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Research Review

Non-water control measures for potato common scab

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Preface

This review was commissioned by the British Potato Council to consider non-water based control options for potato common scab.

The Main objectives were to:

- Comprehensively review refereed and conference publications and internet sources on non water-based control measures for common scab.
- Contact research groups around the world to identify research projects in progress that would identify other non water-based control measures.
- Objectively assess the information available and interpret for the GB situation.
- Provide a comprehensive report and bibliography.

A workshop was held at CSL to obtain industry views as part of the review process and information incorporated into the document.

Improved control of the potato common scab pathogens is likely to depend on efficient and cost effective integration of existing measures rather that the introduction of completely novel measures, as outlined at the end of the review.

Non-water control measures for potato common scab
A literature review

1. Introduction

Although Great Britain has a maritime climate, water for agricultural use is becoming an increasingly scarce resource. This is especially true in the vicinity of some of our most fertile land. A raft of legislation and related initiatives are coming together to change the rights and responsibilities of water users. These include the EU Water Framework Directive (2000/60/EC), Water Bills in England & Wales and Scotland, Catchment Area Management Strategies, Diffuse Pollution Regulations, the Groundwater Directive and various other environmental directives. Their impact for the potato industry has been summarised in a BPC report 'Changes to water policy and their effect on the potato industry' (Tompkins & Clayton, 2003). The net result is that water restrictions on abstraction will increase and the cost of using water will rise. Less availability and more expensive water potentially imposes severe restrictions on potato production.

Water is needed for yield but also for quality in potato production. Common scab is one of the main diseases that will affect quality in potatoes where irrigation is not available. The causal organism is widely distributed and is thus a threat in almost all soils. Cultivar resistance can effectively limit development of the disease but in the driest years infection can occur even on highly resistant cultivars. The use of water during the period of tuber initiation has provided an effective control measure where properly applied. However, with increased restrictions on water use, alternative approaches to the control of common scab are needed.

This literature review was commissioned to examine non-water measures for the control of common scab. The review is divided into two parts. Firstly, the taxonomy of common scab initiating *Streptomyces* species is described. Although the causal organism has been referred to as *Streptomyces scabies* (now renamed as *Streptomyces scabiei*), there are in fact a number of *Streptomyces* species associated with the disease. Their association with different symptoms and their differing biology are described.

Secondly, the non-water control measures found in literature and internet searches are described. Researchers have been investigating potato common scab, and reporting their results, throughout the world since the 1800's. The literature is extensive, international and often historic. However, the non-water control measures fall into 12 categories, each of which is discussed in detail.

After the bibliography, there is a section describing potential avenues for future research. The first part of this section records the potential avenues for future research identified by the authors. The second part lists the areas of potential practical value endorsed1 by agronomists attending a workshop on common scab on 2nd July 2004. [It may be better to combine these to avoid repetition?]

2. Taxonomy of scab forming S*treptomyces* species

2.1. The causal agents

There is now no doubt that potato common scab is caused by a wide range of *Streptomyces* species. Historically this was recognised since the 1920's in North America, Europe and USSR, but very few of the strains have been maintained and it is now impossible to determine whether the identifications made were correct. Bradbury (1986) lists 38 plant pathogenic *Streptomyces* spp. Of these, 23 are reputed to be pathogenic to potato, although some of the evidence is based only on pathogenicity tests (Millard & Burr, 1926). Many of the species listed as being pathogenic were from the old USSR and were either linked to symptoms or to soil conditions. Because reference strains or accurate descriptions were not available, many of these were not included in the Approved Lists of Bacterial Names (Skerman *et al*., 1989). However, a few were and these included *S. scabies, S. aureofaciens, S. clavifer, S. collinus, S. globisporus, S. griseus, S. intermedius, S. longisporus, S. rimosus, S. sampsonii, S. setonii, S. tricolor,* and *S. violaceous.*

Streptomyces is perhaps the largest genus of bacteria having many hundreds of species. Most are soil and plant rhizosphere species. They are well known for their ability to compete with other microorganisms either by producing antibiotics or in other ways. They are responsible for the commercial production of many of our antibiotics e.g. streptomycin. The taxonomy of the genus is confused partly due to its large size but partly due to technical difficulties. Hence, common scab has tended to be linked with the term '*Streptomyces scabies'* and although it was recognised that this was a species complex, the name stuck and over time *S. scabies* became synonymous with common scab. This was especially true in the USA and UK and, for example, the seminal work on the role of water in control of common scab by D. H. Lapwood and his colleagues at Rothamsted Research Station in the 1970's (Lapwood *et al*., 1973), refers only to *S. scabies.*

Much of the old literature differentiates the proposed species on the basis of symptoms and biological conditions. The newer literature supports this but also includes modern classification criteria such as 16S rRNA sequencing and DNA:DNA homology to further support the existence of many different species. Table 1 includes all the validly published species which cause potato scab. There is clearly a strong link between species and symptom type, soil conditions and perhaps geographic location. Many species are also pathogenic to other, often unrelated, plant species e.g. beet, radish and carrot.

More recently, a further 9 pathogenic species have been described, including *S. acidiscabiei, S. caviscabiei, S. turgidiscabiei, S. europaeiaescabiei, S. stelliscabiei, S. reticuliscabiei, S. luridiscabiei, S. puniciscabiei* and *S. niveiscabiei.*

Common scab of potatoes can be caused by many different *Streptomyces* species, although *S. scabiei* is perhaps the most widespread and common.

2.2. The validly named species for which pathogenicity is undisputed

The most common pathogen worldwide is probably *S. scabiei* as defined by Lambert and Loria (1989a or b? – Reference for b is missing). This causes typical common scab. Typical common scab is also caused by *S. acidiscabiei* (Lambert and Loria, 1989a) and *S. europeaiscabiei* (Bouchek-Mechiche *et al*., 2000a). Most of the other species cause different symptoms (see below and Table 1). These include *S. reticuliscbiei* (Bouchek-Mechiche *et al*., 2000a) and *S. stelliscabiei* (Bouchek-Mechiche *et al*., 2000a), *S. turgidiscabies* (Miyajima *et al*., 1998), *S. caviscabies* (Goyer *et al*., 1996a). Three new species from Korea have recently been described, all of which have erumpent common scab symptoms that appear to be more corky than those caused by other species. These are *S. luridiscabiei*, named for its pale yellow spores, *S. puniciscabiei*, named for its white to purple spores and *S. niveiscabiei*, named for its snow white spores (Park *et al*., 2003). *S. aureofaciens* has been found to cause russet type scab in several different countries. *S. setonii* has been found to cause common scab symptoms in India.

Other species no doubt will be named in the next few years since common scab has worldwide significance and better determinative methods are now available. Several key workers have unclassified strains in their collections.

Many of the pathogenic species have strains that are not pathogenic. These include *S. scabiei*, *S. turgidiscabiei*, *S. aureofaciens*, and *S. setonii*. It is likely that other species also contain non pathogenic strains. *S. aureofaciens* has been suggested to belong to the genus *Kitatospora* rather than *Streptomyces*. A recent study has recommended its retention in *Streptomyces* but showing a close relationship to *Kitatospora*. However, this illustrates the complexity of the genus and the fact that pathogenicity is found in unrelated species within it.

There are 10 validly named pathogenic species for which pathogenicity has been clearly demonstrated in the recent literature and unsubstantiated reports of several other pathogenic species. Some of these species contain non pathogenic strains.

2.3. Nomenclatural anomalies

The Latin binomial, *Streptomyces scabies* is grammatically wrong and has been renamed as *Streptomyces scabiei*. Although this has been corrected for *S. acidiscabies*, now *S. acidiscabiei*, to our knowledge, it has not yet taken account of *S. turgidiscabies* and *S. caviscabies* which should be *S. turgidiscabiei* and *S. caviscabiei* respectively. The most recent 6 published species (Bouchek-Mechiche *et al*., 2000a; Park *et al*., 2003) all take the scabiei epithet into account. The continuation of this review refers to the validly published names.

2.4. Geographic distribution

It is likely that *S. scabiei* has worldwide distribution. Since some of the newly named species are not yet well known, their distribution is not yet known. *S. acidiscabiei* was first described from North America but is now known from Japan and Korea (Song *et al*., 2004). *S. caviscabiei* was first reported from Canada but is believed to occur elsewhere. *S. turgidiscabiei* was first reported from Japan and more recently from Finland (Kreuze *et al*., 1999) and from Sweden and Denmark (Lehtonen *et al*., 2004) but may well be synonymous with *S. reticuliscabiei* currently recorded only from France. *S. europaeiscabiei* is recorded from France, Netherlands and Russia.

S. stelliscabiei is recorded so far only from France. *S. aureofaciens* is recorded from Switzerland, Canada, Finland. *S. luridiscabiei*, *S. niveiscabiei* and *S. puniciscabiei* are currently known only from Korea and within Korea all currently known strains come from Jeju Island (Park *et al*., 2003).

In a recent Defra funded study on several hundred UK strains isolated from a range of scab symptoms on potato, great diversity was shown based on fatty acid profiling and genetic fingerprinting (D. E. Stead, unpublished). However, there was no good correlation between the results from the two methods nor from the reference strains of all species apart from the recently described Korean species. Thus it was not possible to prove, based on the selected methods, whether any of the newly described European species occurred in the UK.

Thus in Europe, four or five of these species are known to exist. In the few studies that have looked at diversity of scab forming species in Europe, all have shown some diversity. A recent French study (Bouchek-Mechiche, 2000a), named several new species occurring in France. It also revealed as yet unclassified strains. These authors refer to several other strains found by others that almost certainly represent new species that cause scab lesions. They also speculate that *S. acidiscabiei* and *S. caviscabiei*, although not found in their survey in France, perhaps occur but at lower frequency. A survey of scab forming species in Finland (Kreuze *et al*., 1999) also found the first record of *S. turgidiscabies* outside Japan and the first record of *S. aureofaciens* for Finland. These authors also found some as yet unclassified strains. A further study on Finnish strains (Lehtonen *et al*., 2004) showed that *S. turgidiscabiei* was perhaps even more common than *S scabiei* in some potato production systems. They also showed that some strains from Sweden and Denmark belonged to *S. turgidiscabiei.*

Thus it is highly likely that some of these species occur in the UK in addition to *S. scabiei*. To date there are no European records of the acid tolerant species. However in the recent Defra study, the reference strains of *S. aureofaciens*, which occurs perhaps widely in Europe, grew well at pH 4.5, although this result differs from other published work and needs confirmation.

S. scabiei probably is the most widespread and common species and probably has worldwide distribution. Whereas some of the recently described species seemed to have limited distribution, more recent work implies that some of these are much more widespread.

Little is known of the status in the UK. Although it is clear that *S. scabiei* occurs, the diversity found in the recent Defra study implies that several other species do exist. The import of seed potatoes from the EU and the proximity of some of the more recently described species in France and Netherlands implies that *S. turgidiscabies*, *S. europaeiascabiei*, *S. stelliscabiei* and *S. reticuliscabiei* will almost certainly be present. It is also clear that some of these are taxonomically different and have different epidemiological characteristics.

