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Common scab and its control in seed-potato crops

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Abstract

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In the Netherlands, common scab of potato is usually caused by *Streptomyces scabies*. Non-pathogenic strains of *S. scabies* exist and a pathogenicity test is the only way of distinguishing between pathogenic and non-pathogenic isolates. Three types of scab were distinguished on the variety Bintje and called: 'normal', 'superficial' and 'russet'. The anatomy of lesions and reaction to external conditions differed in normal and superficial from in russet scab.

Different ways of control have been tested: by chemicals, antagonists, crop rotation and irrigation. Control by irrigation proved most effective, if the soil was kept near field capacity for four weeks after tuber formation. Irrigation altered the microbial population of the soil. The ratio of pathogenic actomycetes to bacteria shifted and discouraged scab development.

Contents

1 Introduction

Common scab is not one of the most important potato diseases in the Netherlands, but it is of great importance to the potato-seed export-trade, because many countries have strict regulations regarding the occurrence of scab on imported seed. Rejection for export means an enforced sale on the home market at much lower prices. Therefore in 1953 the Institute of Phytopathological Research (Instituut voor Plantenziektenkundig Onderzoek, IPO, Wageningen) was required to study the control of common scab. In 1955 the author joined the investigations, which were then mainly directed at the possibilities of chemical control (van Emden & Labruyère, 1958) and took charge in 1959. Investigations on chemical control were continued and the results are given in Chapter 6. Work was also done on the causal organism (Chapter 2) and on the processes of infection (Chapters 3 and 4). Because of the wide range of types of scab lesions on potato tubers there was a need to study whether these were caused by one or by more pathogenic actinomycetes (Sections 2.2 and 3.1).

Since chemicals rarely gave satisfactory control, other ways had to be found. Research on the soil microflora showed the possible use of antagonists, mainly actinomycetes, but this proved impracticable (Chapter 7).

Overhead irrigation during the time of tuber formation, however, proved a satisfactory method in many respects (Section 8.1). The mechanism of scab control by irrigation may be explained by differences in the interaction between bacteria and actinomycetes in wet and dry soil (Section 8.2).

In this publication the Dutch Potato Scab Committee, represented by several research institutes, the extension services of the main potato seed producing areas, the General Netherlands Inspection Service for Field Seeds and Seed Potatoes and the practical farmers, is mentioned. Although the Committee did not have any official status, it promoted the coordination of scab research in the Netherlands very successfully, especially after 1962. The author thanks the Committee for the many useful discussions and valuable suggestions.

In this publication I have mainly concentrated on the results of work done or initiated by myself, but whenever necessary, due acknowledgement is made of data or information supplied by others.

2 Cause of common scab

Common scab is a disease which attacks all the underground parts of the potato plant of which the tubers are most important, because of their commercial value.

The various types of scab on tubers have been known by different names, generally referring to the type of lesion caused. For example 'Flachschorf', 'Tiefschorf', 'Buckelschorf' and 'Buckeltiefschorf' (Frank & Krüger, 1896), 'variabler Schorf' (Wollenweber, 1920), 'pitted scab', 'raised type of scab' (Jones, 1931), 'ordinary scab', 'deep scab', 'superficial scab', 'elevated scab' (Emilsson & Gustafsson, 1953) and 'russet scab' (Harrison, 1962).

In the Netherlands the name given may refer to the lesion type or to the source of infection, for example, 'greideschurft' indicates a type of scab from land previously under grass for many years, whereas the Dutch synonyms for deep or pitted scab are 'pok' or 'pokschurft', for raised or elevated scab 'knobbelschurft' and for superficial and sometimes russet scab, 'roest'.

Scab lesions of all types arise as discrete spots and are generally star-shaped, because the infected tissue cracks as the tuber expands. This is most obvious with deep and least with superficial scab. When lesions coalesce the star-shaped appearance is lost and extensive areas of the tuber may be severely affected. Russet scab lesions are less discrete and commonly cover much of the tuber surface, and we propose the Dutch name 'netschurft' for this type of scab.

