BRITISH POTATO COUNCIL

A review to investigate novel ways to control or manage powdery scab disease in potatoes

Blair M McKenzie

Scottish Crop Research Institute

2005

Contents

SUMMARY

This review examines the science defining and controlling the environment around the roots and tubers of potatoes. The soil environment is considered in the context of understanding and controlling the soil organism and pathogen *Spongospora subterranea*, the cause of powdery scab of potatoes. The review is based three sources of information:

1) well documented understanding of soil science,
2) anecdotal evidence gathered from interviews with a range of people involved in potato production and processing, and
3) literature associated with potato agronomy and *S. subterranea* pathology.

Brief comment is made on the need to understand the soil medium when sampling for inoculum.

The review synthesizes the information assembled into a flow chart covering aspects of field selection and potato production. The flow chart covers three phases in sequence:

- the plant character
- pathology
- soil science including agronomy.

For each of the questions in the flow chart a score is assigned on the basis of risk for powdery scab, and comment made on the usefulness of the questions in providing insight for management.

The discussions developed from the flow chart are used to suggest novel and integrated ways to manage powdery scab and to identify gaps in understanding.

BACKGROUND

Powdery scab of potatoes, caused by the organism *Spongospora subterranea*, is one of the most important disease problems for the cultivation of seed and ware potatoes, especially in cool wet years. This review concentrated on the areas of field selection, cultural practices and integrated crop management, while acknowledging opportunities for plant breeding as a means of disease control.

While there have been previous reviews of powdery scab, this review focused on *S. subterranea* as a soil organism and as such used understanding of soil science in relation to other soil organisms to inform ideas on disease development. The areas of soil science considered were texture versus structure, soil water, aeration, temperature, soil mechanical properties, soil pH, redox and soil biology.

A flow chart covering aspects of field selection and potato production was developed. The flow chart covers three phases in sequence: the plant character, pathology and soil science including agronomy. For each of the questions in the flow chart a score is assigned on the basis of risk for powdery scab, and comment made on the usefulness of the questions in providing insight for management. The questions in the flow chart are in plain language, with alternative ways to express the questions often provided in the text. The discussions developed from the flow chart are used to suggest novel and integrated ways to manage powdery scab and to identify gaps in understanding.

INTRODUCTION

The biology of the powdery scab pathogen-plant interaction has been studied in some detail. A European workshop, held in 2000 at the SAC in Aberdeen, brought together researchers from at least 7 countries, and resulted in the Proceedings of the First European Powdery Scab Workshop (ISBN 09-0587-516-8). Amongst the conclusions from the workshop was a table of management options for an integrated approach to control powdery scab and associated viruses. The topics listed in this table were: field selection, cultural practices, cultivar resistance or tolerance, biocontrol, seed, hygiene, soil, legislation and seed certification, and integrated crop management. Some of these are clearly outside the scope of a review e.g. legislation, while others are clearly central e.g. field selection.

It is in the areas of field selection, cultural practices and integrated crop management that this review will focus, while acknowledging opportunities for plant breeding as a means of disease control. The workshop identified issues such as disease history, soil characteristics e.g. soil pH, inoculum concentration, and a range of cultural practices associated with the production of potatoes that are important for disease occurrence and severity. Practices that seemed to provide most opportunity were those involved in field selection, seed-bed preparation, planting, crop rotation and irrigation.

S. subterranea BIOLOGY AND POWDERY SCAB

This review will not dwell extensively on the biology of *S. subterranea*, a topic which has been thoroughly reviewed by Harrison *et al*. (1997) amongst others.

However a few comments are necessary to provide context for the review. The organism, *Spongospora subterranea* is responsible for powdery scab. The organism remains in soil as thick-walled resting spores, typically about 4 μm in diameter. These resting spores are usually clumped together into porous cystori, which are commonly termed spore balls and are typically between 40-80 μm in diameter. The spores may persist in soil for more than ten years. When water is present and other less well defined conditions are favourable the resting spores germinate, releasing zoospores. Harrison *et al*. (1997) speculate on the possible causes of germination and survival strategies associated with simultaneous or staggered germination.

The released zoospores (also about 4 μm in diameter) swim through, or move with the soil water, until they encounter a root or root hair, or they expire. On encountering a root hair the flagella of the zoospore are withdrawn and stylet is forced into the root hair. This begins the process of disease infection of the root. The plasmodium formed inside the root hair develops and subsequently releases, into the soil solution, up to 8 more zoospores that can each further infect the root or other tissue.

Powdery scab results from the zoospores infecting recently initiated tubers. The infections process is likely to be similar to that for roots described above (Harrison *et al*. 1997) but the exact process is less clearly documented. The result is scabs developing on the surface of the tuber, but which may penetrate well into the tuber itself. Consequences of the disease are blemish effects on the tubers, which may have major, detrimental effects on marketability.

SOIL SCIENCE

Spongospora subterranea is a soil organism as well a pathogen of potatoes. As such, there is a need to understand the physical, chemical or biological medium in which the organism resides. An understanding of ways to manipulate soil properties or processes coupled to knowledge of the organism may suggest management options to influence either the infection or spread of powdery scab. The information in this section is largely based on what is known from other soil organisms, with the limited information specifically on *S. subterranea* mainly considered later. It is not an extensive review of soil physics or chemistry, rather a description of selected properties that have been invoked as involved in the incidence or severity of powdery scab.

Texture versus Structure

Soil is defined by two properties – soil texture, the relative amounts of the primary particles sand, silt and clay; and soil structure, the arrangement of the primary particles with organic matter and the pore space containing water and air. Soil structure manifests as secondary particles, commonly called aggregates and the pore spaces between and within these aggregates. A good structure for the growth of roots of most plants is an aggregated soil with aggregates typically of diameter 0.5 – 2.0 mm. For most purposes, including potato production, soil texture is fixed, while soil structure is changed by many agricultural activities including cultivation and machinery traffic. The separation of clods and stones with their forward burial into wheelings, as occurs in potato production, is one of the few agricultural practices sufficiently intensive to influence soil texture, but even then only on a local scale. Soil properties have typically been studied at the macroscopic level of fields or perhaps crop rows, but soil organisms are typically microscopic (e.g. *S. subterranea* spore balls are mostly between 40-80 μm diameter and the individual spores around 4 μm diameter).

The driver for studying soil at the microscopic level has been to understand soil function. An example of which is the sorption-desorption reactions of nutrients to clay or organic matter, which will, in turn, influence the macroscopic management. The motivation for the scientific study of soil at the macroscopic level is related to understanding and manipulating crop production. Examples include decisions on lime or fertilizer application based on mean values of pH or nutrient concentrations throughout the entire field. The intention here is to relate the different scales to understand how *S. subterranea* behaves in soil, and how the soil might be managed to decrease the incidence and severity of powdery scab symptoms.

Soil is a three dimensional medium. The soil profile is a vertical section, with agricultural soils typically revealing 2 or more horizons or layers. The surface or A horizon generally contains more organic matter and thus has more the biological activity than the subsoil or B horizon. Typically the depth of the A horizon is around 30 cm, coinciding with the depth of cultivation. Root growth commences in the A horizon and tuber development is largely confined here. It is likely therefore that, even with the extensive soil manipulation involved in potato production, the spore balls and the zoospores that emerge from the spore balls, will be confined to the A horizon, unless movement in water transports them to the subsoil. This has obvious implications for where in the soil infection of roots can occur.