2.5. Taxonomic Methods and their use in identification

Traditionally, nutritional and physiological tests were used with host tests to confirm species identification and this was the basis for naming new species. More recently, nutritional kits have been used to support DNA studies (Bouchek-Mechiche *et al*., 1998; Bouchek-Mechiche *et al*., 2000a), fatty acid profiles have been used (Faucher *et al*., 1993; Stead, unpublished), morphology of spores and mycelium together with pigment analysis (Faucher *et al*., 1992; Faucher *et al*., 1993; Loria *et al*., 1997) and numerical taxonomy based on many different characters (Lambert *et al*., 1989b, Faucher *et al*., 1993). Although all these methods have value, they have not been able to resolve the differences between groups within the *S. scabies* complex. However, since non-pathogenic Streptomycetes are commonly associated with potato tubers, microscopic and plating analyses such as for pigmentation and spore morphology are useful rapid screens for partial characterisation. Most pathogenic species have rows of 10–50 smooth cylindrical spores on terminal mycelial strands that are either flexuous or spiral in form. These characteristics are presented in Table 2.

Molecular methods have been more discriminating. A range of techniques have been used including RFLP (Doering-Saad *et al*., 1992; DNA hybridisation (Bouchek-Mechiche *et al*., 2000a; Healy & Lambert, 1991), 16S rRNA sequencing (Takeuchi *et al*., 1996; Park *et al*., 2003;Song *et al*., 2004), PCR and PCR-based genetic fingerprinting (Sadowsky *et al*., 1996; Stead, unpublished). In sum, genetic fingerprinting separates clusters of strains but this does not necessarily correlate with species. PCR of specific genes has the same limitations, 16-23 S rRNA spacer sequencing does not differentiate all species and 16S rRNA sequencing differentiates most but not all species. DNA:DNA homology is the gold standard with taxa sharing less than 70% homology being worthy of separate species rank. However this is a labour intensive technique requiring a high level of skill to guarantee consistent results. It may be used for taxonomic studies but not for routine identification.

A recent paper (Lehtonen *et al*., 2004) reviews the literature on diagnostic methods and recommends species specific PCR assays for 3 species occurring in Finland. These protocols are based on 16SrRNA sequences. However the authors recognise that 16S sequences cannot be used to differentiate all pathogenic species and cannot differentiate *S. scabiei* from *S. europaeiaescabiei* or *S. reticuliscabiei* from *S. turgidiscabiei.*

Streptomyces taxonomy is complex. The methods needed to identify them accurately appear to rely on potentially expensive, time consuming methods that require a high level of molecular expertise and expensive equipment. A novel approach is to develop species specific PCR primers for *in situ* detection without the need for isolation. However, current methods cannot differentiate all pathogenic species.

2.6. Taxonomic position of pathogenic species

Phylogeny is the study of the molecular evolution of organisms and relies on a molecular clock of some description. Currently, the sequence of the 16S ribosomal RNA gene is the gold standard. Phylogenetic trees based on several studies using similar sequences from the 16S rRNA gene show a similar picture but not all include the same strains or the same precise sequence (Takeuchi *et al*., 1996; Park *et al*., 2003; Song *et al*., 2004). Scab forming strains fall into several clusters:

1. The S. diastotochromogenes group containing several soil non-pathogens plus S. scabiei, S. europaeiscabiei and S. stelliscabiei

2. The Kitosatospora spp group containing S. aureofaciens although Groth et al. (2004 reference missing) recognise that S. aureofaciens should remain in Streptomyces
3. The S. griseus group which also contains S. setonii and S. luridiscabiei
4. The S. acidiscabiei group
5. The S. turgidiscabiei group which also contains S. reticuliscabiei. These may be synonymous (L. Gardan, personal communication)
6. The S. ambofaciens group which as well as containing many saprophytic species also contains S. niveiscabiei and S. puniciscabiei

It is clear that pathogenicity is present in completely unrelated taxa within the genus *Streptomyces* in a diverse way. This will undoubtedly have great relevance to most methods for control of scab.

2.7. Symptom type

The term common scab is used for a wide range of symptoms but is generally intended for scab lesions which are erumpent but with some form of cratering. The degree of erumpentness has been associated with different species. Historically, Millard and Burr (1926) recognised *S. tumuli* coming from particularly erumpent scab lesions and more recently, Miyajima *et al*. (1999), described *S. turgidiscabies* from turgid erumpent lesions in Japan. The *S. scabies* complex is responsible for much typical common scab, but it is only recently that this complex has been taxonomically revised. Bouchek-Mechiche *et al.* (2000a) described *S. stelliscabiei* for those pathogenic strains producing a typical star like crater within an otherwise typical erumpent scab lesion. See also below.

Pitted scab is also a well recognised symptom, describing a non erumpent, often deeply pitted crater-like lesion. Again, historically, Millard and Burr (1926) recognised *S. virodgenes* as producing pitted scab. More recently, Goyer *et al*. (1996a), described *S. caviscabies* from Canada as the cause of deep pitted scab, separating this from the pathogens that cause shallow pitted and erumpent scab.

Other symptoms include netted scab, a new name for an old disease in Europe (Scholte & Labruyere, 1985) and russet scab. These are often confused with each other. Scholte and Labruyere (1985) argued that there were two forms based largely on those from USA which they termed russet scab and those from Europe which they termed netted scab. *S. aureofaciens*, a well established scab pathogen is often associated with russet scab. Bouchek-Mechiche *et al.* (2000a) recently proposed a new species causing netted scab in Europe and named this pathogen, *S. reticuliscabiei*. Bouchek-Mechiche et al. (2000b) also note that netted scab in Europe can be caused both by *S. retuliscabiei* and by another species that they described in Bouchek-Mechiche et al. (2000a) - *S. europaeiscabiei*, which predominantly caused typical common scab. The difference appears to be partly cultivar-based. Bouchek-Mechiche (2000a) also present evidence from their own work and that of others of several as yet unnamed novel species that cause russet and netted scab. Kreuze *et al*., (1999) found that *S turgidiscabiei*, named for its erumpent lesions often causes deep pitted lesions on cv. Bintje.

There are three basic common scab types – erumpent, pitted and superficial. There is some correlation with the causal *Streptomyces* species; there is some correlation with potato cultivar; there is also some correlation with environmental conditions. Thus for example, a strain that causes one symptom in one cultivar may cause a different symptom in another or in the same cultivar grown under different conditions. The naming of some species has been based on the symptom associated with the early findings. Some recent studies have shown different symptoms under different conditions. Most species probably cause different symptoms under different conditions.

2.8. Environmental impact

Several of the early proposed species were based on scab formation under different environmental conditions. Scab in the USSR at low soil temperatures was thought to be caused by *S. candidatus* a different species to that caused by *S. violaceus* at higher temperatures. A recent study by Bouchek-Mechiche et al. (2000b) recognised 3 groups of French strains based on pathogenicity and temperature. The largest group contained all strains of *S. scabei, S. europaeiscabiei* and *S. stelliscabiei* from typical common scab lesions in potato, carrot and radish and these were most virulent at 20-30^{o}C. The second group were *S. reticuliscabiei* from netted scab lesions were pathogenic to both tubers and roots of only a few potato cultivars but did not infect carrot or radish and were most virulent at 17^{o}C. The third group were *S. europaeiscabiei* strains from netted scab lesions on cv. Bintje that caused netted scab at 20^{o}C and deep pitted scab at 30^{o}C. Their conclusion was that scab control must take account of the species present in the soil.

Soil pH has always been regarded as a means of scab control since '*S. scabies*' was thought to infect tubers only under neutral to alkaline soil conditions. This philosophy was proved to be flawed when acid tolerant strains were found in N. America. Lambert and Loria (1989a) described *S. acidiscabies* which causes typical common scab symptoms but is found at pH down to 4.5. At the same time they showed that the '*S. scabies'* complex was heterogeneous but that a large number of strains centred around the type strain and were prevalent in alkaline soils. They called this central group *S scabies*, leaving no taxonomic home for all the other common scab strains. More recently, Park *et al*. (2003) have described three new species from Korea, all of which cause typical common scab under acid conditions. For the four acid tolerant species, the range of pH tolerated is from c. 4.5 – 9.0, whereas *S. scabies* (Lambert & Loria, 1989b) has a range from c. 6.0 – 10.0.

Storage conditions may also influence the incidence of the different species. Lehtonen *et al*. (2004) found that both *S. scabiei* and *S. turgidiscabiei* often occurred in the same lot of potatoes and indeed in the same lesions. The relative incidences of the two pathogens changed during the 2– to 24–week storage periods when a much higher proportion of scab lesions tested positive for *S. turgidiscabiei* than for *S. scabiei*. These findings suggest that that *S. turgidiscabiei* may be more tolerant to handling of tubers prior to storage (e.g. washings) and to the storage conditions than *S. scabiei.*

Even the use of irrigation for control may be dependent on the type of species present since there are differences in use of water to control common and netted scab. Labruyere (1971) found that whereas increased irrigation caused reduction in common scab it caused an increase in incidence and severity of netted scab. It is now considered that netted scab is often produced by species other than *S. scabiei*, including *S. reticuliascabiei.*

Although there is very little published work on the epidemiological differences between the scab forming *Streptomyces* species, it is clear that these can be significantly different. Successful control will be dependent on a better understanding of the epidemiology of all the scab forming species present in the UK.

2.9. Survival and spread

It is now clear that the pathogenic species compete well in soil and that survival in soil is the major means of spread from one crop to the next (Loria *et al*., 1997). As shown below, other crops can harbour many of the strains belonging to many of the pathogenic species. Survival and transmission on seed tubers is far less important in terms of its contribution to the amount of scabbiness in a crop but import of seed is the major means of introducing new species into another geographic area (Pavlista, 1996; Wilson *et al*., 1999; Stevenson *et al*., 2001; Afek & Orenstein, 2002). There is very little published work on the more recently described species but Lehtonen *et al*. (2004) showed that both *S. scabiei* and *S. turgidiscabiei* survived well on seed but that there were cultivar dependent differences. It is likely that there will be differences in ability to survive both at strain level and at species level.

It is generally considered that seed-borne inoculum contributes a negligible amount to scabbiness of potatoes, whereas soil-borne inoculum is predominant. However, seed-borne inoculum is almost certainly relevant to dispersal of new pathogenic species to fields and areas where they are absent. There is an important need for further study, especially since there are no examples of statutory control for the pathogenic species.

2.10. Host range

Although there have been many studies on host range of *Streptomyces* species, it can be difficult to interpret accurately because the strains used were not well characterised. However, there is no doubt that many strains can cause common scab symptoms on several unrelated hosts. Bradbury (1986) lists beet, carrot, parsnip, radish and sweet potato as other commonly affected crops. From a taxonomic view, it is clear from recent studies that *S. scabiei, S. europaeiscabiei* strains can have broad host ranges. (Bouchek-Mechiche *et al*., 2000a & b; Loria *et al*., 1997; Lambert & Loria, 1989b). Indeed rotations of potato and beet are known to increase scab incidence caused by *S. scabies* (Loria *et al.*, 1997). Although S. acidiscabies is known naturally only from potato, Lambert (1991) demonstrated successful host tests with turnip, radish, beet, rutabaga and carrot but not parsnip.

