures, rather than simply rainfall per se. and he concluded that favourable conditions for the disease were the combination of inoculum in the soil, periods of low (12-13°C) soil temperatures from June-September and periods of 2-3days continuous rainfall separated by short intervals of dry weather. Read *et al.* (1995) found in a national survey of powdery scab levels that disease was scarce in all areas surveyed in 1989, and generally limited to crops in Scotland and western England in 1990. It was thought likely that these locations were the only areas with suitable climate conditions in the unusually dry years over which the survey was conducted.

The British Potato Council- funded reference crops (1998, 1999 and 2000) provide interesting data on the occurrence of powdery scab in relation to variations in soil temperature, precipitation levels and irrigation treatments, with seed from the same stocks planted at 4 sites in the UK over 3 seasons. The level of seed inoculum of *Sss* was determined through visual assessments (and was present on seed in all three years), however at this time there was no robust method for determining levels of soil inoculum so this parameter could not be quantified. A brief comparison of the two extreme sites (Cambridge and Dundee) follows.

In all three years, very little disease developed at the Cambridge site, and then primarily in the irrigated treatment. Around the period of tuber initiation soil temperatures were lower at the Dundee site than at Cambridge (*c*. 17.6°C in Cambridge but only 14.2°C in Dundee). In 1998, the incidence of powdery scab at the unirrigated site at Dundee was 17.5 %. In this year, Dundee had considerably more rainfall around the period of tuber initiation than Cambridge. In 1999 and 2000, very low levels of powdery scab were found at the unirrigated Dundee site. During the period of tuber initiation rainfall was low at both sites limiting disease development in these years. However, in 2000, Dundee also had an irrigated treatment in which relatively high levels of disease developed. Therefore it appears that the lower soil temperature in Dundee may be more conducive to powdery scab development than soil temperatures found at Cambridge. At the Dundee site, disease developed given sufficient moisture either through rainfall or irrigation, whilst it remained limited at the Cambridge site even when adequate moisture was available in the irrigated treatments.

Other studies from Europe and around the world have also reported links between cool damp conditions and disease development. Melhus *et al.* (1916) noted that in Maine, periods of rainfall followed by cool damp and cloudy conditions during the growing season provided suitable conditions for infection (which is of course essential for subsequent disease development). They also noted that the disease was not solely restricted to the northern US as these conditions occurred further south in Florida where potatoes were planted in January-February and harvested April-May. Kole (1954) reported that the severity of powdery scab varied from year to year in the Netherlands with weather conditions. Powdery scab was rare in dry summers but could become serious in normal or wet summers. Christ & Weidner (1988) reported disease in one year in an area of Pennsylvania but subsequently failed to find disease in trials in later years and other areas, attributing this to warmer drier conditions. Similarly, Iftikhar *et al.* (1993) reported that the prevalence of powdery scab in the North West Frontier Province of Pakistan was higher in spring, when temperature and rainfall were more favourable, than in autumn.

Weather: Summary Point

- **The development of powdery scab tuber symptoms is favoured by cool soil temperatures and wet conditions**

Soil pH

We have found no further literature to cause us to contradict the statement made by Harrison *et al.* 1997, that "the literature concerning the effects of pH on the severity of powdery scab is confusing and contradictory and there is little evidence to suggest that *S. subterranea* is greatly influenced by pH within the range normally found in arable soils"

Some studies have failed to find a relationship between soil pH and disease incidence and severity (Kole 1954; Parker 1984a; Falloon *et al.,* 2005). In contrast, Cooper *et al.* (1976) reported that powdery scab incidence was very low below pH 5, when pH was reduced to 4.6 following treatment with sulphur. Brereton (1991) also reported a tendency for powdery scab incidence and severity to be reduced at lower soil pH, within a range of pH 5.1-6.7. In most instances the addition of sulphur in order to reduce pH has been associated with substantial reductions in disease incidence (Melhus *et al.,* 1916; Cooper *et al.,* 1976; El Fahl & Calvert,1976) and severity (Hughes, 1980). However, in a sulphur deficient soil, the addition of low rates of sulphur increased disease severity (Hughes, 1980).