The amount of solid soil material per unit total volume is the bulk density, ρb, of the soil, expressed as kgm^{-3}. In general, the bulk densities of soils used for potato production lie between 1.1 and 1.4 kgm^{-3}, with surface soils generally having lower values than subsoils. By definition, and as used in the recent review "Soil compaction and potato crops" (Hatley *et al*. 2005) soil compaction is an increase in soil bulk density with a related decrease in pore space. Thus the greater the bulk density the more compact the soil. In addition, when a soil is compacted the loss of pore space is usually at the expense of the largest pores. This has implications for the storage and movement of water, including the creation of relatively dense impermeable layers that may cause localized waterlogging when excess rainfall or irrigation occur.

Soil Water

The quantity and movement of water in soil is important for *S. subterranea* – which is an organism that relies on water for all stages of the life cycle, apart from the resting or spore ball phase. For this reason this review will establish the language needed to understand water in soil, but will not dwell on methods required to measure or control soil water. Most simply, the volumetric water content of a soil, θ, can be expressed as the volume of water per unit volume of soil (v/v). The water content can also be expressed by weight, θg, as the mass of water per unit mass of solid material (g/g). The two measures are connected by the bulk density ρb, of the soil. While water content is a useful macroscopic measure of soil water status, the amount of information revealed by it at the microscopic level is limited.

While the idea of soil water content has many applications the movement of water in soil and the availability of water to plant roots are controlled by the energy state of the water. The energy of water stored in soil is commonly called "suction". This suction can be thought of as the amount of work that must be done to bring the water to a freely available state at the soil surface. In soil physics theory there are a number of terms that comprise the suction, including gravity related depth in the soil and the amounts of solutes in the water, but for the purpose of potato production these are dominated by the attraction of the water into the soil pores. This attraction of water into the soil pores, depends on the interaction of the water with the soil pores and their geometry, and is termed the matric suction (or in some places suction tension). Typically the symbol ψ is used to represent matric suction.

Because work must be done to release the water from soil, the suction can be expressed per unit mass or water, per unit weight of water or per unit volume of water. Consequently there are a number of unit systems possible. This review will generally confine the units to a height or head in meters or centimeters. Under this scale field capacity would normally be taken as

1m (i.e. 100 cm, or 10 kPa) suction and wilting point as 150 m (or 1500kPa) suction. For plotting relationships involving suction it is common to use a log scale. For a more complete description of the development of soil water physics the reader is referred to any of the many texts related to the subject e.g. Marshall *et al*. (1996), or Hillel (1998).

The soil water characteristic is the relationship between the soil water content and the matric suction (usually expressed in log form). It describes how much water is stored in the soil and how easily it is available to plant roots. Methods to determine such relationships are also set out in numerous texts, such as those suggested above. Because potatoes are grown in relatively sandy soils the complications that arise in understanding water retention curves associated with soils that swell and shrink extensively need not be considered.

Figure 1

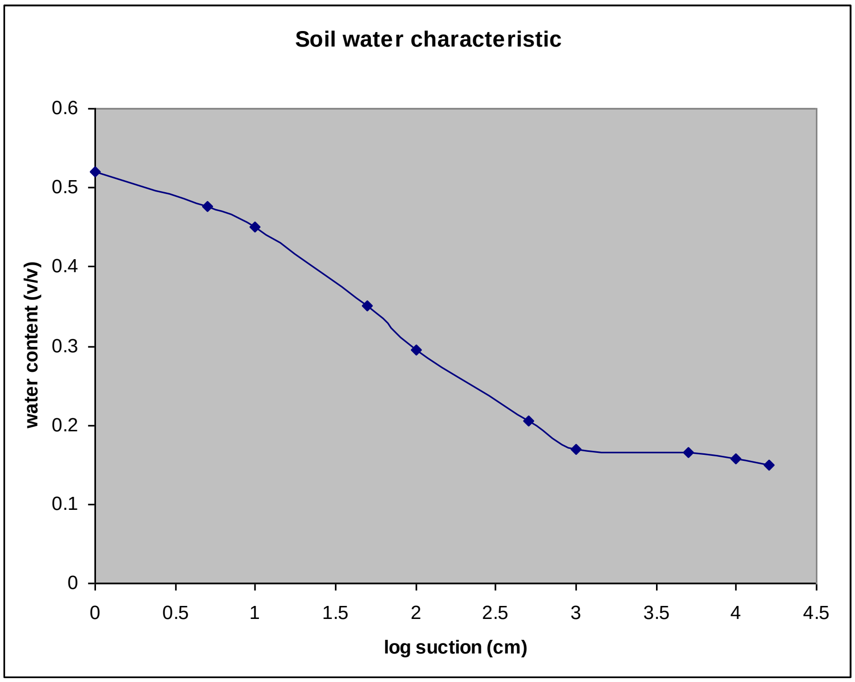


Figure 1 is an example of a typical soil water characteristic. Field capacity, for the example here corresponds to a log suction of 2, i.e. a water content of 0.3. The drier end of the characteristic is controlled by the soil texture while at the wetter end the soil structure dominates the relationship.

The effect of the soil water characteristic on the organism *S. subterranea* and its ability to cause powdery scab symptoms can now be considered. As well as providing information about the availability of soil water to plants and soil organisms, including *S. subterranea*, the water characteristic also provides information on the sizes of pores in the soil. As noted above soil structure is the arrangement of soil particles and their grouping into aggregates, and thus the pore spaces between and within soil aggregates. Pores in soil are sometimes viewed as interconnected tubes of varying diameters and lengths. The filling of a pore with water, or the draining of water from that pore, depends on the diameter of pore and can be presented as the equation:

$D = 4 \sigma / \psi$

Where:
D is the equivalent pore diameter
σ is the surface tension of water, and
ψ is the matric suction.

Thus the soil water characteristic, with the matric suction axes re-designated as equivalent pore diameter, can also be seen as a pore size distribution for the soil. Examples of this relationship are presented in Table 1

Table 1

Matric suction (m)	Significance	Equivalent pore diameter (μm)	Comment
1	Field capacity	30	Size of small spore ball
10		3	Slightly smaller than zoospores
100		0.3	
150	Wilting point	0.2	

The importance of this relationship for *S. subterranea* is that the zoospores move through water-filled pores to infect potato roots. 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 beyond that which limits the locomotion of protozoa, will cause them to encyst. 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 centimeters, even when following a possible chemical signal in the water. Anecdotal evidence (E. Anderson pers comm.) suggests that zoospores of *S. subterranea* can move far further than Harrison *et al*. (1997) suggest, with distances of more than 0.5 m being suggested. This brings the possibility of movement between crop rows, with implications for epidemiology. It is worth commenting that soil pores tend to be tortuous and that the tortuosity becomes greater in smaller pores. So that the straight line distance the zoospores can swim in soil is likely to be much less than observed in tests done in free water. Similarly, the distance over which any chemical signal from roots to zoospores can operate is likely to be very limited. There is clearly a need to resolve the differences in the suggested range that zoospores can swim.

While soil physics has developed systems of equations to describe the movement of water into and through soil, these describe macroscopic flow and are of limited applicability at the individual pore scale. So, while there have been studies of the distribution of soil organisms through soil by water these have mainly considered macroscopic movement of human pathogens (e.g. Gagliardi and Karns 2000). What is needed for our understanding of the movement of microorganisms in soil is appropriate models that can consider the movement as mass transport.

However, the zoospores exist in water, held within pores, and this water may be also moving. Some water movement may be in response to the gravity related suction when the soil is wetter than field capacity leading to flow through the soil profile. The movement of water in smaller, more tortuous pores will be slower than in larger pores. However, other movement may be in response to gradients in matric suction established by plant roots drawing water for transpiration. The complexity of the situation is further exacerbated when one considers that plant roots modify the pore size distribution around them. During growth and expansion roots must compact the soil in their immediate vicinity, changing the pore size distribution. It is therefore not surprising that, the extent of the contribution of this water movement to roots has on the infection process is unknown.