Some strains and taxa are probably restricted to potato. These appear to include *S. turgidiscabiei, S. caviscabiei, S. reticuliscabiei, S. stelliscabiei,* and possibly the three newly described species form Korea, *S. luridiscabiei, S. puniciscabiei and S. niveiscabiei.* Indeed, some of these may be restricted to pathogenicity on particular potato cultivars.

Research in Canada (Goyer & Beaulieu, 1997) showed that all *S. scabies* isolates were pathogenic on carrot and radish but pathogenicity on beet, parsnip, turnip and potato was variable. Even though *S. acidiscabies* and *S. caviscabies* had only previously been isolated from potato, it was demonstrated that isolates of these species could also infect other crops, such as radish, carrot, parsnip and turnip.

There is increasing evidence for differences in cultivar resistance to different *Streptomyces* species (Lehtonen *et al*., 2004; Bouchek-Mechiche *et al*., 2000a & b) Bouchek-Mechiche (2000b) showed that *S. reticuliscabiei* was not pathogenic to radish or carrot but was pathogenic to a few potato cultivars including cvs. Desiree and Bintje but not Charlotte.

Some *Streptomyces* species and strains have wide host ranges; others appear to have narrow host ranges perhaps within potato cultivars. These differences have significance for breeding resistance and for use of rotations in control but require further study. A key issue here is whether symptomless presence or infections are as important as symptomatic lesions as a source of inoculum for survival.

2.11. *Association with other* **Streptomyces** *species*

Several early studies reported by Bradbury (1986) refer to association of pathogenic species with other saprophytic species and in subsequent host tests; symptom development was dependent on the presence of up to 5 different non-pathogenic strains. A more recent observation (Lehtonen *et al*., 2004) is that in Finland, at least two species are found commonly not only in the same crop but also the same scab lesions. The significance of this type of interaction requires further study.

2.12. *Virulence factors*

For some time, virulence has been associated with phytotoxins. Speculation that scab symptoms were due to the production by the bacterium of a phytotoxin date back to 1926 (Fellows, 1926). However it was not until 1989 that these phytotoxins were isolated, purified, identified and shown to able to induce symptoms (King *et al*., 1991). The main compound is Thaxtomin A but another 10 minor compounds have been characterised (Loria *et al.,* 1997). Thaxtomin A is produced by many of the pathogenic species but not all. Altering its structure in these pathogenic strains results in loss of virulence. However, there are pathogenic strains which do not produce these thaxtomins. The thaxtomin production is linked with a gene called the nec1 gene (Bukhalid *et al*., 1998). Park *et al*., 2003 demonstrated the presence of the nec1 gene in strains of *S. scabiei*, *S. acidiscabiei* and *S. turgidiscabiei* but not in the three Korean species or in any of the saprophytic species tested. Bukhalid *et al*., 2002 have also shown that horizontal transfer exists for this gene and its flanking regions between strains of several species in the *S. diastatochromogenes* group, which includes *S. scabiei* The significance of this remains unresolved but it is clear that there is a pathogenicity island containing several genes associated with pathogenicity (Bukhalid *et al*., 2002) which can transfer horizontally between species. It is also clear that some species e.g. *S. scabiei* contain non pathogenic strains, strains which presumably have lost or never had the pathogenicity island. These authors noted that whereas the DNA sequence of the nec1 gene was identical in all the strains they identified as *S. scabiei*, there was great genetic variation between the strains, implying that there may be even greater diversity of *Streptomyces* species than currently accepted.

Pathogenicity is governed by a series of genes, many of which are located on a pathogenicity island. This part of the DNA can be passed from strain to strain and also between species, apparently unrelated species within the genus *Streptomyces*. The best known of the genes involved is the nec1 gene, which is involved in thaxtomin A production. This phytotoxin plays an important role in virulence but is not essential for pathogenicity, since some strains that do not have the nec1 gene are pathogenic. A key question is how many of the soil inhabiting *Streptomyces* species are able to accept and incorporate the pathogenicity island into their own chromosome and cause scab. Another key question is whether there are significantly different pathogenicity islands that may account for the different symptom types or whether symptom types are due to switching on/off of specific genes within the pathogenicity island.

2.13. Control

Almost all work on control has been done on the *S. scabies* complex or on *S. scabiei* itself. Bouchek-Mechiche *et al*. 2000b make the point that the type of *Streptomyces* species has rarely been taken into account in work on epidemiology of scab formation and in the use of that information in, for example, cultural control. Their paper and that of Lehtonen *et al*. (2004) clearly show that the pathogenic species now known to occur in Europe differ substantially in their ecological requirements. The most obvious example is control by lowering soil pH e.g. by adding elemental sulphur. Will control of *S. scabiei* by this means simply create a niche for one of the acid tolerant species? Four of these are now recognised although they are not yet recorded in Europe.

Almost nothing is known of how to control the newly described species and all current methods assume the pathogen is *S. scabiei*. Even for this pathogen the data collected appear contradictory. Successful scab control must take account of the species present. Key work is needed on cultivar resistance, effects of pH, soil type, temperature, storage etc.

Table 1: *Streptomyces* species causing scab symptoms in potato

Name	Authority	Host	Known Distribution	Symptom
Streptomyces acidiscabies	Lambert & Loria, 1989b	Potato	USA, Canada, Japan	Common scab - raised
Streptomyces aureofaciens	Duggar, 1948	Potato	Canada, Finland, Holland, Switzeland,Germany	Netted and Russet scab
Streptomyces caviscabies	Goyer, Faucher & Beaulieu, 1996	Potato	Canada,	Deep pitted scab
Streptomyces collinus	Lindenbein, 1952	Potato	India	Common scab
Streptomyces europaeiscabiei	Bouchek-Mechiche et al., 2000b	Potato, other vegetables	France, Netherlands, Russia	Common scab
Streptomyces intermedius	(Krüger 1904) Waksman, 1953	Potato, beet	Germany	Common scab
Streptomyces luridiscabiei	Park et al., 2003	Potato	Korea	Corky scab - raised
Streptomyces niveiscabiei	Park et al., 2003	Potato	Korea	Corky scab - raised
Streptomyces puniciscabiei	Park et al., 2003	Potato	Korea	Corky scab - raised
Streptomyces reticuliscabei	Bouchek-Mechiche et al., 2000b	Potato	France	Netted scab
Streptomyces scabiei	(ex Thaxter 1892) Lambert & Loria, 1989a	Potato, other vegetables	Worldwide	Common scab - mostly raised
Streptomyces setonii	(Millard & Burr 1926) Waksman, 1953	Potato	Russia	Common scab
Streptomyces steliiscabiei	Bouchek-Mechiche et al., 2000b	Potato, carrot, radish	France	Star-shaped common scab-raised
Streptomyces turgidiscabies	Miyajima et al., 1998	Potato, other vegetables	Japan, Scandinavia	Pitted scab

Table 2: Diagnostic properties of *Streptomyces* species causing potato scab as reported in the literature

Name	Spore chain shape	Spore colour	Spore Type	Melanin produced	Soluble pigment produced	*Nec* gene present	Growth at pH 4.5
Streptomyces acidiscabies	flexuous	white -pink	Smooth	no	yes	yes/no	Yes
Streptomyces aureofaciens	flexuous and spiral	red brown - grey	Smooth	no	no	?	No?
Streptomyces caviscabies	spiral/flexuous	grey-white	smooth?	no	no?	?	No
Streptomyces collinus	spiral	grey	Smooth	?	?	?	?
Streptomyces europaeiscabiei	spiral	grey	smooth?	yes	no	?	No
Streptomyces intermedius	spiral	bluish -grey	Smooth	no	weak	?	?
Streptomyces luridiscabiei	flexuous	yellow -white	Smooth	yes	no	no	Yes
Streptomyces niveiscabiei	flexuous	white	Smooth	no	no	no	Yes
Streptomyces puniciscabiei	flexuous	pale orange	Spiny	yes	no	no	Yes
Streptomyces reticuliscabei	flexuous	grey	smooth?	no	no	?	No
Streptomyces scabiei	spiral	grey	Smooth	yes	yes	yes	No
Streptomyces setonii	straight -flexuous	yellow-grey	Smooth	no	no	?	?
Streptomyces steliiscabiei	spiral	grey	smooth?	yes	no	?	No
Streptomyces turgidiscabies	flexuous	grey	Smooth	yes	no	yes	Yes?

3. Non-water control of scab-forming *Streptomyces* spp.

3.1. Resistant cultivars

Cultivar resistance is an important tool in controlling common scab of potatoes and tables of cultivar resistance are published, for example by the National Institute of Agricultural Botany (NIAB)/ British Potato Council (BPC) (Anon., 2004). Appendix 1 lists current GB cultivars and their resistance rating to common scab. Mishra and Srivastava (2001) working in India consider that satisfactory and eco-friendly control cannot be achieved without genetic resistance, which is not only cheaper but also stable and thus acceptable to farmers. Rich (1983) is unequivocal: “The most effective method of scab control is to plant resistant cultivars”.

Numerous cultivars with different levels of resistance have been identified worldwide through useful field screening programs. Both durable horizontal resistance (Gergely *et al*., 2003) and simply inherited sources of resistance (Murphy *et al*., 1995) appear to be available. *Solanum phureja* has been identified as a useful source of scab resistance in the production of *S. tuberosum* cultivars (Maine *et al*., 1993) although resistance levels tend to decrease on backcrossing with *S. tuberosum*.

Although many new potato cultivars come with resistance to common scab, no commercially important potato cultivars are immune to infection and the level of resistance is usually not high. One early study of resistance levels amongst 684 potato cultivars from a world collection indicated that none was immune and only 1.3% (Ackersegen, Akebia, Arnika, Carnea, Hindenburg, Kotnov, Patrones, Reichskanzler [Chancellor] and Sarka) were strongly resistant. The remainder could be allocated to seven categories of lower resistance, and almost 75% of the total showed intermediate levels of resistance (Zadina *et al*., 1975).

In multi-location trials on 23 potato clones in the USA (Haynes *et al*., 1997) significant environment, genotype and genotype x environment effects on heritability of resistance to common scab were observed. It was concluded that scab resistance was unstable whereas scab susceptibility was stable across environments and that new sources of scab resistant germplasm would be required to obtain genotypes with high levels of scab resistance that are stable across environments. The fact that even resistant cultivars will become infected given high inoculum levels or favourable environments, means that currently available resistant cultivars will best be used as part of an integrated control system.

The value of common scab resistance in different cultivars may vary with a number of variables including *Streptomyces* species or isolate, soil moisture content and soil pH (Haynes *et al.*, 1997). Mishra and Srivastava (2001) found good correlation between the resistances of 27 potato cultivars to common scab over two years. Hooker (1981) reports that physiological specialisation of subculture isolates of *S. scabies* has been demonstrated in glasshouse trials. Selective pathogenicity by biotypes in the field, however, is of little importance and relative resistance of potato cultivars remains relatively constant over a wide range of natural soil populations.