A number of studies have also reported increases in disease incidence and severity (Melhus *et al.,* 1916; Wenzl & Reichard, 1974; Cooper *et al.,* 1976; El Fahl & Calvert 1976; Hughes, 1980) following the addition of lime and nitrochalk. However, Wenzl & Reichard (1974) and Wenzl *et al.* (1972) found the addition of calcium oxide and basic slag resulted in a decrease in the incidence of disease.

There is some evidence to suggest that the effect of applying sulphur or lime treatments is influenced by the method of incorporation, existing soil pH (El Fahl and Calvert 1976) and timing of intervention (Hughes 1980). Apparent variability in the findings may relate to the fact that modifying soil pH will alter other variables which may influence powdery scab. The forms of lime used (calcium oxide, hydroxide, carbonate and silicate) encourage flocculation of colloidal particles, improving soil structure and drainage, which may explain disease reduction associated with lime addition. It may also be that soil pH interacts with other variables to determine disease development (Harrison *et al.,* 1997).

It has been suggested that soil pH may influence the incidence and severity of powdery scab by influencing the aluminium content in soils (Shimada & Mizuno, 2000; Nakayama *et al.,* 2007) where low soil aluminium levels are conducive to disease development. There is also evidence of a similar effect with regards to the level of zinc in solution in the soil (Brereton, 1991). Merz (1989) found that root infection was not influenced by the pH level of the nutrient solution in which the spore balls were maintained.

Soil pH: Summary Points

- **There is little evidence to suggest that *S. subterranea* is greatly influenced by pH within the range normally found in arable soils**
- **Some evidence to suggest that low pH associated with the addition of sulphur reduces powdery scab.**
- **Increasing pH, associated with the application of lime or nitrochalk may increase the risk of powdery scab**

Soil Type

Although soil type is often thought to influence the incidence and severity of powdery scab the factors involved are unclear. It is generally believed that powdery scab is worse on light sandy soils. There some soil types and localities where, despite planting powdery scab infected seed tubers, the disease consistently failed to develop. One such area and locality are the clay soils of Essex.

Physical characteristics that affect water content are important and chemical characteristics, some of which influence soil structure, may also be involved (Harrison *et al.*, 1997). However, the existence of suppressive soils has not been demonstrated, or indeed, factors associated with soil type (other than those relating to soil moisture content) that consistently suppress the development of powdery scab identified.

Melhus *et al.* (1916) found that in a field in which soil texture and characteristics varied greatly powdery scab was closely correlated with a grey Washburn silt-loam. Ramsey (1918) also identified a "low, gray" type of soil as being particularly favourable for disease development. Some studies found disease to be more prevalent in or restricted to sandy/sandy peat soils (Kole 1954; Forsund, 1971; Bus, 2000). Conversely, others have linked the disease to loam/clay soils (Hims 1976a; Tuttobene, 1986). de Boer (2000) noted that incidence of disease was significantly lower in sandy soil than a clay loam held at the same water potential. However they acknowledged that despite sandy soils having a lower water holding capacity, powdery scab could be severe under high irrigation regimes needed to cultivate potatoes in sandy soils of semi-arid regions in Australia. van de Haar (2000) noted that although powdery scab could be found on all soil types in the Netherlands it was particularly prevalent on sandy or organic soils.

van de Graaf *et al.* (2005, 2007) found no significant difference in incidence or amount of disease in roots and tubers in a loamy sand, sandy loam or silty clay at the same water potential, but symptomless root infection was significantly higher and incidence and severity of root galls significantly lower in the silty clay than in other soils.

Parker (1984a) found no significant correlation between disease incidence and the levels of organic matter, extractable potassium and phosphate in soils and Brereton (1991) found no evidence of a relationship between disease incidence and severity and the levels of extractable P, K or Mg in soils. However he found that disease incidence and severity tended to be lower in soils with high levels of zinc in solution. Using multivariate analysis, Crump *et al.* (2006) found different soil factors to be important in their relationship with powdery scab in different areas of Australia. In one area, higher pH, higher exchangeable cations (EC) and higher total soluble salt were associated with increased disease. In another area it was higher nitrogen and lower zinc and in a third area higher phosphorus, potassium, sodium, manganese, iron, sulphur, cobalt, molybdenum and K:Mg ratio were associated with high levels of disease.