All these symptoms of common scab had long been known before the cause was found. At the end of the 19th century Thaxter (1891, 1892) attributed the cause to *Oospora scabies,* an organism with certain parallels between fungi and bacteria. According to Cunningham (1912) the scab organism had to be placed in the genus *Streptothrix.* Lutman & Cunningham (1914) considered the causal agent to be identical with *Actinomyces chromogenus* Gasparini. With the increase in knowledge of the actinomycetes, Güssow (1914) introduced the name *Actinomyces scabies.* In 1943 the organism was transferred to the genus *Streptomyces* by Waksman & Henrici (1943) and is now generally known as *Streptomyces scabies* (Thaxter) Waksman et Henrici. Since Thaxter's type culture was no longer available a neotype was chosen and described (Waksman, 1961, pp. 274–275). According to Corbaz (1964), Waksman and Henrici's description does not fit most of the isolates obtained from lesions of scabby potato tubers. Corbaz deposited a culture which he considered to be *S. scabies* at the 'Centraalbureau voor Schimmelcultures' (CBS, Baarn), under number C.B.S. No. 135.64, which has smooth spores in long regularly-spiralled chains and melanoid pigments are produced in culture. *S. scabies*

(type culture IMRU 3018) of Waksman also shows a strong tyrosinase reaction.

Although *S. scabies* is considered as the main causal agent of common scab, other actinomycetes may be involved. Wollenweber (1920) and Millard & Burr (1926) named a number of other *Actinomyces* species and more recently Corbaz (1964) mentioned three other *Streptomyces* species, *S. griseus, S. aureofaciens* and *S. flaveolus*. Both Harrison (1962) and Mygind (1965) have isolated the causal agent of russet scab, which they considered different from *S. scabies* as did Bonde & McIntyre (1968) with an isolate from soils low in pH.

Among isolates of *S. scabies* physiologic specialisation is described by de Bruyn (1939), Leach et al. (1939), Schaal (1940a, 1940b), Taylor & Decker (1946, 1947), Thomas (1947), Emilsson & Gustafsson (1953), Gregory & Vaisey (1956), Hoffmann (1954, 1959), Weber & Menzies (1962) and Mygind (1962).

In view of the differences of opinion it was decided to investigate whether common scab of potatoes in the Netherlands is caused by one or several *Streptomyces* species.

2.1 Materials and methods

To study the causal agent of common scab a large number of strains were isolated either from soil or from tubers of different potato varieties from different sites in the Netherlands.

Sometimes mycelium could be taken directly from the surface of scab lesions on freshly harvested tubers, but when no mycelium was present the tuber was disinfected with calcium hypochlorite and rinsed with sterile water, before removing a piece of scabbed tissue aseptically. After grinding in a glass mortar with a small amount of sterile water, the suspension was further diluted and plated out on a agar medium containing tyrosine. Small colonies showing the tyrosinase reaction were transferred to test-tubes or small Petri dishes (7 cm in diameter), for colonies producing a dark soluble pigment (positive tyrosinase reaction) may be *S. scabies*, but those not are unlikely to be the pathogen. When isolating from soil, and after the first dilution, a mixture of phenol and water (1 : 140) was used to eliminate bacterial contamination (Lawrence, 1956). The final dilution (usually $1 : 10^5$) was plated out on a agar medium containing tyrosine, as in isolation from tubers.

Because the tyrosinase reaction gives no certainty about the pathogenicity of the isolates, the following pathogenicity test had to be carried out:

Pure cultures were incubated at 28° C in Petri dishes (15 cm in diameter) filled with 'Perlite' saturated with a modified Say-solution (20 g sucrose, 1.2 g *l*-asparagine, 0.6 g K_2HPO_4, 10 g Difco yeast extract, 1000 ml water). After 10–14 days the Perlite, rich in mycelium and spores, was used to inoculate steam-sterilized pot soil (a mixture of sand and peat soil, enriched with stable manure, as used at IPO) by mixing thoroughly. The mixture was then put in polyethylene bags, and placed in earthenware pots (12.5 cm in diameter and 15 cm in height). The contents of one Petri dish were used per pot. The polyethylene bags were only partially filled