The limits of currently available sources of genetic resistance to scab are demonstrated by the French fry processing industry in Tasmania where incidence of common scab has steadily increased since the late 1980’s. This is despite Russet Burbank, which is recognised as possessing moderate resistance dominating production (more than 80%) (Wilson, 2001a). Trials by Wilson (2001a) have demonstrated differences in the resistances of clones of Russet Burbank to common scab, although differences between cultivars were greater than differences between the Russet Burbank clones.

Future development of higher levels of resistance will largely depend on an increased understanding of the host pathogen interaction. Recent research on the mechanisms and genetic control of pathogenicity in the scab-forming Streptomycetes is relevant in this respect. Pathogenicity of *Streptomyces* spp. on potato is largely dependent on the ability of strains to produce at least one of two major phytotoxins, thaxtomins A and B (Lawrence *et al*., 1990; King *et al*., 1991). Interestingly, glucosylation appears to be a mechanism of thaxtomin A detoxification and is related to scab resistance and susceptibility in potato (Acuna *et al*., 2001). Therefore, there may be useful marker genes in potato related to an ability to glucosylate the toxins which will aid in effective selection of resistant genotypes. In a more direct approach, scientists at the Tasmanian Institute of Agricultural Research are aiming to develop extreme resistance to common scab within existing potato cultivars through exposure of cell lines to the toxins and regeneration of potato plants from those which survive the treatment (Wilson, 2001a; 2001b). Goto (1981) concluded that the concentration of reducing sugars in peel extracts is positively correlated with scab severity and may therefore be a useful indicator during screening of new breeding material for resistance.

The ability to cause scab symptoms is believed to be inherited between *Streptomyces* spp. by horizontal transfer of a pathogenicity island containing the gene nec1 (which is involved in pathogenicity and physically linked to the thaxtomin A biosynthetic genes) and a transposase pseudogene ORFtnp (Bukhalid *et al*., 1998; Healy *et al*., 1999). Resistance in potato genotypes to thaxtomin activity may therefore be expected to be broad-based across all scab-forming streptomycete strains. However, phytotoxin production was found to vary differently between scab-forming isolates of *Streptomyces scabiei* and *acidiscabiei* in response to changes in pH, temperature and calcium or phosphate availability (Natsume *et al*., 2001). It may therefore be important to ensure stability of resistance in potato across the range of variability within the pathogenic Streptomycetes.

Durable horizontal and simply inherited sources of resistance to common scab are available. However, no commercially important potato cultivars are immune to infection and the level of resistance is usually not high. Significant environment, genotype and genotype x environment effects on heritability of resistance to common scab can be observed and whilst scab resistance is unstable, scab susceptibility is stable across environments.

Relative resistance of potato cultivars remains relatively constant over a wide range of natural soil populations. However, the effectiveness of common scab resistance in different cultivars varies with a number of variables including *Streptomyces* species or isolate, inoculum level, soil moisture content and soil pH. Pathogenicity of *Streptomyces* spp. on potato is largely dependent on the ability of strains to produce at least one of two major phytotoxins, thaxtomins A and B

3.2. Reducing seed-borne inoculum

The relative importance of infection borne on seed tubers and in the soil has been disputed. However, it is generally considered that populations of scab-forming Streptomycetes introduced on seed are likely to be far outnumbered by those already present in field soils (Lapwood *et al*., 1973). In a previous review of the literature, Pavlista (1996) concluded that common scab occurs ubiquitously even on unfarmed land and that common scab infected seed potatoes are therefore not very important as a source for field contamination. Despite this, when considering an integrated approach to scab control, it is advisable not to introduce new pathogen populations to an environment in which measures have been taken to suppress the existing populations. Thus it is commonly advised to avoid planting seed tubers affected by common scab, particularly on common scab-prone soils with low levels of *Streptomyces spp.* or virgin soils (Lapwood, 1973; Brenchley & Wilcox, 1979). Planting infected or contaminated seed with common scab can be regarded as an effective mode of transmission of new scab-forming and possibly more aggressive pathogen strains of *Streptomyces* (Loria, 2001).

On soils not prone to common scab, heavily infected seed can be planted without ill-effects (Brenchley & Wilcox, 1979; Adams & Hide, 1981; Pavlista, 1996). In soils prone to common scab, and where the pathogen is already present, inoculum present in soil is probably sufficient to make inoculum carried on seed insignificant. The frequent occurrence of common scab on horticultural crops (carrots, swede, beetroot) grown from true seed, which does not carry the pathogen, supports this view. Conflicting findings include Stevenson and James (2003) who planted infected seed on a site with a history of common scab and found more scab on harvested tubers than where healthy seed was planted. Wilson *et al.* (1999) demonstrated that both seed and soil borne inoculum were important and concluded their relative importance depended on locality, soil type, environment, pathogen population and cultural practice.

It is generally considered that populations of scab-forming Streptomycetes introduced on seed are likely to be far outnumbered by those already present in field soils. It is concluded that common scab occurs ubiquitously even on unfarmed land and that common scab infected seed potatoes are therefore not very important as a source for field contamination. However, planting infected or contaminated seed with common scab can be regarded as an effective mode of transmission of new scab-forming and possibly more aggressive pathogen strains of *Streptomyces* Thus it is commonly advised to avoid planting seed tubers affected by common scab.

3.3. Crop rotation

There are many conflicting reports in the literature of the effects of crop rotation on common scab incidence. This is probably due to the greater effects of environmental variation between the various studies. For example, Vruggink (1976) determined that the influence of soil type on the numbers and species of actinomycetes appeared to be more important than that of the previous crop grown (including grass, wheat, potato, lucerne and sugar beet). In the UK, the severity of common scab generally decreased as the number of preceding potato crops increased (Hide & Read, 1991). In Poland, increased proportions of potato in crop rotation did not result in increases in infections of the tubers and vegetative parts by *Streptomyces scabies* (Piskorz & Roszak, 1989). In Belorussia, cultivation of potato after lupin decreased common scab, whereas scab incidence was considerably higher in potato crops after maize (Sidorevich, 1977). In the USA, rotation with small grains, maize or alfalfa is usually recommended and Rich (1983) suggests that soy beans and rye are also good rotational choices. However, Li *et al.* (1999) demonstrated that a potato-oat-potato rotation increased scab in comparison with continuous potatoes. Rotation with red clover is also thought to increase scab incidence in the following potato crop. Powelson *et al.* (1993) recommend avoiding rotations with carrot, beet, spinach, turnip and radish.

There are conflicting reports in the literature of the effects of crop rotation on common scab incidence, probably due to the greater effects of environmental variation. In consequence there is little strong evidence on which crops reduce or increase common scab risk. There is some evidence to indicate that increased cropping by potatoes does not increase the risk of common scab.

3.4. Effects of cultural practices

Waterer (2002b) investigated effects of manipulating planting and harvest dates with the aim of reducing the period during which the potato crop was exposed to conditions favourable to common scab. The disease was reduced by minimising the period the crop was in the ground i.e. planting late and harvesting early but yields were unacceptably reduced. Late harvesting resulted in greater increases in common scab than early planting possibly because conditions in autumn are more favourable to scab. Leaving the crop in the ground for longer periods after foliage destruction or desiccation increased common scab incidence.

In general, optimum temperatures for growth of *S. scabies* are relatively high (25-30 ^{o}C) and losses to common scab tend to be worst in warmer areas or growing seasons (Hooker, 1981; Loria *et al.*, 1997). See also temperature effects on *Streptomyces* species in Section 2.8.

There is little evidence to indicate that manipulating planting or harvest date can provide a reliable and practical control measure to reduce common scab.

3.5. Soil pH

Reports of the effects of soil pH on scab incidence have sometimes been conflicting, again reflecting possible larger effects due to environmental and/or pathogen variation. In most reports the pathogen is referred to as *S. scabies* and the interpretation of results therefore do not take into account more recently identified variation in pH tolerance between different scab-forming *Streptomyces* spp.

In Tasmania, an observed pH threshold in the range 5.0-5.2, below which common scab did not develop (Lacey & Wilson, 2001), was in accordance with similar findings elsewhere and in Maine, where scab incidence was similarly correlated with soil pH (Lambert & Manzer, 1991). Other scab-forming *Streptomyces* spp. have lower pH tolerances. *S. acidiscabies* is characterized by its ability to cause common scab in acidic environments (Goyer *et al*., 1996b). In Finland, pathogenic strains identified to *S. scabies* grew at pH 5.0 but not at pH 4.6, whereas other pathogenic strains (now recognised as *S. turgidiscabiei*) grew down to pH 4.4 but not at pH 4.2 (Lindholm *et al*., 1997). In Korea, newly classified scab-forming spp. *Streptomyces luridiscabiei*, *Streptomyces puniciscabiei* and *Streptomyces niveiscabiei* have also been shown to be tolerant of low pH down to pH 3.5 (Park *et al*., 2003a & b).

Greater severity of common scab in soils of high pH has long been recognised (e.g. Waksman, 1950; Lapwood, 1973; Brenchley & Wilcox, 1979; Loria, 2001). Whether the effect of liming in increasing levels of common scab results from increased calcium levels in soil or from increased alkalinity has been controversial. Lambert and Manzer (1991) compared the effect of dolomitic lime and gypsum on common scab and concluded that scab incidence was related to soil pH and not calcium concentration. However, Horsfall *et al.* (1954) found scab severity and calcium content of tubers were positively correlated but Lambert and Manzer (1991) reported higher levels of calcium in tissues showing scab symptoms than healthy tissues and suggested increased calcium content in tubers was, therefore, an effect and not the cause of scab. Findings of other earlier workers are also critically reviewed by Lambert and Manzer (1991). Elucidating the roles of calcium and alkalinity in increasing severity of scab may appear of little practical benefit, however, Lambert and Manzer (1991) point out that low calcium levels in potato soils may reduce crop quality by increasing susceptibility to soft rots, internal rust spot and subapical necrosis. Where soil calcium levels require enhancement to negate these problems this may be better carried out by adding gypsum than lime.

Waterer (2002a) investigated effects of very high pH on common scab. Over a pH range of 7.0 to 9.0 there was little effect on total tuber yields but severity of scab lesions declined as pH increased above 8.5. Marketable yields after grade out to scab were highest at pH 9.0. Percentage of tuber surface covered by scab lesions declined by 2-3% and proportion marketable increased by 10-20%.

Lacey and Wilson (2001) have suggested the apparent relationship between soil pH and severity of common scab may reflect cropping practice. They suggest heavily cropped soils, which are prone to common scab, are more likely to be heavily limed and to receive appreciable quantities of potassium fertilisers. Nevertheless they emphasise the robust relationship between pH and common scab disease and recognise the utility of simple soil pH tests in identifying fields where common scab may be troublesome.

A soil pH below about 5.2 was generally regarded as scab suppressive as long ago as 1918 (Gillespie, 1918) and similar findings across the world have continued to be reported to the present (e.g. Lambert & Manzer, 1991; Lacey & Wilson, 2001). This indicates the robustness of this threshold over the range of soil types and pathogen species studied.