Soil Type: Summary Points

- **The existence of "suppressive" or indeed "conducive" soils has not been demonstrated**
- **There is no evidence to suggest that soil type has a major impact on powdery scab development if free draining soils are maintained at field capacity.**

Inoculum

Powdery scab may be seed-borne (Hide 1981; de Boer *et al.* 1982; Read *et al.* 1995) or soil-borne (Letham *et al.* 1988; Merz *et al.* 2006) with the result that planting disease free and uncontaminated seed-tubers in infested soil (Letham *et al.* 1988; Merz *et al.* 2006) or infected tubers in uninfested soil (Eraslan and Turhan 1989; Falloon *et al.* 1996; de Nazareno and Boschetto 2002) can lead to the development of disease in progeny tubers. However, the relative importance of these two sources of inoculum has never been clearly demonstrated (Harrison *et al.* 1997). Furthermore, a number of studies have shown that disease may not develop where temperature and/or soil moisture conditions are unfavourable, even where soils are known to be infested or diseased tubers are planted (Melhus *et al.* 1916; Ramsey 1918; Hughes *et al.* 1980; Christ and Weidner 1988; Iftikhar *et al.* 1993; Nakayama *et al.* 2007).

In uninfested soils, transmission of the pathogen from infected tubers to progeny does not appear to be straightforward. Burnett (1991), Keiser *et al.* (2007a) and results from British Potato Council-funded projects 807/211 (2002) and R253 (2008) found no consistent correlation between the level of seed tuber infection and subsequent disease levels on progeny tubers. Other studies have reported lower incidence and severity of disease on progeny tubers compared to the seed stock from which they were grown (Braithwaite *et al.*, 1994; de Nazareno & Boschetto, 2002).

There is evidence to suggest that even symptomless tubers may be contaminated (de Boer *et al.*, 1982; Harrison *et al.*, 1993; van de Graaf *et al.*, 2005). Although it is not always clear whether such tubers are actually infected or simply contaminated by contact with diseased tubers (de Boer *et al.*, 1982; Harrison *et al.*, 1993). A distinction should be made between latent infections where the tubers are infected with the pathogen but disease symptoms are not expressed, and surface contamination following contact with, for example, infected tubers or contaminated farm machinery. Latent infections may be associated with conditions that are unfavourable for disease development, such as sub-optimal temperatures and low inoculum concentrations (van de Graaf *et al.*, 2005). However, more research is required to ascertain the importance of such infections in causing subsequent contamination of soil and disease in progeny crops. Falloon *et al.*, (1996), attributed the occurrence of disease when tubers free from powdery scab symptoms were planted in

a soil (in New Zealand) in which potatoes had not previously been grown, to symptomless infection of the seed tubers. This is an area where more work is clearly needed to determine the risk associated with symptomless but infected seed. The British Potato Council- funded project R253 (2008) found that out of 124 seed stocks sampled, 56 (45%) were found to have some level of symptomless contamination. Symptomless contamination was classified as stocks which displayed no disease symptoms yet had detectable levels of *S. subterranea* as determined using real-time PCR. It was not possible in this study to ascertain if these stocks caused disease as they were predominantly planted into infested soils.

It is not entirely clear whether a relationship between soil inoculum concentration and disease incidence and severity exists given the contradictory findings of a number of studies.

Under laboratory conditions, both Burnett (1991) and Brereton (1991) found evidence of a positive relationship between numbers of plasmodia detected in root hairs and increasing inoculum concentration. Burnett (1991) reported curvilinear relationships in which the rate of increase declined above a threshold of 1 spore balls/ml nutrient solution and 3.33 sporeballs/g soil, whilst Brereton (1991) found the rate of increase in infection with inoculum level increased up to the maximum concentration tested (0.25 spore balls/g soil). In a subsequent experiment Brereton (1991) reported that the mean number of plasmodia/root section continued to increase with increasing inoculum concentration up to the maximum concentration tested (250 spore balls /g soil), with no evidence of levelling off. In contrast, van de Graaf *et al.* (2007) found no evidence of a significant relationship between root infection or root galling and inoculum concentration within a range of 5-50 spore balls/g soil.