Aeration

The pore space in the soil is fluid filled, and that fluid is water, air or a combination of the two. Thus an increase in soil water content, will decrease the air-filled content of the pore space. The air in the soil reflects the composition of the normal atmosphere at the soil surface. As aerobic organisms (e.g. plant roots and soil animals) use the oxygen in the soil air, they release carbon dioxide changing the composition of the soil air. If replenishment of the soil air does not occur the, oxygen deficiency may occur. Low oxygen concentration slows tuber development and thus prolongs the period of susceptibility to powdery scab.

Replenishment of the oxygen and release of carbon dioxide takes time because these gases must move through the tortuous pore spaces to the soil surface. The processes that lead to recharge of the soil air are diffusion – movement due to differences in the concentrations of individual gases, and mass flow – movement due to sucking in or pushing out air that is in the soil, without discrimination between gases. The main driver of replenishment of the soil air by mass flow is change to the soil water content. Thus as water drains from the soil, air is drawn in to replace the water. While mass flow of air is important diffusion of gases in response to localized concentration gradients in the dominant mechanism by which the oxygen enters the soil and carbon dioxide escapes. Diffusion of e.g. oxygen through water is approximately one ten thousandth the rate of diffusion of oxygen through air. Thus having significant air-filled pore space is important to ensure oxygen supply to soil organisms including plant roots.

From this, it can easily be seen that soil conditions will have a major impact on the supply of air to organisms living in the soil. Waterlogging, the state where water cannot drain from the soil, leads to oxygen deficiency because mass flow drawing fresh air into the soil cannot occur and diffusion of gases cannot occur through the water filled pores. From Table 1 it can be seen that at field capacity pores larger than 30 μm diameter will be air filled. To maintain soil in an aerated condition pores larger than 30 μm diameter are important, particularly if the pores are continuous to the soil surface. Compaction of the soil, e.g. by machinery leads to the loss of pore space and in particular the loss of large pores open to the soil surface – that are important for aeration. Prevention of compaction and stopping the soil becoming waterlogged are thus important for aeration.

It is worth noting that at the microscale, say of the size of the zoospores of *S. subterranea*, there may be great variability in the soil. This variability will obviously be less in soil that has gone through e.g. extensive cultivation operations to achieve a homogenous seedbed. Nevertheless it is likely that within the soil profile microsites will exist that will provide niches suitable for a wide range of soil organism. Roots growing in soil will be respiring – using oxygen and releasing carbon dioxide. While the respiration by individual roots is unlikely to cause major gradients in gas concentrations, these may be sufficient to act over the short distances needed to attract *S. subterranea* zoospores.

The paragraphs here, based on texts such as Leeper and Uren (1993) cover the principles of aeration, and are useful ways to think about large scale processes. The key determinants of oxygen concentration in soil are replenishment, particularly by diffusion, and the demand for oxygen by roots and soil organisms. The demand for oxygen will also depend on the activity of these organisms – which will respire much more quickly in warm soil, than in cold soil.

Temperature

Temperature is a key determinant of the activity of soil organisms, including *S. subterranea*, controlling both the physiology of the organism and also the chemical environment in the soil solution. The temperature of the soil is, in turn, controlled by the amount of energy reaching the soil surface, the movement of that energy into the soil, mainly by conduction, how the energy is dissipated through the soil and how the energy is lost from the soil by convection or as latent heat. The loss as latent heat from the soil is often overlooked but can be understood as evaporation of water from soil requires the water to undergo a change of state from a liquid to a gas, and this change of state requires energy which is derived from the soil, cooling the soil in the process.

Soil temperature changes in response to daily and annual cycling. These are typically presented in soil physics as waves to match the general temperature cycling in the atmosphere. Solutions to differential equations, based on soil thermal properties with incoming and outgoing energy, are in the form of sin waves. While the mathematics of the solutions is not relevant here, some of the observations of the understanding of soil temperature regimes are relevant to understanding the behaviour of *S. subterranea* in soil.

Daily temperature cycles, driven by weather, are far more variable than annual temperature cycles, driven by climate. In both cases however the greatest variability occurs at the soil surface, with an increasing effect of the soil acting to dampen the amplitude of the temperature wave. The implication of this is that even a few centimeters into the soil temperature extremes will be ameliorated to an extent that the amplitude is only a few degrees. Temperatures of 11-18^{0}C, at 10 cm soil depth, are generally considered optimal for powdery scab.

There are several practical ways to select sites for soil temperature regimes or to manipulate the soil temperature. Manipulating the soil temperature will, usually, change other soil properties. Sites with a southerly aspect, (i.e. that are south facing in the northern hemisphere) will tend to be warmer and hence drier than those with a northerly aspect. Examples of common methods of manipulation of soil temperature are to cover the soil with different coatings. Dark coating e.g. black plastic can be applied to increase the soil temperature, while white plastic may increase reflectance of heat and thus prevent the soil heating. Insulating materials e.g. fleeces may be used to protect the soil surface from frosts, and to prevent the loss of heat resulting in decreased temperatures. Ridging the soil so that the ridges have increased exposure to the sun e.g. setting the ridges to face south in the northern hemisphere increases the opportunity for the soil to be warmed by the sun. Irrigation has been used as a frost protection method because more energy is needed to overcome the latent heat associated with evaporation – before the soil freezes.

Soil Mechanical Properties

Considerable work has been done on the role of soil mechanical properties on roots and to a lesser extent on larger soil organisms, such as earthworms (Greenwood and McKenzie 2001). Strong soil is a major limitation to the elongation of plant roots (Bengough and McKenzie 1997). While *S. subterranea* will not directly be influenced by the physical strength of the soil, the disease severity may be increased if root growth is slowed by strong soil that prevents roots elongating, or if the increased soil strength results from soil compaction associated with the loss of large soil pores. As noted above, it is likely that most spore balls are located in the soil A-horizon or seedbed, and thus the more rapidly root tips can elongate out of the seed bed the less chance there is for the tips to be infected.

Also noted above, it is the large continuous soil pores that are responsible for draining excess water from the profile, preventing waterlogging, and in allowing mass flow and diffusion processes to keep the soil well aerated. Large pores may also permit the movement of zoospores through soil. The extensive cultivation needed to prepare a seedbed for potato production is likely to interrupt pore continuity and may, if wet conditions occur, prevent drainage of excess water.

The mechanical properties of soil include aggregation and the processes of aggregate formation and disruption. Aggregates of the size suggested to be suitable for seedbeds, typically 0.5 – 2.0 mm diameter, are susceptible to breakdown by the processes of slaking and dispersion. Slaking is the breaking down of aggregates into smaller aggregates when relatively dry soil is suddenly wet by water. The propensity of aggregates to slake is increased by the loss of organic matter from the soil, associated with mineralization, and hence is associated with cultivation. Dispersion is the physical separation, in water, of primary soil particles from one another. Dispersion is usually associated with the clay mineralogy and cation chemistry of the soil. Because most of the soils used for potato production in the U.K. are relatively sandy, coupled with the use of lime and/or gypsum, suggests that soil dispersion is limited. The two processes, separately, or in combination, can lead to surface crusting and interrupt the movement of water and air into the seedbed. They also lead to slumping of the seedbed, creating regions of increased bulk density, which in turn can be associated with poor drainage and waterlogging. If the soil remains in a dense, wet condition, loss of any residual aggregation occurs and a massive structure is generated, which is extremely difficult to repair.