Mizuno *et al.* (2000 or 1997? If 2000 then reference is missing) suggested the suppressant effect of low soil pH on scab is due to its effect on availability of aluminium. Application of ammonium sulphate (an acidifying fertiliser) effectively suppressed common scab in soils containing at least 0.2 to 0.3 mg/l Al but was less effective on soils of low soluble Al concentration. They suggested manipulation of available aluminium levels in soil was better achieved through manipulation of pH than by applying aluminium compounds directly. Successful manipulation of soil pH may depend on the buffering capacity of the soil.

Regulation of soil pH using acid-producing fertilizers such as ammonium sulphate and avoidance of the use of alkaline-producing lime or manure amendments is generally recommended to reduce common scab. In field studies in Korea, an application of sulphur powder to a low-pH soil reduced the disease incidence from 70 to 0% (Park *et al*., 2002a). In Japan, acidification of the soil to pH <4.5 (soluble Al > 0.3 mg per litre) was achieved through application of ammonium sulphate but only when the fertilisers were spread on the surface as opposed to applications directly in the rows (Mizuno *et al*., 1997).

Studies around the world have generally discovered that common scab is very limited below pH 5.0-5.2 and the frequency of this finding indicates the robustness of this threshold over a range of soil types and pathogen species. However, other scab-forming *Streptomyces* spp. have lower pH tolerances including *S. acidiscabies, S. turgidiscabies, S. luridiscabiei, S. puniciscabiei* and *S. niveiscabiei*. These more acid loving species do not appear to be common in the UK. Whether the effect of liming in increasing levels of common scab results from increased calcium levels in soil or from increased alkalinity has been controversial. However, it is concluded that common scab incidence was related to soil pH and not calcium concentration, although a low concentration of the latter can affect tuber quality. In one study over a pH range of 7.0 to 9.0, the severity of common scab declined as pH increased above 8.5. It is suggested the suppressant effect of low soil pH on common scab is due to its effect on availability of aluminium. Manipulation of available aluminium levels in soil was better achieved through manipulation of pH than by applying aluminium compounds. Successful manipulation of soil pH may depend on the buffering capacity of the soil. Regulation of soil pH using acid-producing fertilizers and avoidance of the use of alkaline-producing lime or manure amendments is generally recommended to reduce common scab. An application of sulphur powder to a low-pH soil has effectively reduced the disease incidence to low levels.

3.6. Suppressive soils

According to a recent review by Weller *et al*. (2002), agricultural soils suppressive to soil-borne plant pathogens occur worldwide, and for several of these soils the biological basis of suppressiveness has been described. Two classical types of suppressiveness are known. General suppression owes its activity to the total microbial biomass in soil and is not transferable between soils. Specific suppression owes its activity to the effects of individual or select groups of microorganisms and is transferable. It is particularly useful to consider the interaction of physical, chemical and biological mechanisms of specific suppression in relation to the potential for induction of suppression to common scab in field soils.

Soils suppressive to potato scab have been reported, for example by Menzies (1959) and Lorang *et al.* (1989), usually after several years of potato monoculture. Menzies (1959) showed that soil suppressiveness was eliminated by steaming soil and could be transferred to a conducive soil by mixing in 10% suppressive soil. Liu *et al.* (1996) isolated a relatively high proportion of suppressive strains of *Streptomyces* from lenticels of potatoes grown in suppressive soils. Roles of resource competition and antibiotic production by suppressive strains in biological control of potato scab are unclear. Work by Neeno-Eckwall *et al.* (2001) using antibiotic resistant pathogenic *Streptomyces* strains suggests both may be important. Many suppressive *Streptomyces* strains exhibit antibiotic activity against pathogenic *S. scabies.* Suppressive strains produce a diversity of antibiotics. Assuming antibiotic production is important in biological control, use of strain combinations in practical biological control will reduce the chances of selecting pathogenic strains resistant to antibiotics produced by suppressive strains. Strain combinations may also be more effective in colonising soil under a variety of environmental conditions. Formulation of a compatible mix of suppressive strains is complex and described by Liu *et al.* (1996). Pot trials by Liu *et al.* (1995) showed introduction of suppressive strains reduced scab on potato tubers.

Two classical types of suppressiveness are known. General suppression owes its activity to the total microbial biomass in soil and is not transferable between soils. Specific suppression owes its activity to the effects of individual or select groups of microorganisms and is transferable. Soils suppressive to potato scab have been reported usually after several years of potato monoculture. One mechanism may be the development of suppressive strains of Streptomyces which compete for resources and produce antibiotics.

3.6.1. Physical mechanisms of specific suppression

In terms of soil structure, it is well known that light, well-drained soils favour scab development more than water retentive loam or clay soils (Grzeskiewicz *et al*., 1990; Park *et al*., 2002b). Maintenance of adequate soil moisture, particularly when tubers are most susceptible to infection (during initiation and early development), is widely known to decrease scab incidence (Lapwood *et al*., 1973). Control is thought to be largely due to suppression of the scab-forming organisms by increased populations of antagonistic soil bacteria on the surface of the developing tuber (Adams & Lapwood, 1978).

Recent research in Korea confirmed that water stress imposed for the first two weeks after planting or for two weeks during the tuber formation stage increased the incidence of common scab more than that imposed during the tuber enlargement and maturation stages (Park *et al*., 2002b). Irrigation reduced disease incidence by about 50% but a good drainage was also important to suppress common scab. In contrast, some scab-forming streptomycetes, e.g. the species now known as *S. caviscabei*, have been observed to cause high disease levels in well-irrigated soils (Goyer *et al*., 1996a).

It is well known that light well-drained soils favour common scab development more than water retentive loam or clay soils. This effect is related to the water retentiveness of soils. However, some *Streptomyces* spp., particularly *S. caviscabei* have been observed to cause high disease levels in well irrigated soils.

3.6.2. Chemical mechanisms of specific suppression - effects of crop nutrition

The effects of plant nutrients on common scab of potato have been extensively reviewed by Keinath and Loria (1989) including 65 references. It is often unclear whether differences in mineral balance play a direct role or whether they are side-effects indicating other active mechanisms of pathogen suppression, e.g. reduced pH or increased water status.

3.6.2.1. Nitrogen

Nitrogen levels do not appear to directly affect potato scab (Keinath & Loria, 1989) but many nitrogenous fertilisers acidify soil and this indirect effect may reduce levels of potato scab, although the effect is not universal (see references in Keinath & Loria, 1989).

Nitrogen fertilisation may also indirectly affect incidence of potato scab by altering timing of tuberisation. High levels of nitrogen may delay tuberisation to a period when soils are drier and more favourable to crop infection by *S. scabies*. (Lapwood & Dyson, 1966). Li *et al* (1999) found that skin coverage by common scab was higher in crops grown at very low (0) or very high (175-210 kg/ha N) rates of nitrogen than at intermediate rates of 70-140 kg/ha N.

Some soil amendments may also have direct chemical effects on pathogen suppression. Studies conducted in Poland during 1982-84 showed that higher nitrogen doses (up to 200 kg N/ha) increased potato infection by *Streptomyces scabies* (Czajka *et al*., 1992). High nitrogen organic amendments have been shown to suppress common scab due to release of ammonia and nitrous acid into the soil, particularly under low pH conditions (Lazarovits *et al*., 2001) – also see organic amendments.

3.6.2.2. Phosphorus

Keinath and Loria (1989) considered phosphorus to have little direct effect on potato scab but use of phosphatic fertilisers which increase soil pH (such as basic slag) can make scab worse.

3.6.2.3. Calcium and Potassium

Most work reviewed by Keinath and Loria (1989) suggests increased scab resulting from addition of calcareous liming materials to soil results from changes to pH and not calcium levels. There is, however, limited evidence that high calcium levels, in the absence of changes in pH, may induce scab (Davies *et al.*,1976b; Goto, 1985). Goto (1985) concluded that the content of exchangeable calcium is a more reliable parameter than the soil pH to evaluate the severity of potato scab.

Keinath and Loria's review concluded that in isolation, application of potassium does not affect common scab. It has been suggested that calcium : potassium ratios are important in determining severity of common scab. This idea was reviewed and tested by Doyle and Maclean (1960) who manipulated Ca : K ratios independently of soil pH without any effect on scab.

A strong correlation between soil pH and exchangeable cations, particularly calcium, was found in Tasmania (Lacey & Wilson, 2001). Common scab was not observed on potatoes grown in soil with combined exchangeable Ca, Mg and K at 12 cmolc/kg or less.

3.6.2.4. Sulphur

Use of sulphur to control potato scab is one of the first known uses of a soil nutrient to control a plant pathogen (Keinath & Loria, 1989). Most studies suggest the effect results from reduction in soil pH caused by sulphur (McCreary, 1967; Keinath & Loria, 1989). Davies *et al.* (1974), however, demonstrated reductions in scab severity following application of sulphur or gypsum (calcium sulphate) even though the effect of treatment on soil pH was small because of a highly buffered soil. Although reductions in common scab achieved by Davies *et al.* (1974) were statistically significant they fell short of commercial control.

3.6.2.5. Manganese

Keinath and Loria reviewed many trials investigating effects of manganese application on potato scab. Whilst some trials showed beneficial effects of manganese application, many did not. The discrepancy is demonstrated by trials in Scotland. McGregor and Wilson (1966) found that 31 kg/ha manganese sulphate banded in the furrow significantly and consistently reduced scab at four trial sites, however, Gilmour *et al.* (1968) consistently found no significant effect with 57 kg/ha manganese sulphate applied in the same way, also at four sites.

Keinath and Loria (1989) concluded; "The results of field trials apparently have not been favourable enough to warrant the use of manganese sulphate for scab control". They also point out that manganese can be toxic to potato and that on well-aerated soils manganese may be of limited effectiveness. They do, however, consider that manganese sulphate should be tested further in field trials. In particular, the interaction of manganese application with other soil factors such as pH and manganese content before application should perhaps be studied. Although writers such as

McGregor and Wilson (1966) and Gilmour *et al.* (1968) report soil analyses, differences in technique make comparison difficult. Gilmour *et al*. (1968) also report use of dung at two of their sites.

The similarity between conditions inhibiting scab and those which increase availability of manganese in soil, particularly acidic and moist soils, is enticing and intriguing. The connection may extend to the effects of organic matter: increased microbial activity (following green manuring) increases availability of manganese but humus will adsorb manganese. Effects of green manuring on soil microbiology probably offer a more direct explanation of its effects.

In Poland, addition of manganese to ammonium sulphate, especially in the form of chelate, significantly reduced infection (Grzeskiewicz *et al*., 1990). In India, a significant reduction in common scab development and an increase in tuber yield were achieved following applications of manganese sulphate (Saha *et al*., 1997).