Similarly, van de Graaf *et al.* (2005), in inoculated pot experiments, and Merz *et al.* (2006), in field trials correlating multiple spot sites of soil inoculum and disease, found no evidence of a relationship between soil inoculum concentration and the incidence and severity of disease on tubers. In contrast, Qu *et al.* (2006a) found a significant relationship between soil inoculum levels and disease incidence when they tested 17 field soils in America and found them to be contaminated with *Sss* at levels between 0 and 14,400 sporeballs / g of soil, using a competitive PCR assay, and Shah *et al.* (2005) found that a significant asymptotic relationship existed between inoculum concentration (ranging from 0-12000 spore balls /g soil) and the severity of disease in tubers. When watered to field capacity, Parker (1984a) found residual soil inoculum resulted in disease incidence and severity similar to that obtained in pots to which additional inoculum had been added. Similarly, Christ (1989) compared field plots with natural inoculum levels to plots to which additional inoculum had been added and found no difference in disease levels between the two.

Nakayama *et al.* (2007) using a competitive PCR technique (Bell *et al.*, 1999) tested 29 potato fields in Japan and found the highest spore ball density to be 105 spore balls / g soil. They found no evidence of a significant relationship between spore ball density in the soil and tuber disease severity but did find a significant positive relationship between the amount of disease on the roots of plants and tuber disease severity. This would accord with the conclusion of Burnett (1991) that initial soil pathogen concentration was of less importance than the build up of inoculum during the root multiplication phase.

Harrison *et al.* (1997) argued that it was reasonable to assume the severity of powdery scab was positively correlated with the quantity of *S. subterranea* coming into contact with developing tubers and that the relationship would be asymptotic, with less disease for a given level of inoculum as the proportion of uninfected tuber surface decreased. However, they also noted that field observations suggest initial spore ball levels play a minor role in determining the amount of disease that develops since under favourable conditions low levels of spore balls can give rise to high numbers of zoospores. Initial inoculum level may be of greater importance where conditions for pathogen

multiplication are unfavourable. This observation is in contrast to the findings of the British Potato Council- funded project R253 (2008), in which a relationship between soil borne inoculum and disease was found only in the year in which conditions were conducive to disease i.e. in 2007 which had a relatively cool wet summer. In the two previous years (2005 and 2006) little powdery scab had been recorded on the monitored stocks as the summers were relatively dry. In this study, the maximum level of *S. subterranea* infestation found in 122 soils sampled within the UK was 148 spore balls / g of soil. Merz (1993) surveyed 78 soils from potato producing areas of Switzerland and reported that soils highly contaminated with *S. subterranea* had inoculum densities greater than 500 spore balls / g of soil as determined using a baiting technique (Merz 1989). The wide variation in spore ball levels found between individual studies is likely to be associated in part with the different methodologies used.

Inoculum: Summary Points

- **Inoculum is both seed- and soil- borne**
- **The relative importance of these two inoculum sources is not fully understood**
- **More research is required to ascertain the importance of symptomless tuber infections in causing subsequent contamination of soil and disease in progeny crops**
- **The relationship between inoculum level and disease is not fully understood – this is likely to be an interaction between environmental conditions, root infection, primary and secondary infection cycles, host resistance and disease**
- **Methods exist to quantify soil inoculum and symptomless tuber infections**

Spore ball survival and germination

Spore ball dormancy is an important factor in the survival of *S. subterranea* in soil, but very little is known about it. Any factor that affects the dormancy or germination of resting spores or the survival of spore balls will alter the potential for disease development. If germination is inhibited, fewer zoospores are released in a given time and subsequently we would expect less disease to develop and vice versa, assuming other factors are unchanged (Harrison *et al.*, 1997).

S. subterranea sporeballs are not killed by air-drying prior to storage (Jones and Harrison 1969). Kole (1954) suggest that the germination of resting spores and subsequent incidence of root infection may be increased by the use of previously dried infested soil and inhibited by the storage of soil under moist conditions. Freezing of soil was not found to stimulate germination (Kole 1954). Little is known about the possible role of exudates from higher plants or soil micro-organisms in suppressing resting spore germination (Harrison *et al.*, 1997). However, Fornier (1997) found exudates of fat hen reduced the number of zoospores released. There is some evidence to suggest that although not a fundamental pre-requisite for germination host plant root exudates may stimulate/regulate primary zoospore release (Kole 1954; Fornier and Burgess 1996; Merz 1997).