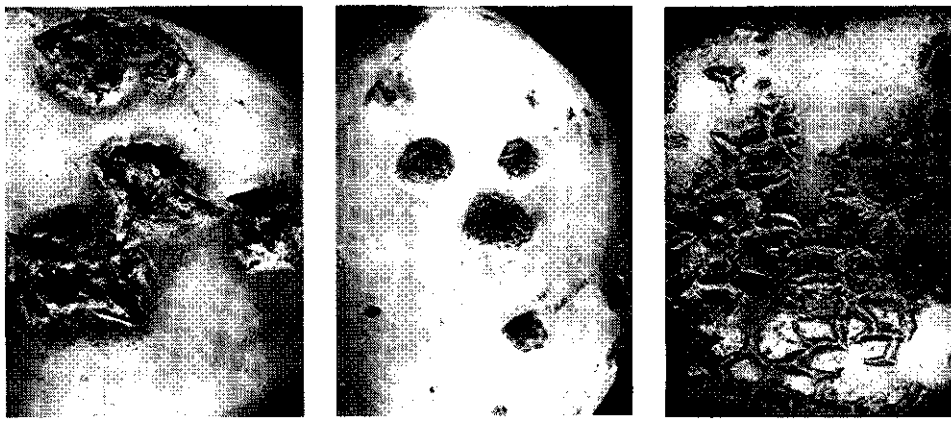

Fig. 1. Lesions of common scab on Bintje: normal (left), superficial (middle), russet (right).

so that the tops could be rolled back allowing about 10 cm to potrude above the level of pots to prevent cross contamination by splashing when watering, found previously by Hoffmann (1959). At first four replicates were used, but with no contamination two replicates proved sufficient. A disinfected sprout, usually of Bintje, sometimes Eigenheimer, rooted in Perlite, was planted in each pot which was watered normally until tuberisation began. Watering was then kept to a minimum to allow infection to occur. During growth young infected tubers could be seen by manipulating the bag to expose the tubers. After about $2^1/_2$ month tubers were harvested and the amount and type of scab was assessed. Pathogenic isolates were distinguished on scab-susceptible Bintje by symptoms as either 'normal', 'superficial', or 'russet' scab (Fig. 1) (described in detail in Chapter 3).

In later tests inoculum was produced in liquid culture in flat 100 ml medicine bottles containing 50 ml potato dextrose with 0.7% peptone, which were shake-cultured at 24–28° C for 10–14 days. Mycelium was then filtered, homogenized in a high speed grinder (Ultra Turrax) for 2–4 sec, mixed with a small quantity of quartz sand, and then used to inoculate the sterile pot soil.

2.2 Results

The survey of tuber and soil isolates revealed that on the same medium a wide range of mycelium, spore and substrate colour (mycelium and spores generally shades of grey), and of colony texture, velvety or granular, could be obtained. Spore chains were most often spirally wound, but showed considerable variation (Fig. 2A–H).

From soil we obtained many tyrosinase positive isolates which were culturally and microscopically indistinguishable from the pathogenic isolates, but proved to be non-pathogenic in the pathogenicity test.