3.6.2.6. Boron

Makheshwari and Saini (1994) showed that soil application of boric acid at 3 kg/ha at planting more than halved scab levels on harvested tubers. Keinath and Loria (1989) reviewed four papers: in one application of boron slightly reduced scab, in one scab was increased and in two there was no effect. Workers in India have reported boric acid is effective as a seed tuber treatment (see Section 3.8)

3.6.2.7. Copper

Keinath and Loria's review (1989) concluded that although copper does control potato scab it's commercial use is limited by harmful effects on plant growth and yield.

3.6.2.8. Iron and Zinc

Work reviewed by Keinath and Loria (1989) suggested that zinc is not useful in controlling common scab. Limited work on iron failed to demonstrate any effect of soil applications, although, some of the physiological aspects of iron may merit study.

It is often unclear whether differences in mineral balance play a direct role or whether they are side-effects indicating other active mechanisms of pathogen suppression, e.g. reduced pH or increased water status.
Nitrogen levels do not appear to directly affect common scab but many nitrogenous fertilisers acidify soil and have an indirect effect. Nitrogen fertilisation may also indirectly affect incidence of potato scab by altering timing of tuberisation to a period when soils are drier and more favourable to infection by *S. scabies.*
Sulphur has been shown to have some effect but most studies suggest the effect results from reduction in soil pH.
The effect of Boron and Manganese on common scab is inconsistent but some studies have shown a reduction. The use of Manganese may be worthy of further study.
P, Ca, K and Zn are not considered to have any effect on common scab.

3.6.3. Biological mechanisms of specific suppression

A number of organisms antagonistic to scab-forming streptomycetes have been shown to reduce scab symptoms under field conditions. *Streptomyces melanosporofaciens* strain EF-76, a geldanamycin producer, was effective with and without chitosan, a polymer derived from chitin that elicits plant defence mechanisms (Beausejour *et al*., 2003). In China, potato common scab, caused by *S. scabies*, was greatly reduced using *Streptomyces* strains, isolated from suppressive soils of potato scab, in experiments conducted in the laboratory, greenhouse and in the field (Liu *et al*., 1997). Some 22 additional non-virulent potato isolates of *Streptomyces* spp., with antagonistic activity higher than PonSSII, significantly reduced scab in pot experiments (Liu *et al*., 1996). All virulent strains and 54% of the non-virulent suppressive strains in this study were classified as *S. scabies*.

Research at the University of Minesota has shown that antibiotic production by non-pathogenic *Streptomyces* spp. is important in the suppression of scab-forming streptomycetes but competition effects also lead to disease suppression when antibiotic production is deactivated (Neeno-Eckwall *et al*., 2001). In co-inoculation experiments with pathogen and suppressive strains, higher total streptomycete population densities were correlated with lower amounts of disease. It is noteworthy that mutants of the pathogenic *Streptomyces scabies* strain RB4 that are resistant to an antibiotic produced by the potato scab-suppressive isolate *S. diastatochromogenes* strain PonSSII arose spontaneously at a frequency of 10^{-4} (Neeno-Eckwall & Schottel, 1999). These results indicate the occurrence of a high frequency of phenotypic and potential genotypic instability in the pathogen strain. Overall the studies at the University of Minnesota have found scab biocontrol inconsistent but they are aiming to enhance control using locally adapted antagonistic strains, increased inoculum doses, using purified antibiotics in association with suppressive *Streptomyces* spp. and integrating biocontrol with crop rotation (www2).

In green-house and field experiments in Germany, the incidence of common scab was decreased up to 73% by seed treatment with different suppressive strains of *Bacillus subtilis* formulated as water-soluble granules (Schmiedeknecht *et al*., 1997**)**. In field trials, the incidence of common scab was decreased by up to 67% with different *Bacillus* strains, equivalent to the effects of fungicide treatments including pencycuron and tolclofos-methyl (Schmiedeknecht *et al.*, 1998). As well as producing antibacterial and antifungal compounds *Bacillus subtilis* metabolites may promote plant growth or induce resistance or tolerance (Schmiedeknecht and Bochow (1998). In Russia, commercial biocontrol agents trichodermin (*Trichoderma lignorum* [*T. viride*] strains IST and L-17), and Planriz (*Pseudomonas fluorescens* str. AR-33) successfully controlled common scab with beneficial effects on plant growth, development and yield (Evstratova and Nikolaeva, 2001).

In studies on the mechanism of biocontrol it has become apparent that some organisms are able to break down or glucosylate the thaxtomin phytotoxins produced by scab-forming streptomycetes. One isolate of *Ralstonia pickettii*, and two isolates identified as *Streptomyces mirabilis* were shown to utilise thaxtomin A and protected growing plants against common scab when inoculated onto potato tubers (Doumbou *et al*., 1998). An isolate of the fungus *Aspergillus niger* was also shown to break down the Thaxtomin A toxin (Lazarovits *et al*., 2004). Thaxtomin A and B, the two major phytotoxins associated with the common scab of potato disease, were transformed into C-14 linked beta-glucosides when individually incubated with cultures of *Bacillus mycoides* (King *et al*., 2000). The biotransformation products were much less phytotoxic than the parent compounds. In Canada, workers at the Université de Sherbrooke have filed a patent for bacterial strains which degrade the toxin produced by common scab-inducing pathogens (www1).

Phage technology may lead to new opportunities for biocontrol of the common scab pathogens. Two distinct groups of actinophages that infect common scab pathogens have been identified from field soils in Hokkaido, Japan (Ogiso *et al*., 1999). Two types of actinophages, including both temperate and lysogenic types, were also isolated from soil samples in Egypt using *Streptomyces scabies* as indicator strain (El-Sayed *et al*., 2001). In Western Australia, McKenna *et al*. (2001) used a highly virulent polyvalent phage against *S. scabiei* to significantly disinfest seed potatoes and thereby reduce contamination of soil from seed-tuber-borne inoculum as well as reduce progeny tuber infection. In a pot experiment use of the *Streptomyces* phage reduced levels of surface lesions of scab on daughter tubers from 23% to 1.2%.

Antagonistic *Streptomyces spp*. have been shown to reduce common scab. The antagonistic action is ascribed to antibiotic production and sometimes competition. However, studies have found common scab biocontrol by *Streptomyces spp*. inconsistent. Other biocontrol agents found to be effective include strains of *Bacillus subtilis, Trichoderma lignorum* [*T. viride*] strains and a *Pseudomonas fluorescens* strain. In studies on the mechanism of biocontrol some organisms were able to break down or glucosylate the thaxtomin phytotoxins produced by scab-forming streptomycetes. These included *Ralstonia pickettii*, two isolates of *Streptomyces mirabilis* and *Aspergillus niger*. Actinophages that infect common scab pathogens have been found and under experimental conditions found to reduce levels of common scab.

3.7. Organic Amendments

Literature on effects of organic amendments on common scab is unclear: there are many anecdotal reports and hypotheses advanced upon little firm evidence. Manures variable in source, storage and application are spread onto variable soils with different cropping history so the emergence of contradictory reports is perhaps unsurprising.

Many authors do not recommend application of animal manures or other animal wastes to land intended for potato production. For example, Powelson *et al.* (1993) assert that, by increasing organic matter content of soil, manures provide a food base for the common scab pathogen which subsequently survives well in soil. They claim common scab is often severe after manure application and that *S. scabies* survives passage through the digestive tract of animals and is distributed with manure.

In theory, organic amendment of light well drained soils to increase water holding capacity is likely to increase suppressiveness to common scab, particularly if other factors, such as pH and antagonistic biological activity are also favourably affected.

Canadian researchers Conn and Lazarovits (1999) reviewed literature related to effects of animal manures on scab. They found that although “Manure application has almost invariably been linked to increased levels of potato scab since the turn of the century [ie. Since 1900]”; there was no clear experimental evidence to support this assertion. In their experimental work, fresh chicken manure was highly effective in reducing incidence of potato scab to near zero levels at two sites in the first year after application reduced scab incidence. However, at one site common scab incidence on potato tubers grown in the third year after manure application had doubled. Pig manure was also effective. The overall effect of cattle manure was neutral. Possible mechanisms for the affect of manure are also discussed including effects on soil pH and possible toxic effects of ammonia production on plant pathogens. Manures also increased microbial populations of soils which may result in increased competition for existing nutrients or increased populations of antagonistic organisms. See also Bailey and Lazarovits (2003) for discussion of mechanisms involved. Direct application of the findings of Conn and Lazarovits (1999) is complicated by the high rates of manure application used (at or above the likely practical maximum rate). However, possible mechanisms such as annual applications of smaller amounts of manure could be investigated.

Workers in the same laboratory also investigated effects of soymeal and meat and bone meal on common scab of potatoes (Lazarovits *et al.* 1999). In the year of application both soymeal and meat and bone meal greatly reduced scab levels. Total yields were significantly reduced but, because of greater marketable proportion, marketable yield did not differ from control. Effects of treatment on yield might be ameliorated by application further in advance of planting. Reduced disease levels were also found in the second year after application but by the third year disease levels were at least equal to, and sometimes higher than, untreated plots.

In Japan, amendments with compost and sulphur (Funakoshi & Matsuura, 1983), or an antibiotic biofertilizer produced from swine faeces containing *Streptomyces albidoflavus* (Hayashida *et al*., 1989), inhibited development of the pathogen. In Pakistan, organic amendments alone or in combination with urea and ammonia nitrate reduced common scab, caused by *Streptomyces scabies*, of potato (Faqir *et al*., 1995).

Ammonium lignosulfonate a by-product of paper pulp making, at approximately 6 t/ha solids reduced severity of potato scab by 50-80% in the year of application. Four sites with different soils were used and treatment did not appear site specific. On some sites use of ammonium lignosulfonate suppressed potato scab for a second year. Although ammonium lignosulfonate provides nitrogen to crops it can be phytotoxic (Soltani *et al.* 2002).

In contrast to general caution in texts about effects of animal manures on common scab, green manures are often recommended because decomposing organic matter supports microbial activity antagonistic to scab (O'Brien 1925, Gram & Weber, 1951). An alternative hypothesis is the "preferential food" theory: easily decomposable green manures provide a readily available food source which *Streptomyces* being mainly saprophytic prefers to potato tubers (Millard, 1923).

Green manure crops such as rye, millet and oat have been reported to reduce incidence of scab (Powelson *et al.*, 1993). Soybean green manure has been shown to reduce potato scab (references in Lazarovits *et al.*, 1999). On the other hand, some ploughed down legumes, particularly red clover, encourage development of scab (Powelson *et al.* 1993) but this may be due to the lime requirement of clover to enable it to establish (Butler & Jones 1949). Earlier work reviewed by Rogers (1969) appears inconsistent with green manures reducing scab in some trials but not others. Green manures may affect scab through their effects on soil microbiology or through effects on the availability of manganese. Rogers (1969) suggested the inconsistent results may arise through variations in populations of actinomyces antagonistic to *S. scabies,* conditions unsuitable for multiplication of antagonistic actinomycetes, low levels of manganese in soils or alkaline soils binding available manganese. In his experimental work Rogers (1969) demonstrated that 5 t/ha grass meal applied at planting reduced scab but measurements of soil microbial populations and manganese levels suggested that neither may fully explain the control obtained.