S. subterranea has been shown to persist for long periods (at least 5 years) in the soil in the absence of potato cultivation (Melhus *et al.*, 1916, Foxe 1980; Letham *et al.*, 1988) but it is believed to persist for much longer. Merz *et al.* (2007) reported that testing with ELISA one year after a field trial indicated soil infestation levels had halved, with a further decline to undetectable levels one year later. Work carried out as part of the British Potato Council- funded project 807/211 (2002) found that spore ball survival declined rapidly in soils maintained at 20°C but remained high when soils were kept at 4 °C.

Alternative hosts may also play a role in maintaining inoculum in infested soils. Apart from potato and related Solanaceae species, the host range of *S. subterranea* includes other crop plants, such as oilseed rape, sugar beet and spinach, and a large number of common UK weed species, including chickweed, poppy, nettle and fat-hen (Jones and Harrison, 1969; Jones and Harrison, 1972). Until recently, *S. subterranea* had only been detected as zoosporangia in the roots of alternative hosts (Jones and Harrison, 1969; Jones and Harrison, 1972; Andersen *et al.*, 2002) and the role of alternative hosts in the survival of *S. subterranea* between potato crops was viewed as debatable (Jones and Harrison 1972; Harrison *et al.*, 1997). However a study by Qu and Christ 2006a, found four out of 16 crop and weed species infected with *S. subterranea* subsequently produced root galls, with spore balls detected on 3 species (yellow mustard, oats and tomato). It is therefore possible for *S. subterranea* to complete its lifecycle in the absence of potatoes. This new knowledge gives rise for the need for more information on the affects of crop rotations and the occurrence of weed species on the persistence of soil inoculum. The incidence of powdery scab was found to be higher where potatoes have been grown previously, irrespective of the length of rotation (Burgess & Wale 1996). This suggests that either spore balls do not decrease markedly over time, or that once soils have become infested their levels may be actively maintained through the infection of alternate hosts.

The presence of volunteers would also prolong persistence of soil inoculum. This is illustrated by the observation of Jones & Harrison (1972), who found some evidence of a link between areas of high PMTV infectivity in fields in Scotland and the location of old potato clamps, resulting in an accumulation of *S. subterranea* close to gates and walls, with little PMTV infection in field centres.

Spore Ball Survival and Germination: Summary Points

- **Spore balls can persist in soil for many years**
- **It is possible for *S. subterranea* to complete its lifecycle in the absence of potatoes. This gives rise for the need for more information on the affects of crop rotations and the occurrence of weed species on the persistence of soil inoculum.**

Determining Levels of Soil Inoculum

A major factor contributing to the dearth of information on the relative importance of different sources of inoculum and the environmental factors influencing infection and disease development, has in part been due to our inability to accurately detect and quantify *S. subterranea* inoculum levels in soil.

With the development and validation of a new technique to effectively extract and subsequently quantify target DNA in soil (Potato Council- funded project R253 (2008)), new research possibilities have opened up which would enable us to investigate some of the epidemiological questions regarding the development of powdery scab which remain unanswered. Disease risk assessments where inoculum levels on seed and in soil are associated with a level of disease risk are now possible.

It is realized that standardisation of testing methods is crucial if inoculum levels are to be linked with disease risk. As part of a current Potato Council- funded project (R411), three institutes in the UK (SCRI, SAC Aberdeen and CSL) are carrying out comparative tests to ensure standardisation of test results and interpretation, for future diagnostic service providers.

Determining Levels of Soil Inoculum: Summary Point

- **A reliable method for the quantification of soil-borne inoculum has been developed and validated**

4 Strains

Significance of variation or 'strains' of *Spongospora subterranea*

Due to the difficulties in controlling powdery scab, as previously outlined, the development of integrated control strategies that incorporate host resistance are considered to be the only option for sustainable disease management. The requirement for cultivars with resistance that is durable both over time and locations is interlinked with the ability of the pathogen to evolve and overcome that resistance. The current lack of information relating to the existence of physiological races, pathotypes or variation in populations of *Sss*, combined with a lack of understanding of how environmental factors and the pathogen interact to cause infection and symptom development lead to uncertainties over the future efficacy of control measures.

If different *Sss* strains exist, and vary, for example in their virulence on different host species, pathogenicity, ability to overcome resistance, and in their interactions with the environment and PMTV then there are direct implications for the efficacy of both breeding programmes and control strategies.