Several people in the industry have mentioned impressions of compacted layers, or even "pudding basins" of dense soil formed underneath the seedbed (E Anderson pers comm.). These features are attributed to using heavy machinery and tilling the soil in a too wet state. Observations such as these are not confined to the potato industry, and the compacted layers at depth may be a result of using heavy harvesting machinery from previous crops, at times when the soil was too wet to support the high axle loads or to resist shearing. Economic pressures to sow crops within limited time exacerbate the risk of working the soil in an inappropriate condition. The optimum soil water content at which soil should be worked to form a seed bed is just drier than the plastic limit. The plastic limit is defined as the gravimetric water content below which the soil is friable and crumbles and above which the soil is plastic. The plastic limit is typically taken as approximately a matric suction of 650 cm. (As an example in Figure 1, log 650 = 2.8, and corresponds to a water content of around 18%).

Spore balls of *S. subterranea*, can remain viable and in the soil for periods of years. During that time, to all intents and purposes, they are part of the soil, and as such, will be influenced by the dynamic processes of aggregation and aggregate breakdown. This review will not consider all the processes that change the structure of the soil, but it is clear that even the processes already mentioned must mean that spore balls are likely to become associated or bound to clay or other minerals or to soil organic matter. Where and how spore balls sit within the soil structure does not appear to have been considered. For example if spore balls are bound to other soil organic matter they are more likely to experience attack by other soil organisms than if the spore balls are bound to clay particles within soil aggregates. Implications of the location of sporeballs within the soil structure will again briefly be considered in the section on sampling of soil.

Soil pH

pH is the hydrogen ion concentration of the solution expressed as a log scale. Soil pH is the driver of most chemical reactions in soil and controls the availability and/or toxicity of several elements e.g. phosphorus becomes less available as the pH moves away from 7 in either direction while Mn deficient at high pH becomes toxic at low pH. Of interest here is the nature of Zn in soil, since it has been associated with soils that are suppressive to powdery scab. Zinc exists in soil as Zn^{2+}. Zn is part of the soil solution, is an exchangeable cation associated with soil mineral particles and in forms unavailable to plant roots. Zn in the soil solution is highly dependent on the soil pH (Jeffery and Uren 1983) and thus its availability is greatly affected by agricultural practices such as liming – the addition of calcium carbonate to soil. Typically Zn concentrations of 6 $\mu g\ g^{-1}$ are considered sufficient to help suppress powdery scab, but this is greater than the usual concentrations in Scottish soils used for potatoes (E. Anderson pers comm.).

While general macroscopic understanding is useful, as noted above the soil is not a homogenous medium and there will be extensive variation at the microscale. This becomes particularly important when considering the interactions between *S. subterranea* and potato roots. While potatoes are noted as being generally intolerant of high pH (i.e. intolerant of alkalinity) conditions in the rhizosphere of potato roots may be different from the bulk soil. The general idea that plant roots exude less carbon in acidic conditions, has lead to suggestions that there will be less substrate available for the general microorganism population under low pH. While there is a great deal of yet to be understood about rhizosphere processes, it is interesting to speculate on competition for sites to attach to roots between *S. subterranea* and other soil microorganisms.

Redox

Plants and other photosynthetic organisms derive their energy from sunlight. Heterotrophic organisms, like *S. subterranea*, derive energy from the oxidation of reduced substrates, in the process using oxygen as a "terminal electron acceptor" and with the production of water. While some soil organism can use terminal electron acceptors other than oxygen this is not an option for *S. subterranea* – an obligate aerobe. Under even localized waterlogging, changes in the soil biology associated with redox changes, will cause major differences in the nature and availability of many ionic species within the soil solution.

Soil biology

S. subterranea is not the only organism in the soil and as such has to exist in an environment where competition and predation exist. Several authors (e.g. Newsham *et al*. 1995) have noted diminished disease severity where roots are in a symbiotic relationship with mycorrhizae. In these cases the infection of the root by the fungus seems to act to prevent the establishment of disease or root feeding organisms. However mycorrhizae are adversely affected by cultivation. Cultivation breaks up the hyphal networks, diminishing the amount of hyphae in the soil. For potato production where multiple cultivation passes are used the amount of mycorrhizal inoculum available is likely to be very small. I know of no studies relating mycorrhizal infection of potato roots and the severity of powdery scab.

While often overlooked earthworms play an important role, not only in physically modifying the soil, but also in modifying and breaking down organic matter in the soil. Geophagous earthworms live by ingesting and digesting soil organic matter. In that process the organic matter is ground in the crop of the earthworm. The crop is part of the alimentary canal, which usually contains coarse sandy material to help breakdown recalcitrant organic matter. Whether spore balls of *S. subterranea* could survive such a system that has evolved to digest soil organic matter is unknown. Of course, earthworm populations are severely detrimentally influence by cultivation and may take many years to recover. Thus, activities involved in the production of seedbeds for potato production may also wipe out earthworm populations.

SAMPLING OF SOIL

There is extensive literature on sampling soil for a wide range of purposes; a task that increasingly uses geostatistics to understand soil processes and define sampling strategies (Webster and Oliver 2001). In any sampling exercise the critical questions are 1) what is being sampled for, 2) what information is required and, 3) what is the medium from which the sample must be collected? This review will not extensively examine the considerable literature on soil sampling, rather consider some information appropriate to understanding the organism *S. subterranea* and the powdery scab in soil.

Sampling strategies for soil properties vary depending on what information is being sought. An entirely different regime would be selected if samples were being collected in a search for a contaminant than if sampling for a general indication of e.g. soil pH in a field. In the same way, different sampling strategies for *S. subterranea* would be adopted if the information sought was "is the organism present in the soil in this field", than if the information sought was "what is the inoculum concentration in the soil in this field". Likewise if the soil sample collected is to be used for direct assay the approach may be different than if the collected sample were to be used in conjunction with bait plants. So any sampling strategy associated with spore balls of powdery scab in soil will need to define the question or questions being asked, in the same way that strategies for understanding manifestation of the disease would need to define the question being asked. In these examples the two things, inoculum and manifestation of the disease may be related, but similarly may not. I will now briefly consider some examples of what might be sampled for and why, assuming that the medium is soil associated with potato production.

A simple first sampling might be to obtain a general understanding of the concentration of inoculum in the soil. For this a traditional sampling strategy, taking several samples at a range of sites across a field, perhaps using a grid or "W" strategy to locate sites for collection could be employed. Samples collected in this way might be combined and sub-sampled to decrease the numbers of samples for measurement. With appropriate measurement of the sample, this might provide an indication of the general concentration of inoculum in the field. Note, that nothing is said in this procedure about spatial distribution (including depth), nor about spatial or temporal variability. Processes, such as preparation of a seedbed for potato production, tend to homogenize the surface soil and may decrease the amount of sampling that must be done compared with sampling soil pre-cultivation.

It would appear that little is known about how and where the spore balls remain in soil. There are numerous hypotheses that are associated with this gap in the literature. For example, are the spore balls associated with organic matter or aggregates in the soil, do they move deeper in the soil with time, or is there distribution associated with other soil properties? To answer these scientific questions on the nature of the soil organism, more detailed and precise sampling would need to be developed – but such sampling is likely to be necessary to understand *S. subterranea* as a soil organism. This could lead to improved sampling strategies e.g. if *S. subterranea* is bound to soil organic matter then sampling for soil organic matter could target the organism.