White (1928) found that a rye cover crop ploughed under in early spring more effective in reducing common scab than a cowpea cover crop ploughed under the previous autumn. White (1928) suggested this was because more decomposing vegetable matter was present at tuber initiation following working in of a cover crop in the spring. Even so, Rogers (1969) found that by tuber initiation (about 40 days after planting) populations of bacteria and actinomycetes were much less than their maximum numbers at 11-22 days after planting. Czech researchers (Divis & Kristufek, 1998), showed no noticeable effects of organic amendments and green manures on scab incidence in their experiments.

The effect of volatile compounds generated from brassica residues has been investigated in South Africa (www3). In pot trials dried cabbage reduced scab index from 47.9 to 27.9. In contrast workers in Tasmania (www4) found increases in disease incidence when canola was used as a green manure and only occasional, but inconsistent, reduction in common scab incidence from other green manures. Exploiting green manures fully could involve extensive screening of potential species both for effects on scab and cost and reliability of the green manure itself. Medicinal plants could be candidates: Ushiki *et al*. (1998) showed that geraniin, an antimicrobial product from the roots of *Geranium pretense*, was inhibitory to *Streptomyces scabies.* Application of dried root and powdered residue or mixed cropping of geranium and potato in pots all reduced the proportion of tuber area affected by scab although few effects were statistically significant. In addition Takenaka *et al*. (1997) showed that new antimicrobial substances with activity against *Streptomyces scabies*, rosmic acid and rosmanol-related compounds, were present in leaves of rosemary (*Rosmarinus officinalis* L.).

Literature on effects of organic amendments on common scab is unclear. Manure application has almost invariably been linked to increased levels of potato scab since since 1900 but there is no clear experimental evidence to support this assertion. In theory, organic amendment of light well drained soils to increase water holding capacity is likely to increase suppressiveness to common scab, particularly if other factors, such as pH and antagonistic biological activity are also favourably affected. Canadian research has demonstrated that high levels of certain animal manures can substantially reduce common scab. Possible mechanisms include effects on soil pH and toxic effects of ammonia production. Other manures claimed to be effective include compost and sulphur, an antibiotic biofertilizer produced from pig faeces containing *Streptomyces albidoflavus*, organic amendments alone or in combination with urea and ammonia nitrate, ammonium lignosulfonate a by-product of paper pulp making.

Green manures have frequently been associated with reduced common either because decomposing organic matter supports antagonistic microbial activity or easily they provide a readily available food source which the pathogen prefers to potato tubers. It has also been suggested that control is mediated through increased availability of manganese. Attempts to monitor soil microbial populations and soil chemistry have not always explained the control achieved. Effective green manures reported include rye, millet, oats and soybean. By contrast legumes, particularly red clover, increased common scab although this may be due to liming needed for clover establishment. Results with green manures are not always consistent.

Volatile compounds generated from brassica residues have reduced common scab experimentally but in field experiments their effect was inconsistent. Geraniin, an antimicrobial product from the roots of *Geranium pretense* and rosmic acid and rosmanol-related compounds present in leaves of rosemary (*Rosmarinus officinalis* L.) have been found inhibitory to *Streptomyces scabies.*

There is a need to screen for practical and effective options for green manures.

3.8. Chemical control – seed and soil

Disinfection of infected seed tubers provides an obvious alternative to selecting seed tubers free from infections. Chemical treatment of visually healthy seed tubers may not result in any reduction in scab levels on the harvested crop (Wilson *et al.* 1999). Historically, the most effective chemicals for tuber disinfection were mercuric chloride or organo-mercury compounds (Lapwood, 1973; Brenchley & Wilcox, 1979). Mercury compounds are now unacceptable on environmental and human health grounds. Some mercury containing compounds have, however, been trialled in India relatively recently (Mohanty *et al.* 1978; Singh & Soni, 1987; De & Sengupta, 1992). Hot formaldehyde was used to treat seed potatoes in America in the 1940's and 1950's (Pavlista 1996 – who suggests the treatment was more harmful to the farmers than common scab). One of the most effective chemicals used as a tuber dip until 1900 was copper sulphate (Keinath & Loria, 1989). Workers in India have reported that dipping seed tubers in boric acid gives good control of scab on the harvested crop (De & Sengupta, 1992; Maheshwari & Saini, 1994). Mancozeb and captan have also been suggested as seed treatments (Loria, 2001). Antibiotic treatments have been successfully trialled in India and Korea (Singh and Soni 1987, Park *et al.* 2002a). Platt and Maclean (1997) tested seed treatment with fungicides including thiophanate-methyl, mancozeb, captan, metiram, chlorothalonil and fluazinam. No effects on incidence and severity of common scab were found.

Of the range of seed disinfection measures available, none has been validated across the range of scab-forming species, although it is likely that methods which successfully control one species will also be effective against others.

Chemical treatment of soil is difficult: response may vary with soil type and incorporation of pesticides evenly to depth is problematic. Formaldehyde, urea formaldehyde, manganese sulphate and pentachlorobenzene (PCNB/Quintozene) have been used but only the latter has been extensively tested (Davies *et al.* 1974, Davies *et al.* 1976a, Locci 1994). Breakdown products of PCNB may be carcinogenic and UK approvals for quintozene were withdrawn in 2002.

A series of papers by McIntosh *et al.* (1981, 1985, 1988) reported glasshouse tests demonstrating single foliar sprays of the growth retardant 3,5-dichlorofenoxyacetic acid (3,5-D) and a series of related compounds greatly decreased scab incidence. These materials appear to alter the potato's response to infection by scab (Burrell, 1982). However, many of the spray treatments decreased yields and increased tuber number and deformation. One of these treatments, 3,6-dichloropicolinic acid (clopyralid) more than halved scab index at rates less than 15g/ha (equivalent). At rates of 100g/ha clopyralid is often used as a weedkiller to control volunteer potatoes in brassicas crops such as swede! Foliar sprays of Ethionine (an amino-acid) also reduce scab on potatoes – the concentration of ethionine reaching tubers is sufficient to affect metabolism of scab, but not potato (McIntosh *et al.*,1977, Burrel, 1981). Sawicka (1999) in Poland found the growth regulators Poteitin and Mival had no significant or consistent effect on common scab.

Working with newer fungicides, Wilson *et al.* (1999) demonstrated fluazinam, flusulfamide and fenpiclonil gave good control of common scab when used as a spray or dip on diseased seed at high doses. Mancozeb was also effective as a seed treatment. Soil treatment with PCNB was effective but soil treatment with fluazinam gave only poor control. Flusulfamide dip treatment of tubers is recommended in South Africa together with chlorpicrin and quintozene for soil treatment (Gouws, 2000).

In Wisconsin, Stevenson and James (1995) found seed treatment with mancozeb reduced scabbing on the harvested crop. The insecticide/nematicide ethoprophos in the planting furrow reduced scab on one of two varieties. Fluazinam as a foliar spray or planting furrow drench gave variable results.

Choice of resistant varieties affected scab incidence more than any chemical treatments. In contrast, Hide and Read (1991) reported an increase in scab levels after insecticide/nematicide treatment– in this case oxamyl.

A wide range of seed tuber treatments have been evaluated to achieve a reduction in common scab arising from seed-borne infection. Simple compounds such as mercuric salts, copper salts and boric acid have proved effective but are not acceptable for a variety of reasons. Organic compounds such as mancozeb, fluazinam, flusulphamide and fenpiclonil tuber treatments have shown promise as control measures. Of the range of seed disinfection measures available, none has been validated across the range of scab-forming species, although it is likely that methods which successfully control one species will also be effective against others. Soil applied treatments for control of soil-borne inoculum have generally proved unsatisfactory. The use of growth regulators or retardants have shown some promise in the control of common scab but their effect on the crop has been unacceptable. Choice of resistant varieties can reduce common scab incidence more than any chemical treatments.

3.9. Solarisation

In Aberdeen, Idaho solarisation using sheets of clear polythene from 18 June – 4 August increased the proportion of scab free tubers in the following year's crop from 26 to 50% for untreated seed and from 38% to 46% for disinfected seed (with sodium hypochlorite) (Davies & Somerson, 1986).

Solarisation of soil under polythene has reduced common scab.

3.10. Improved diagnostic methods

Newly available diagnostic tools are already providing the means for accurate detection and identification of the pathogenic *Streptomyces* spp. This will now allow researchers to dissect the microbial composition and complex interactions occurring in soils with a view to better understanding the mechanisms of individual control measures and their efficient integration.

A new selective medium (STR) and procedures for rapid detection and differentiation of potential common scab-inducing strains amongst soil populations of *Streptomyces* have been developed in Canada (Conn *et al*., 1998). In the Netherlands, *Streptomyces scabies* hyphae growing in amended soil, were easily detected using an *in situ* hybridisation technique with fluorescent rRNA probes (Hahn *et al*., 1992)**.** Atalan *et al*. (2000 or 1997?) have demonstrated that a multi-step extraction procedure followed by selective isolation and rapid characterization of streptomycetes using pyrolysis mass spectrometry provide a practical way of determining the phenotypic species diversity of streptomycetes in natural habitats.

New molecular methods are allowing study of the diversity and dynamics of populations of pathogens and potential competitors/antagonists in and around plant tissues. Austrian researchers (Sessitsch *et al*., 2002) have used 16S rRNA-based techniques such as terminal restriction fragment length polymorphism (RFLP) analysis, denaturing gradient gel electrophoresis (DGGE) as well as 16S rDNA cloning and sequencing to study microbial communities inhabiting potato roots and tubers. Interestingly, they showed that a higher abundance and diversity of *Streptomyces scabiei*-related species occurred in a cultivar known for its resistance to *S. scabiei*. Bramwell *et al*. (1998) examined the diversity of streptomycetes causing potato scab using phenotypic identification, 16S rRNA sequences, and pathogenicity measurements. Pathogenicity did not correlate well with taxonomic identification, nor with phylogenetic analysis. This result suggested that neither phenotypic nor 16S characteristics are diagnostic for scab-causing strains. Additionally, phenotypic characterizations were not fully consistent with phylogenetic relationships suggesting a need for better integration of genetic and phenotypic characters in the systematics of this group.

New 16s-23s rRNA probes have been described which can be used to detect and identify newly described scab-forming streptomycetes including *Streptomyces luridiscabiei, Streptomyces puniciscabiei* and *Streptomyces niveiscabiei* (Park *et al*., 2003b). Similar probes are also becoming available for detection and identification of non-pathogenic streptomycetes which also inhabit potato tubers (Doumbou *et al*., 2001). The determination of DNA relatedness among newly described species of *Streptomyces* pathogenic to potato in France, *S. europaeiscabiei* and *S. stelliscabiei* (associated with common scab) and *S. reticuliscabiei* (associated with netted scab) (Bouchek-Mechiche , 2000b) will also allow specific probes to be developed for these organisms. High DNA similarity within *S. turgidiscabies* strains (Miyajima *et al*., 1998) and within *S. caviscabies* strains (Goyer *et al*., 1996a), but low similarities between strains of these species and strains of *S. acidiscabies*, *S. scabies*, *S. caviscabies*, *S. griseus*, *S. setonii* and *S. tendae* will also permit development of specific molecular detection and quantification methods for this newly-described scab-forming organism.