Variation in *Spongospora subterranea* f.sp. *subterranea:* methods and evidence

Little is known about the role of sexual recombination in the life cycle of *Sss*, the existence of different 'strains', or whether genetically distinct strains differ in their ability to cause disease. In the closely related pathogen *Plasmodiophora brassicae*, which causes club root on crucifers both genetic strains and different pathotypes have been described (Manzanares-Dauleux *et al.*, 2001), with implications for breeding durable clubroot resistance. To date we are unable to attribute variable powdery scab symptom development to the existence of different *Sss* pathotypes, although some researchers have suggested that they exist.

According to Harrison (1997), Würzer (1964) provided evidence for genetic variation in *S. subterranea* with respect to the optimum temperature for infection but could not distinguish any pathotypes. Inconsistent resistance of cultivars to powdery scab has been widely reported and this circumstantial evidence has been used to suggest the existence of different strains of inoculum within different geographical regions. For example, Torres *et al.* (1995) noted that cultivars found to be susceptible in a trial at Cusco had been reported as resistant in the UK and the Philippines. Falloon *et al.*, (2003) discuss the variation in susceptibility of cultivars between countries as noted by various authors and attributed to different pathotypes of *Sss*. They conclude that the resistance of a particular cultivar to *Sss* is probably conferred by mixtures of race-specific genes along with combinations of (possibly several) minor genes.

In contrast, Wastie & Stewart (1989) found a good agreement in the resistance ranking of potato genotypes grown in soil infested with *Sss* from a different source in each of two years but provided no evidence that the strain in each source was not the same clone, and Merz (2007) reported that a European resistance trial carried out over four years and involving 5-6 countries in each year found no obvious location x genotype interactions. He suggested that variations in susceptibility could be due to difficulties in identifying symptoms, varietal differences in date of tuber initiation and differences in crop management. Preliminary results (Lees unpublished) show that the ribotype of *Sss* in these European resistance trials, as assessed using the method of Qu *et al.*, (2000), as described below, was predominantly type II, illustrating that without evidence of variation in *Sss* between locations in combination with an understanding of the relationship between variation and phenotype, it is difficult to draw conclusions about differences in host resistance ratings.

Relatively few attempts have been made to date to characterise variation in *Sss*. This is largely due to the intractable nature of the pathogen; the fact that it is an unculturable obligate biotroph (can only be cultured in a host plant) and that it is therefore difficult to obtain sufficient 'clean' DNA for commonly used molecular marker techniques and that sequence information is limited. As little is known about the genetics of *Spongospora,* assumptions about what constitutes an isolate or 'strain' (spore ball, resting spore or zoospore) are sometimes made. In general, analyses are made on single spore balls, but a spore ball may also comprise many genotypes in the form of individual resting spores.

The British Potato Council- funded project 807/211 (2002) investigated genetic variation between *S. subterranea* spore balls from different sources in Scotland using AFLPs, but the results were inconclusive as difficulties arose in obtaining sufficient clean DNA of the pathogen. A diagnostic study by Montero-Astúa *et al.,* (2004) reported geographical variation in lesion symptoms in Costa Rica, they also found variation in DAS-ELISA and PCR results and suggested that genetic variation among *Sss* samples may exist.

Bulman and Marshall (1998), examined genetic variation in the nuclear rDNA internal transcribed spacer (ITS) sequences of *Sss* collections from different locations and showed that collections from Australasia and Europe (named type II) were different from collections from Scotland and South America (type I). Subsequently Qu *et al.,* (2000) and Qu and Christ (2004), also using ITS1 and ITS2 sequences confirmed the existence of the 2 ribotypes (I and II) and stated that genetic groups of *Sss* were associated with particular cultivars in GB without exception, suggesting a genotype x host relationship. However, recent studies in Scotland (Lees unpubl. data) suggest that there is no such relationship with cultivar, but that the ribotype associated with a particular cultivar is dependent on the population detected in the field in which it was planted. Whilst Bulman & Marshall (1998) and Qu and Christ (2004) reported the existence of two different strains, they did not attempt to identify pathotype differences between populations.