With the improvement in assays for the inoculum concentrations in soil we are now in a position to ask questions. In sequence these questions should be:

- Where are the spores in the soil – both at what depth and to what are the bound?
- How does soil preparation change this distribution?
- What factors determine the longevity in soil?

For this review the primary purpose of taking soil samples is to predict the risk and potential severity of powdery scab, based on the inoculum concentration in soil. Some seed growers have ceased growing potatoes on land known to extensively contaminated and invested considerable time and energy finding land not previously used for potato production. In between these extremes of zero soil inoculum and a, so far undefined, concentration too great to permit profitable production there is a presumption that increased inoculum increases disease risk.

FIELD SELECTION AND PRODUCTION FLOW CHART

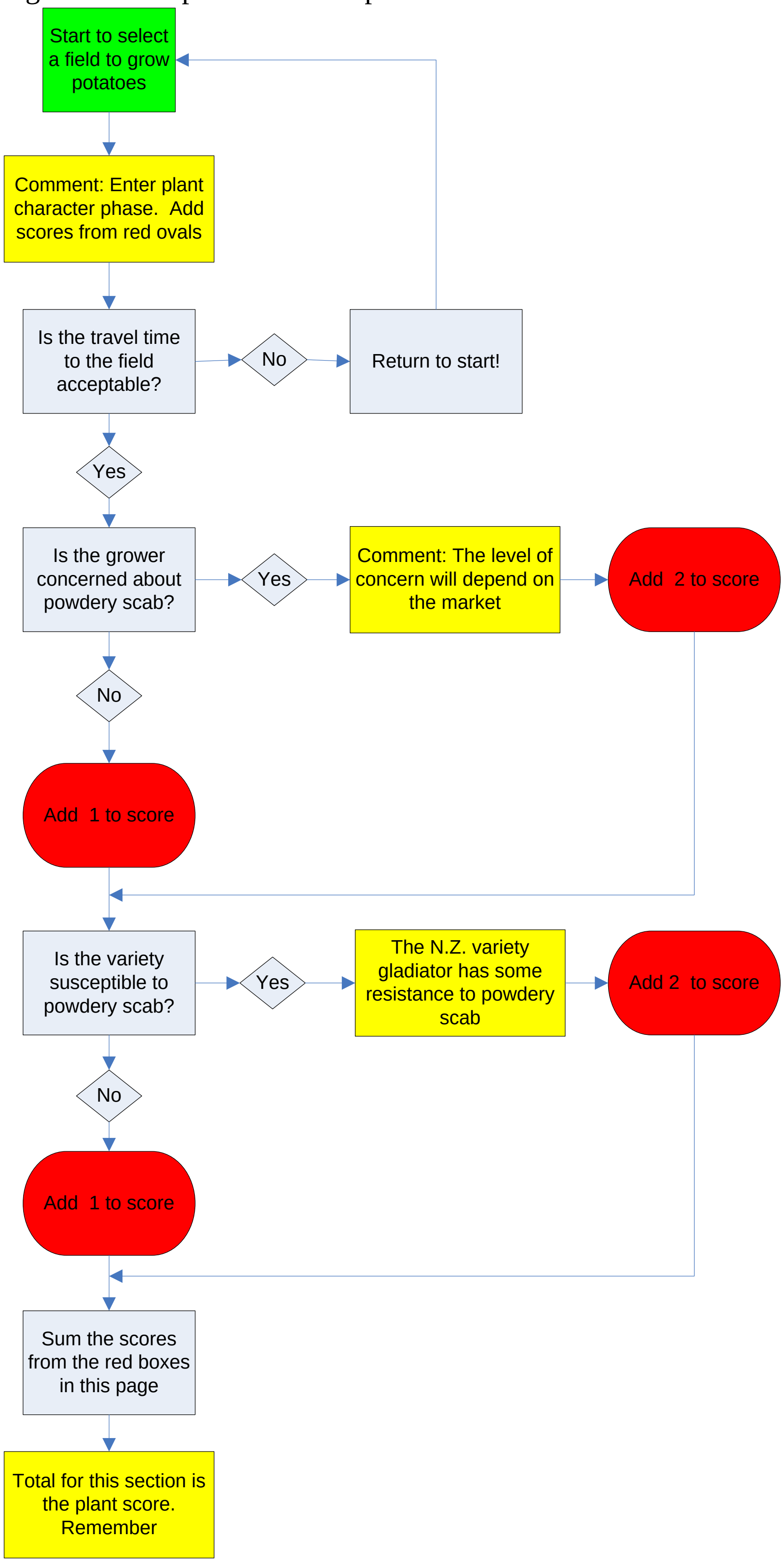
The flow chart, or decision tree, presented as Figure 2 works through a sequence of questions that a grower, intent on minimizing the risk of powdery scab, may consider in producing a potato crop. Developing the flow chart forces appropriate questions to be asked in sequence and identifies areas where insufficient information or understanding is available to satisfactorily answer the question or take action. The questions identified can then be checked further against the existing literature. The flow chart could, with modification, be used as an extension or decision support tool. Similarly, put into the past tense, the flow chart could serve as a case study to unpick what has happened in crops where powdery scab has been identified.

The flow chart is colour coded. This is done for ease of use, and is not an absolute requirement. As set out here the start of each section is in green; comments are in yellow; decision boxes, where questions are posed, are in blue; and boxes where points are scored are in red. The expected sequence is to work through the flow chart starting with the plant character phase (Figure 2a), then the pathogen phase (Figure 2b), and the soil phase (Figure 2c). As written, a score is achieved for each of the three sections which, after all three scores have been obtained, could be multiplied to provide an overall risk. In this scheme a larger number indicates greater risk. The values provided are somewhat arbitrary and are certainly require testing, debate and discussion before wider circulation outside an initial test group. Test groups would comprise focus groups of growers and/or agronomists who would work through the flow chart to "road test" it. In each section consideration is given for the users to introduce a level of concern and it is intended that there is sufficient flexibility that scores could be ameliorated or enlarged to suit individual attitudes.

Figure 2a is the plant character phase. The first question of travel time is not trivial in its own right. Further the question serves to flag practical questions of access and suitability of available land. As the flow chart is designed, no account is given of any differential in the cost of land known to be free of powdery scab versus land that is known to be at risk of the disease. Presumably, as the area of land suitable for potato production but free from powdery scab becomes increasingly limited growers will pay a premium for access to such land. This review made no effort to assess price elasticity with risk of, and cost of management of, powdery scab.

There are other questions that could be added to the travel time to suitable land. Since the profitable production of ware or processing potatoes requires irrigation, it is implicit in the questions of distance to travel that one of the factors in finding suitable land is the availability of irrigation, and that there is no cost differential for water between sites. Similarly, to move machinery incurs a cost, including fuel and depreciation. Fertilizer and other inputs have to be transported, and again these transport costs may be significant. These questions are noted here simply to remind the reader that powdery scab is only one issue in the production system, and hence not treated in isolation.

Figure 2a. The plant character phase



From conversation with growers it is apparent that the concern about powdery scab varied markedly. This concern was based on good or bad experience, the geographic location, for which packing company the crop was being grown, and the intended use of the crop. Hence, the comment that the concern will depend on the market is a surrogate for a wider range of issues. Disease severity is not considered – where minor outbreaks may have little effect on production for some purposes, but greater impact e.g. on production for sales to supermarkets. One view, expressed by several people in the industry, was "in wet years, crops yield well - but you get powdery scab; in dry years, crops yield less well - but there is little powdery scab". People expressing this view saw powdery scab only as taking the absolute premium from top production, but not threatening yield disaster. They tended to make other production issues higher priority.