Polymerase chain reaction (PCR)-based diagnostic assays for *Streptomyces scabiei* together with rapid methods of DNA extraction and purification from soil and plant samples have been developed at the SCRI (Cullen *et al*., 2000). Further useful PCR primers capable of differentiating various European scab-forming species are already available (Kreuze *et al*., 1999; Lehtonen *et al*., 2004). These include primers which amplify the transposable pathogenicity island including the nec1 virulence gene which have already been adapted at CSL for use in quantitative real-time PCR assays (Ward *et al*., unpublished).

New diagnostic tools are providing the means for accurate detection and identification of pathogenic *Streptomyces* spp. These will now allow researchers to dissect the microbial composition and complex interactions occurring in soils with a view to better understanding the mechanisms of individual control measures and their efficient integration. The tools include a new selective medium, an *in situ* hybridisation technique with fluorescent rRNA probes, pyrolysis mass spectrometry and molecular techniques such as restriction fragment length polymorphism (RFLP) analysis, denaturing gradient gel electrophoresis (DGGE) and 16S rDNA cloning and sequencing. New species specific probes and PCR-based diagnostic assays will permit specific molecular detection and quantification methods for each common scab-forming organism.

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www1- www.extension.umn.edu/distribution/cropsystems/DC6122.html

www2- cati.csufresno.edu/cit/rese/90/900804

www3- www.sardi.sa.gov.au/pages/horticulture/pathology/hort_pn_bioscaba.htm:sectID=337&tempID=111

www4- www.tiar.tas.edu.au/domino/tiar/tiar.nsf/rdpr/3v/V20

5. Future research requirements

a. Reviewers comments and proposals

Improved control of the potato common scab pathogens is likely to depend on efficient and cost effective integration of existing measures rather than the introduction of completely novel measures. In this respect, key areas for further research will be:

1. Development of cultivars with high levels of stable resistance or immunity.
    - Improved selection methods targeting resistance to the thaxtomin phytotoxins.
    - Identification of genetic markers for resistance responses in potato plants.
    - Somaclonal selection within existing potato cultivars.
    - Selection of resistance to the full range of known scab-forming streptomycetes.

2. Improved understanding of the mechanisms of suppression of pathogenic *Streptomyces* spp. in soils.
    - Combined use of new molecular methods and traditional approaches to improve understanding of the behaviour of pathogenic streptomycetes and their interaction with complex natural microbial communities (including interactions with non-pathogenic streptomycetes and other antagonistic or competing microflora).
    - Study of the fate of pathogenic streptomycetes in soils following manipulation of pH, water status, nutrient/mineral status and organic content.
    - Identification of molecular markers for selection of potential biocontrol agents.
    - Study potential for biocontrol involving the use of actinophage.
    - Fate of biological control agents on introduction in soils and their interaction with pathogenic streptomycetes.
    - Identification of integrated measures which maximise suppression of pathogenic streptomycetes in soil.

3. Integration of control measures. Most studies on control reported in this review have examined single control factors in isolation. Perhaps with the exception of pH and resistant varieties, few non-water measures have the potential to control common scab completely. However, there are indications in the literature that combinations of control measures can achieve substantial control. Studies are required where promising non-water control measures are integrated to determine their effectiveness.

4. Practical evaluation of novel control measures. Throughout the literature there are examples of novel control measures that have not been evaluated in GB. In order to assess their potential they require testing under unirrigated conditions and in GB soils. These include the use of a range or organic amendments, biological control, the use of manganese and phages.

5. Research to improve understanding of the mechanisms of pathogenicity is ongoing and newly emerging information relating to the above (including the role of thaxtomin and other toxins in pathogenicity and the elucidation of any new virulence factors) should be carefully monitored.

b. Agronomists proposals

The information in this review was described and discussed at a workshop attended by potato agronomists at CSL on 2 July 2004. The key aspects of common scab that this group felt required further investigation were:

- **A survey of the pathogen species currently present in the UK**. This would include identification of species causing different scab symptoms and unexpected scab outbreaks (e.g. under high moisture or low pH conditions). The pathogen variation requires to be determined and compared with known scab-forming *Streptomyces* spp. This should be done early in the season to avoid complication with other symptoms in mature tubers which can be mistaken for scab (e.g. growth cracking). The new range of diagnostic methods should be used and expanded to enable rapid detection and differentiation of the range of pathogenic and non-pathogenic streptomycetes.
- **New molecular methods allowing quantitative detection of pathogenic and non-pathogenic *Streptomyces* on tubers and in soil should be adapted and fully validated**. This would allow generation of data to explain interactions between these organisms and other microbial flora (including biocontrol agents and natural competitors) in response to control measures. The benefits of integrating various control components (e.g. irrigation, manipulation of soil pH, organic amendments, biological control, nutrition including the effects of manganese, seed disinfection, crop rotation, resistant cultivars etc.) could be more accurately assessed according to their direct effects on pathogenic and non-pathogenic *Streptomyces* populations.
- **Improving the efficiency (reducing) of water use**. More detailed information is required on the effects of irrigation on scab control with respect to different cultivars. A basic understanding of tuber development and physiology in different cultivars should be investigated. For example, how long does it take for lenticels to suberise in different cultivars. More efficient irrigation regimes could be devised which are cultivar specific and thus save unnecessary use of water.
- **Understand the impact of crops grown in rotation the UK on common scab development**. Cropping patterns will not change but there is some evidence that some crops can reduce soil populations of pathogenic streptomycetes and reduce the risk of common scab.
- **Develop improved levels of resistance to common scab**. Molecular technology may assist in identifying key resistance markers associated with toxin degradation. Promising Australian results observed in cell selection experiments following exposure to toxin, require careful evaluation. Difficulties may exist in selecting resistant clones amongst current varieties from the point of view of commercial ownership. Nevertheless it is significant that many of the most commonly grown varieties in GB are susceptible to scab (e.g. Maris Piper and Desiree).
- **Investigate control using the application of specific manures and with manganese**. Canadian work has indicated that certain animal manures judiciously applied can dramatically reduce soil populations of streptomycetes and other pathogens. This work requires to be extended and placed in a UK context. Release of manganese from soil has shown promise as a control measure. The mechanisms behind this control method require to be examined.
- **Identification of suppressive soils and stimulation of natural antagonists**. Using molecular tools there is a need to understand the complex population dynamics of pathogenic streptomycetes and antagonistic microbial populations. This will be best achieved by investigating suppressive soils, for example where common scab fails to develop although it was expected.

- **The development of integrated control measures**. As described in the first part of this section, there is a need for experiments to evaluate the integration of a range of potential non-water control measures. Control measures need to reflect the pathogen variation present in the country. It is not worth developing control practices which are pathogen strain or species specific if other strains/species will overcome the protection.

Appendix 1

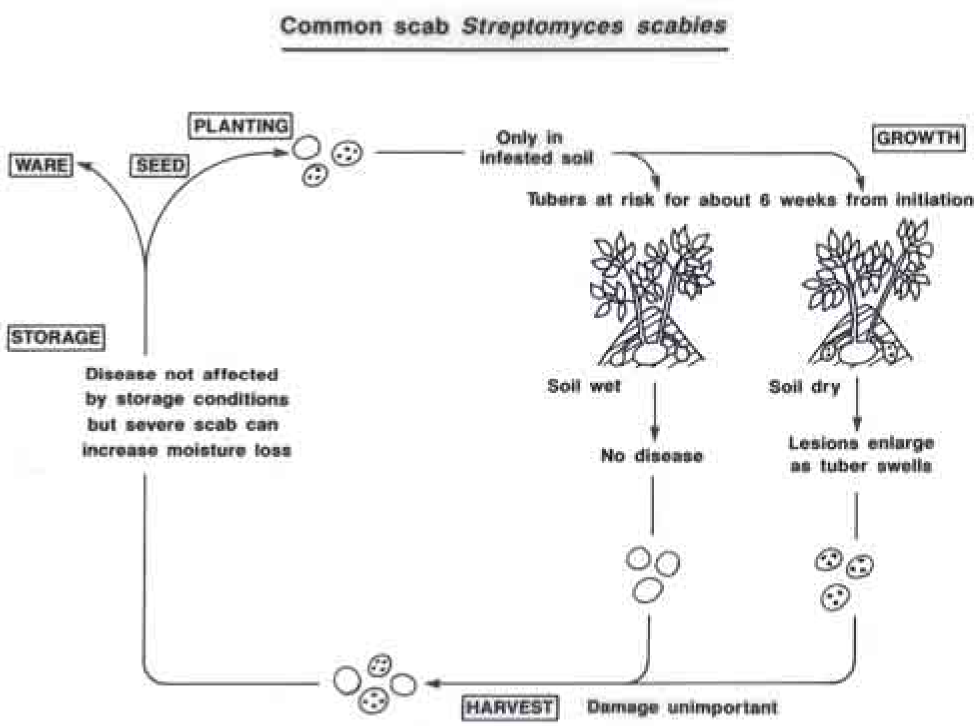
Cultivars listed in the Pocket guide to potato varieties 2004 (Anon. 2004a) and their resistance ratings to common scab. 1 = susceptible, 9 = resistant

Variety	Common Scab
Maris Piper	1
Maxine	3
Spunta	3
Cabaret	4
Charlotte	4
Colmo	4
Desiree	4
Eve Balfour	4
Kerrs Pink	4
Kestral	4
Lady Balfour	4
Navan	4
Stemster	4
Yukon Gold	4
Agata	5
Agria	5
Ambo	5
Arran Comet	5
Avalanche	5
Barna	5
Bintje	5
Caesar	5
Dundrod	5
Fianna	5
Isle of Jura	5
Konsul	5
Marfona	5
Maris Bard	5
Maris Peer	5
Midas	5
Orla	5
Pentland Dell	5
Premiere	5
Rocket	5
Romano	5
Rooster	5
Saxon	5
Ulster Sceptre	5
Valor	5
Victoria	5
Virgo	5
Winston	5
Accord	6
Adora	6

Asterix	6
Atlantic	6
Cara	6
Cultra	6
Estima	6
Harmony	6
Hermes	6
Home Guard	6
Kondor	6
Lady Rosetta	6
Lynx	6
Minerva	6
Nicola	6
Osprey	6
Pentland Javelin	6
Pentland Squire	6
Record	6
Santa	6
Shannon	6
Shepody	6
Slaney	6
Spey	6
Accent	7
Anna	7
Balmoral	7
Claret	7
Cosmos	7
Exquisa	7
King Edward	7
Kingston	7
Lady Christl	7
Lady Felica	7
Melody	7
Morene	7
Nadine	7
Pentland Crown	7
Picasso	7
Stirling	7
Swift	7
Wilja	7
Anya	8
Carlingford	8
Russet Burbank	8
Saturna	8

Appendix 2

Life cycle



Common scab life cycle (reproduced courtesy of the British Potato Council Crop Protection Group – formerly the British Crop Protection Council Potato Treater Group)