Qu and Christ (2006b) went on to look at genetic variation between single spore balls using restricted fragment length polymorphism (RFLP) markers developed from randomly amplified polymorphic DNA (RAPD) fragments obtained from *S. subterranea* spore balls. They developed a number of RFLP probes, which were used to analyse 24 single spore ball isolates derived from 8 locations in the US and Canada. They found genetic variation among, but not within, geographic locations. In contrast, Merz *et al.* (2006) found several polymorphic loci using an ISSR marker amongst spore ball samples collected from tubers of 24 plants, from individual tubers on one plant and from different lesions on one tuber, indicating that spore balls in a given field are not clones.

ISSR markers (Inter Simple Sequence Repeats) are arbitrary markers produced by PCR amplification with a microsatellite primer and are advantageous because no prior genomic information is required for their use. As with all the methods used to date, this is an important point for consideration as, in combination with the inherent problems in dealing with *Sss*, the lack of genome sequence information hinders the development of molecular markers such as SSR that would accelerate population studies in this pathogen.

Genetic variation has been reported on a number of scales, both between geographical regions and within a single lesion, but no knowledge of the existence of pathotypes exists. The next step must be to investigate whether genetically different strains vary in their virulence. In addition, there is little knowledge of the efficiency of virus transmission by the different types of *Sss* and it has been suggested that virus transmission may inhibit powdery scab symptom formation. Current research at SCRI is investigating variation in *S. subterranea* populations in terms of efficiency of transmission of PMTV.

Knowledge of the existence of pathotypes of *S. subterranea* is important for understanding survival in the environment and host resistance in potato, and together with information on virus transmission could be used to develop integrated disease control strategies for both powdery scab and PMTV-induced spraing.

Variation in *Spongospora subterranea:* Summary Points

- **Genetic variation is an important factor to consider in breeding for durable resistance**
- **Genetic variation in *Sss* has been reported on a number of scales, both between geographical regions and within a single lesion**
- **No definitive test for examining variation in *Sss* has been defined**
  - **The absence of sequence information hinders progress in this area**
  - **Links between genetic variation and pathotypes in *Sss* have not been defined**
  - **Studies depend on the existence of a robust test for variation**
  - **Relationships could be defined but this is a significant piece of work; requiring specific expertise**

5 Overall summary

After thoroughly reviewing the literature on conditions which have been associated with the development of powdery scab, it appears that the key requirements are for cool wet soils and a source of inoculum either from infected seed or infested soil. Whilst these conditions are generally associated with cool temperate climates, they are not limited to them, due the use of irrigation which can supply both the necessary water but also cool the top soil (especially if deep bore water is used). Our inability to attribute the occurrence of disease outbreaks to a single factor, such as geographical location, soil type, rainfall or temperature, is almost certainly due to the fact that conditions must be suitable for infection within a particular crop: all these factors may vary over relatively small scales, and high levels of infection occur when suitable conditions coincide with the period of tuber initiation. If all the necessary requirements for infection occur at the right time (tuber initiation), then the biphasic nature of the pathogen enables rapid multiplication of the pathogen and can subsequently lead to high levels of disease (even if initial inoculum levels are relatively low). It must also be noted however, that even when conducive conditions do not coincide with tuber initiation, powdery scab can still develop if a prolonged period of cool wet conditions follows later in the season.

Areas which require future research efforts

Cultivar resistance

- Determining the genotype / environment / pathogen / cultivar interactions. Understanding how different cultivars interact with the environment may assist in cultivar selection for disease management. In addition, understanding how different strains of the pathogen interact with the environment and their host would enable us to breed durable resistance.
- Determining mechanisms of resistance in cultivars would facilitate the breeding to powdery scab resistant cultivars.
- Studying population dynamics of *S. subterranea*/variation in pathogen.

Biological control (impact of soil microbiology on pathogen/disease)

- Suppressive soils – the existence of suppressive soils is at present based on anecdotal evidence and has not been experimentally proven. Work to determine abiotic/biotic factors associated with “suppressive” soils would be beneficial in enabling identification of soils with a low risk of developing disease.
- Rotation- determines the role of alternative hosts in the life cycle of the pathogen and survival of resting spores in the soil. In addition, evaluate impact of crop rotation in terms of the effects of suppressive crops and fallows.

Risk assessment and decision support software

- Determine conditions for required for infection – temperature, water, susceptible period.
- Integration of management strategies.

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