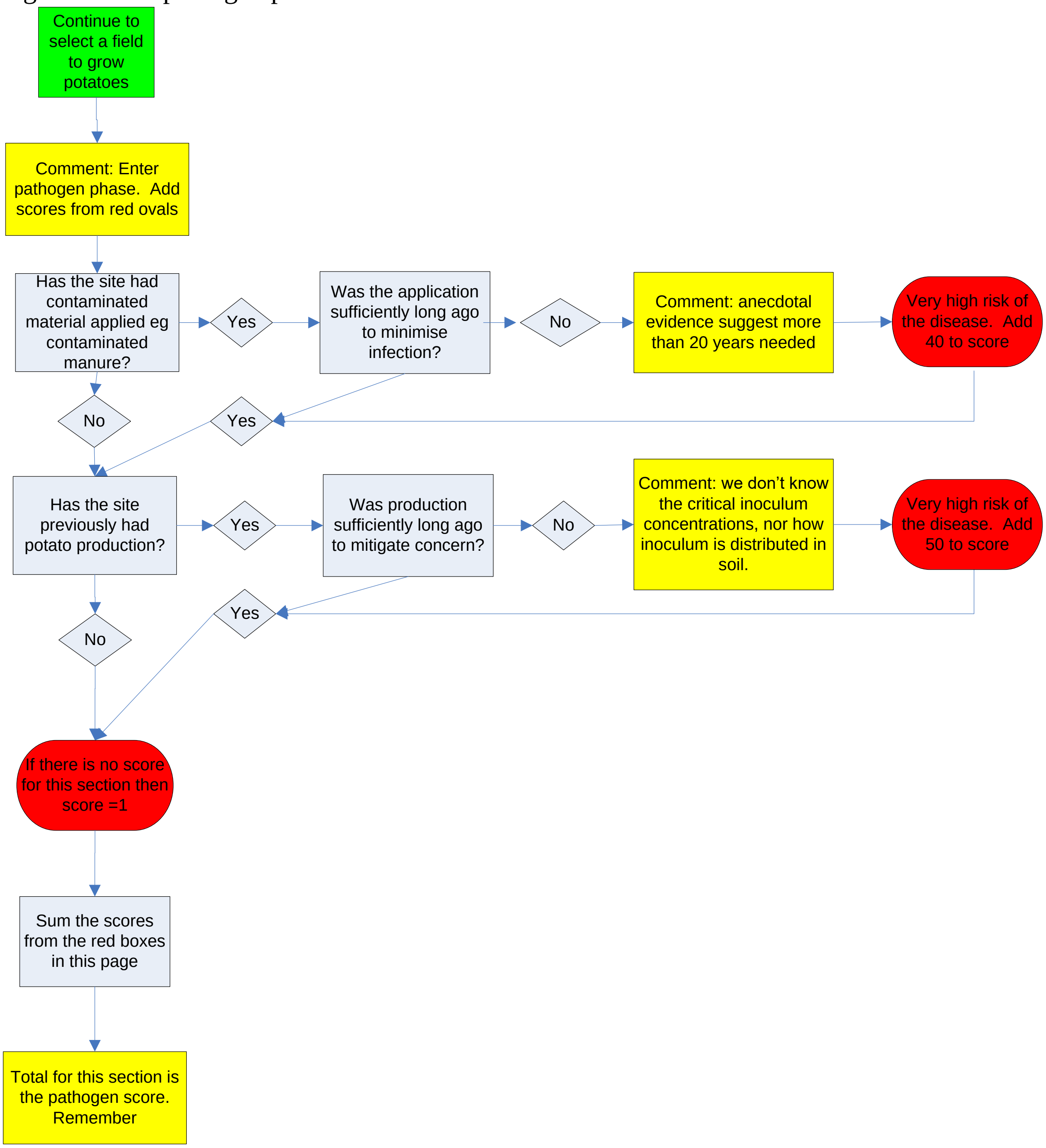
The scores associated with the level of concern are small, but never zero. This, in part, reflects an additional risk associated with powdery scab – virus transmission. Potato Mop Top Virus (PMTV) is associated with powdery scab and should not be overlooked. So, even when growers may be unconcerned about powdery scab, there are other conditions that should be added to make the score greater than zero. No separate questions have been included in the flow chart to specifically cater for viruses.

I have included a question about susceptible varieties because there is at least one variety "gladiator" from New Zealand which has some resistance to powdery scab (J Bradshaw pers comm). For the purposes of using this flow chart as a decision support tool the approach here would be to insert the current list of recommended varieties and to provide a score for each. The current powdery scab rating from NIAB ranges from 1-9, with 1 the most susceptible and 9 least susceptible. Varieties, such as Piper and Nadine are rated as 2, while Hermes in rated as 8. Interest amongst some contractors in Scotland is sufficient to include resistance to powdery scab as a breeding criterion for some commercial operations (J Bradshaw pers comm).

Bradshaw *et al*. (2000) suggested that to breed for disease resistance is difficult due to problems associated with inoculum concentrations and viability of spores. They suggested that beds similar to those used by Wastie *et al*. (1988) were needed to standardize the disease risk. These beds or nurseries provide an opportunity to control inoculum concentrations in soil. Issues associated with inoculum will be further discussed as part of Figure 2b, but the importance of sufficient control in using the organism for scientific purposes is well made.

Figure 2b focuses on the likelihood that concentrations of inoculum in the soil will be sufficient to generate a powdery scab problem. The severity of any epidemic is not quantified here. Inoculum can be introduced to a field by the application of contaminated material. Material that could carry a significant inoculum load includes material spread to land as manure or slurry resulting from livestock being fed contaminated potatoes (S Wale pers comm.). The time that inoculum remains viable in the soil is not quantified and will presumably depend on a range of factors (see Harrison *et al*. 1997 and discussion of Figure 2c). At least twenty years is suggested by several people involved in practical management of powdery scab as the time spores can remain viable in soil.

Figure 2b The pathogen phase



The question "Has the site previously had potato production?" again could be refined, depending on the purpose of the flow chart. Pentland Crown, an old but highly susceptible variety seems to be associated with the build up of very high concentrations of inoculum in the soil. As the inoculum can remain viable in the soil for around twenty years, fields previously used for this Pentland Crown may still pose a greater risk than fields used more recently with less susceptible varieties. With varietal differences suggested, a secondary question, relating to the previously grown variety could easily be inserted. The comment box associated with the question on previous potato production raises the uncertainties in risk associated with the inoculum concentration and distribution in the soil. The implicit assumption with the inoculum is that the risk is the same wherever the inoculum is in the soil, what it is bound to and how long it has been there. Whether these questions are sufficiently important to warrant investigation to the point where they could be used in forming a question for the flow chart is debatable.

That plants other than potatoes can act as a host for *S. subterranea* was not ignored, but was not used as the basis for a question in Figure 2b. Harrison (1997) gives numerous examples of other plants acting as hosts for *S. subterranea* and note members of the Solanaceae and Chenopodiaceae are suitable hosts. For a question to be framed for the flow chart some mechanism of quantification is necessary. While temporal separation between potato crops can easily be assessed (e.g. 5 years since last crop) it is difficult to quantify the impact of weeds and other crops in maintaining or changing the inoculum concentration in the soil.

If alternative hosts were included in the flow chart, one approach might be to include only plants on which the powdery scab life cycle can be completed. Thus it would be necessary to include volunteer potatoes occurring as a weed problem, and coltsfoot (*Ullucus tuberosus*), a weed that reputedly can be used to complete the disease life cycle. A score associated with e.g. grower monitoring of the field could then be included. This however is also problematic, as growers leasing land would not have monitored the field over previous seasons. Other plants, that are hosts, but in which *S. subterrane*a cannot complete its life cycle could still be omitted.