Among pathogenic isolates no correlation could be found between morphology

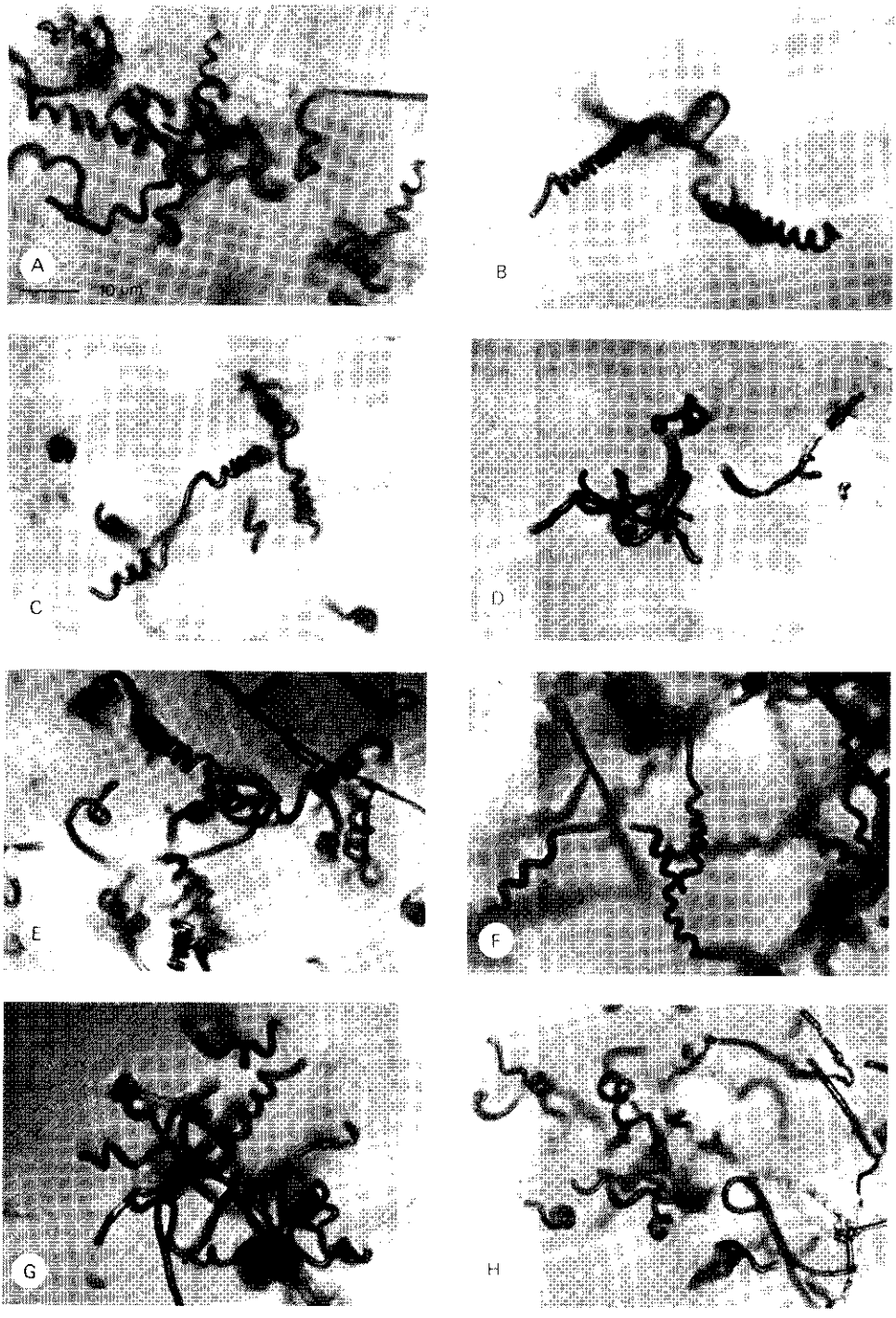

Fig. 2. Variation of spore chains between different isolates causing normal (A–C spiralling and D non spiralling), superficial (E and F) and russet scab (G and H).