Inoculum may also enter the field with the seed. While a question could easily be included into the flow chart for the introduction of inoculum with seed, this was not done for simplicity. It seems unlikely that any guarantee could be given regarding the introduction of inoculum with seed. Grading of potatoes may lead to spores being passed from diseased tubers to clean tubers, with the transmission remaining undetected. Thus there is no easy way to confirm, and thus include a risk score, for contaminated seed.

Figure 2b shows very high scores for the presence of inoculum, and these are somewhat misleading. While it is true that powdery scab cannot occur without a source of inoculum, disease severity is clearly not linearly correlated with inoculum concentration. In fact the incidence or severity of the symptoms of powdery scab on tubers is not correlated with the inoculum concentration in the soil at sowing because of the overwhelming effect of environment.

Figure 2c The soil and environment phase

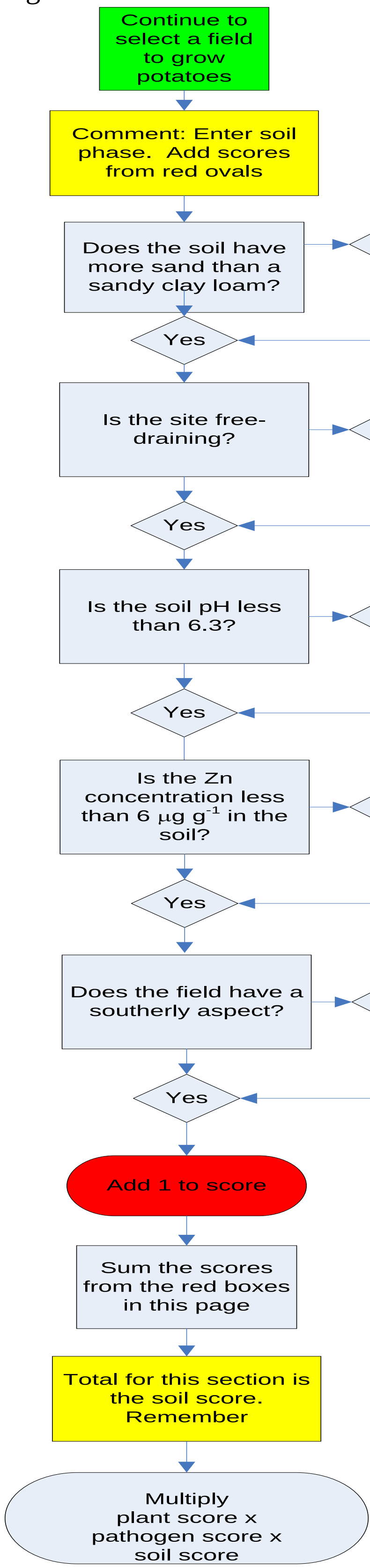


Figure 2c covers the soil or environment related aspects and is thus the basis for management. With the exception of the first question most of the issues or questions in Figure 2c have the facility that they can be managed as part of agricultural production.

The first question in Figure 2c relates to the soil texture. Because texture is a stable property of soil and can fairly easily be determined by hand, it is a useful first indication of the field suitability for potato production. Depending on the user group, the question could e.g. be expressed more precisely as "is the percentage of sand in the A horizon greater than 60%?" Expressing the question in rigorous scientific terms could avoid uncertainty. Whichever way it is expressed, there are, as with previous questions, a number of assumptions and supplementary questions that follow logically. Texture here is of the A horizon. Drainage characteristics, which are texture related, depend more on the texture of the B horizon.

Texture of the A horizon is used as a surrogate for the ability to produce a seedbed. For roots to elongate and for tubers to expand a soft soil is required. If the soil has too much clay then it may require superior management or environmental control to produce a seedbed. There may also be an increased risk that the any seedbed prepared may set hard. Thus the question is listed as of only minor to moderate risk for powdery scab. How to prepare a seedbed, on soils with more clay than the suggested sandy clay loam may become an interest as the areas with powdery scab contamination become increasingly limited.

Whether a site is free draining depends on several factors. These include some e.g. texture of the B horizon, that are fixed, and others that are clearly changed by management e.g. the creation of compacted layers at depth as a result of cultivating the soil with heavy machinery when the soil is wetter than the plastic limit. (For definitions of these terms see the section on soil mechanical properties). Soil can be managed to improve drainage, e.g. by encouraging the formation of biopores or installing artificial drains. There is clearly scope to recommend standards that should prevent waterlogging and thus limit the cycling of wet and dry phases in the soil that some suggest exacerbates powdery scab.

Standards can be set if the same question of drainage is expressed in purely soil physics terms of e.g. "Is the soil hydraulic conductivity greater than 5.5×10^{-6} ms^{-1} at 0.3 m depth?" This links to standards, e.g. documented as part of the U.K. soil survey or as in this e.g. set the U.S. Soil Conservation Service as the minimum requirement for soils to be classed as of moderate drainage, and thus suitable for potato production. The use of such a question in a flow chart used as a decision support tool would require considerable skill in interpretation.

The question of soil pH may be adjusted for different regions in the U.K. Certainly however it has been suggested that the incidence and severity of powdery scab is correlated, all be it weakly, with increased soil pH.

As with the soil pH, the concentration of Zn in the soil influences the incidence and severity of powdery scab. While the mechanisms of this influence are not fully demonstrated, applications of Zn have been one management strategy to help control powdery scab. The mode of action appears associated with germination or activity of zoospores.

Southerly aspect is a surrogate for soil temperature and is manageable only at the field selection stage. For this reason it is given a relatively low score.

The novel use of synthetic chemicals, possibly fungicides e.g. as soil pre-treatments, has not been considered in this review. It is an area that might be explored in the context of the appropriate regulatory frameworks.

As the flow chart is currently formatted the minimum score that can be achieved is 2x1x1 = 2. The maximum score possible under this format is 4x91x61=22,204. As indicated previously these scores are not arbitrary, but nor are they precise. For use of the flow charts as a decision support tool a threshold could be set, below which management could ignore powdery scab in producing a potato crop. What the appropriate threshold should be is would depend not only on the soil science and agronomy but also on the political weighting the disease might have for perceptions of production sanitation in an export context. As such no value will be recommended here.

Above the threshold value, scores could be allocated to each group e.g. low, medium, high and severe risk. For each group management guidelines could suggest management strategies. For the higher risk categories these management strategies may require advance planning so that the soil conditions are improved prior to potato production beginning.

While the flow chart is designed solely for powdery scab, there is clearly opportunity to modify it, not only for other soil borne diseases of potatoes, but also appropriate soil management to meet the current "Good Agricultural and Environmental Condition" (GAEC) standards. This would be done with the idea of incorporating soil factors common to different diseases with GAEC to look for synergies in soil management techniques.

NOVEL MANAGEMENT

That there is a need to have ways to manage or control powdery scab of potatoes is clear. There have been suggestions relating to agronomy and soil management presented as part of extension presentations for many years (e.g. MAFF 1981). Any management strategy must take into account that disease control is only one part of potato production and that powdery scab is only one of several important diseases. Potato production requires the supply of water and nutrients to the crop, and that the soil remain sufficiently soft to allow the easy growth of roots and expansion of tubers.

Two things follow from these observations. First, it is important that the soil be prepared and maintained in the best possible condition, to allow the crop the best window of opportunity to develop. It also follows that after maintaining the soil in best possible condition any control or management technique considered for powdery scab needs to be based on a clear stated mechanism, and should fit in with existing agronomy. Discussion with those involved in the industry provided no suggestion that there was any simple single control measure, either currently available or in development. Fungicide and other pesticide applications are of limited use. Pesticide use is becoming more tightly controlled and thus is unlikely to provide a simple solution to powdery scab. Biofumigation with oilseed rape, had a clearly proposed mechanism, but was tried and found unsuccessful for powdery scab control. Other ideas, whether orthodox or unorthodox, suggested without a defined mechanism proposed, are unlikely to have consistent performance.

As potatoes are grown in rotation, it is possible to see potato production as the sum of more than one year's agronomy. The impact of use and management of the field in the year prior to potato production seems to have limited consideration. Developing the soil over more than one year to a well aggregated, stable, aerated, soft, free-draining, biologically active state is desirable for healthy root growth. Standards exist relating these criteria to root growth for many crops, and they could be established for potatoes. While there is a widely held view that potato production needs, and will always need, multiple cultivations there is an opportunity to use the years preceding the potato crop as an opportunity to develop the soil into the best possible condition. To this end, several simple options might be considered. For example the incorporation of organic matter from preceding crops is likely to stimulate biological activity, including earthworms and mycorrhizae and help stabilize the soil to prevent slaking. The use of minimum tillage in the year or years prior to the potato crop will avoid plough pans developing and improve drainage. Controlling traffic to defined "tram-lines" that ideally would be consistent with the machinery used for potato production will help the soil remain soft and friable. In each of these cases, the improvement in soil condition contributes to a mechanism involved in minimizing powdery scab disease. Thus an integrated, multi-year cropping rotation, focused on achieving the best possible soil condition is likely to help potato production generally, and to managing powdery scab in particular.

CONCLUSIONS AND FUTURE PROSPECTS

Future prospects for understanding and managing powdery scab need to be based on scientifically established mechanisms. The examples presented here range from metabolomics to more conventional laboratory and field experiments done in carefully controlled or measured soil environments.

Harrison *et al*. (1997) discuss the likely causes of germination and survival strategies of zoospores from spore balls. They suggest a range of factors could be important including ionic strength, water potential and signal molecules. Hinch and Weste (1979) observed that zoospores (of Phytophthora) were attracted to roots and that the zone of root elongation was generally most attractive. They suggested that metabolites from the roots were a signal attracting the zoospores. Recently, Johnson *et al*. (2005) have shown isoflavonoid compounds from white clover roots act to attract clover weevils. Identification of the chemical signals involved in stimulating germination of zoospores or guiding the zoospores to roots offers opportunities to interfere with the process. Recent advances in metabolomics of root exudates could be employed to understand the drivers of *S. subterranea* behaviour.

Bradshaw *et al*. (2000) noted the need for control of inoculum concentration to provide standard or defined conditions to study powdery scab development. They noted the work of Wastie *et al*. in 1988 in providing this inoculum control on a sufficient scale to understand the development of the disease along with the development of the crop. Soil properties are interrelated and dynamic rather than static. For example, water and air together occupy the soil pore space and are in constant flux as drainage, plant water use, and temperature cause continual changes. In the same way that inoculum concentration needed to be carefully controlled or monitored at a representative scale to understand disease development, so to, does the soil environment. Thus to understand the soil organism *S. subterranea* we need to have facilities to control or measure the dynamic state of the soil. With the ability to measure the soil environment with sufficient precision a number of simple testable hypotheses become possible. Split root experiments to test or confirm the mechanism of Zn efficacy, or to understand the role that other soil organisms have in protecting potato roots from infection, can be easily be developed. These should provide the mechanistic understanding that can lead to novel managements for powdery scab.

As the availability of land, free from *S. subterranea* from becomes decreases, pressure on heavier textured soils to produce potato crops will occur. In the previous section, I noted that there is a widely held view that potato production needs, and will always need, multiple cultivations. What was not said with this comment is the quantification of what conditions are needed in the soil through the growing season. Rather than defining the cultivation practices needed, we should define the soil conditions needed. Then options on how to get to the required condition, perhaps in the process opening the opportunity on heavier soils less conducive to powdery scab can be explored. Such an approach could be coupled with an exploration, using GIS, soil survey, and mathematical techniques available to interrelate and interpret soil data, of options to produce potatoes, while minimizing the risk of powdery scab.

ACKNOWLEDGEMENTS

I thank numerous colleagues at SCRI, BioSS, SAC and Rothamsted Research for their comments and discussions. In particular I thank, Drs Alison Lees, Stuart Wale and Richard Whalley. I also thank the numerous people in the potato industry who have willingly given their time to talk with someone who was asking, often naive, questions. In particular I thank Eric Anderson of Scottish Agronomy for his tutorials on potato agronomy and production.

REFERENCES

Bradshaw, J.E., Lees, A.K., Stewart, H.E. 2000. How to breed potatoes for resistance to fungal and bacterial diseases. Plant Breeding and Seed Sci. 22, 3-20.

Bengough, A.G., McKenzie, B.M. 1997. Sloughing of root cap cells decreases the frictional resistance to maize (*Zea mays* L.) root growth. J. Exp. Bot. 48: 885-893.

Collis-George, N., 1959. The physical environment of soil animals. Ecology 40: 550-557.

Gagliardi, J.V., Karns, J.S. 2000. Leaching of *Escherichia coli* 0157:H7 in diverse soils under various agricultural management practices. Appl. and Env. Microbiology 66: 877-883.
Greenwood, K.L., McKenzie, B.M. 2001 Grazing effects on soil physical properties and the consequences for pastures: a review. Aust. J. Exp. Agric. 41: 1231-1250.

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

Hatley, D., Wiltshire, J., Basford, B., Royale, S., Buckley, D., Johnson, P. 2005. Soil compaction and potato crops British Council Research Review Ref: R260.

Hillel, D. 1998. Environmental soil physics. Academic Press.

Hinch, J., Weste, G. 1979. Behaviour of *Phytophthora cinnamomi* zoospores on roots of Australian forest species. Aust. J. Bot. 27: 679-691.

Jeffery, J.J., Uren, N.C. 1983. Copper and zinc species in soil solution and the effects of soil pH. Aust. J. Soil Res. 21: 479-488.

Johnson, S.N., Gregory, P.J., Greenham, J.R., Zhang, X.X., Murray, P.J. 2005. Attractive properties of an isoflavonoid found in white clover root nodules on the clover root weevil. in press.

Killham, K. 1996. Soil Ecology. Cambridge University Press.

Leeper, G.W., Uren, N.C., 1993. Soil Science an introduction 5th edition. Melbourne University Press.

M.A.F.F. 1981. Powdery Scab of potatoes. Leaflet 99. Ministry of Agriculture, Fisheries and Food.

Marshall, T.J., Holmes, J.W., Rose, C.W., 1996. Soil Physics 3rd edition. Cambridge University Press.

Merz, U., Lees, A.K., eds 2000 Proceedings of the First European Powdery Scab Workshop. Aberdeen Scotland July 20-22 ISBN 09-0587-516-8.

Newsham, K.K., Fitter, A.H., Watkinson, A.K. 1995. Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. J. Ecol. 83: 991-1000.

Wastie, R.L., Caligari, P.D.S., Wale, S.J. 1988. Assessing the resistance of potatoes to powdery scab [*Spongospora subterranea* (Wallr.) Lagerh.]. Potato Res. 31: 167-171.

Webster R and Oliver MA 2001. Geostatistics for Environmental Scientists John Wiley