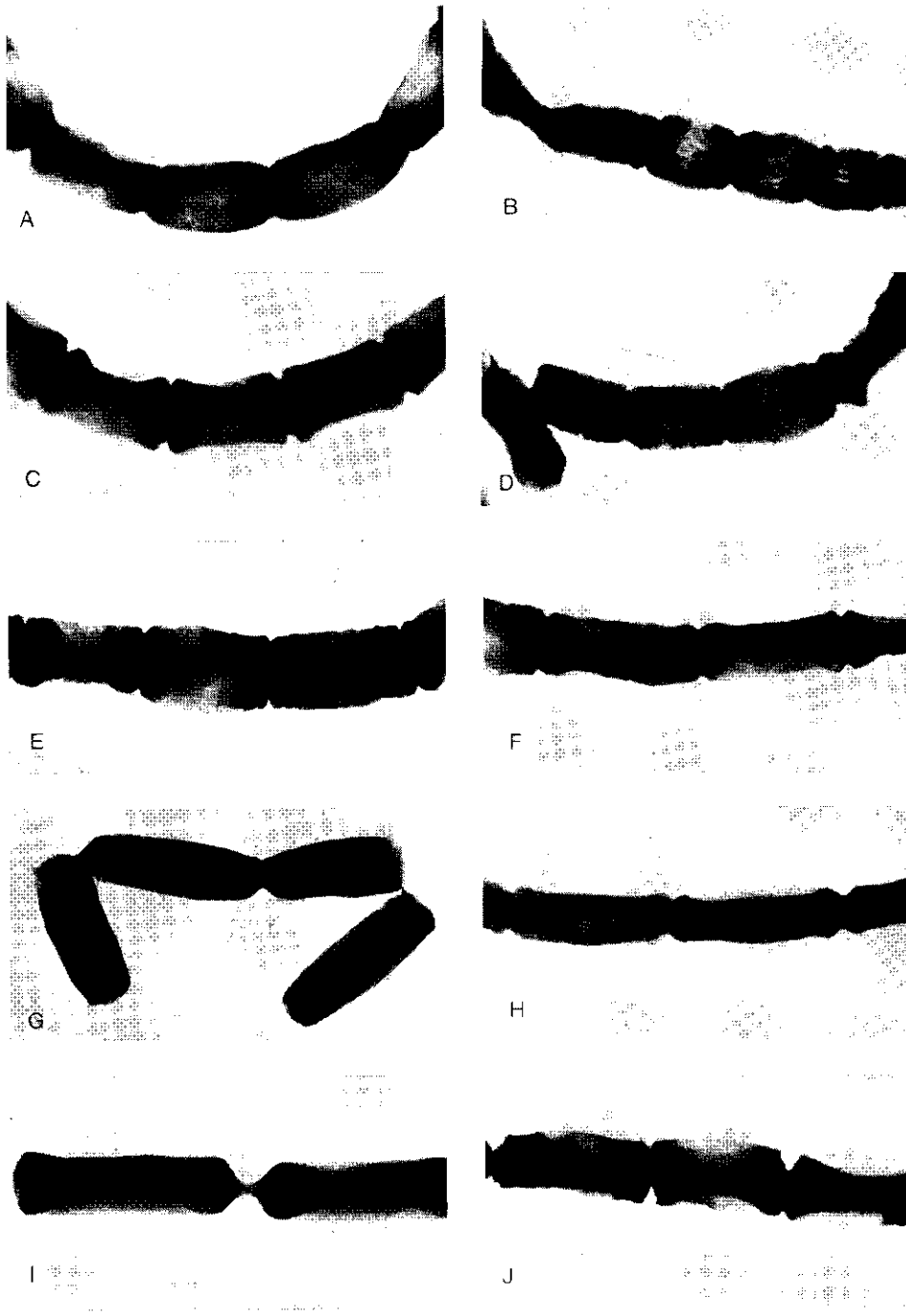

Fig. 3. Variation in spore morphology between different isolates causing normal (A–D), superficial (E–H) and russet scab (I–J) x 10.000 (Photographs: Technical and Physical Engineering Research Service, Wageningen).

of the organism and type of scab lesion caused on Bintje. An isolate giving a particular lesion type on Bintje would always give that type on this variety, but the same isolate might give a different one on a different variety. In general the more resistant the variety the less severe the reaction, but not always. For example, an isolate causing a superficial scab on susceptible Bintje produced a normal type of scab on the more resistant Sirtema.

Russet scab producing isolates showed the characteristic symptoms only on the Dutch varieties Bintje, Climax, Eba and Industrie, whereas other varieties normally were not affected. Only Eigenheimer gave a superficial scab type with a single isolate from this group.

Pathogenic and non-pathogenic isolates from soil could not be distinguished on nutrient media containing tyrosine, for both can give a positive tyrosinase reaction. The percentage of non-pathogens is not constant, for example, in a soil infested with the russet scab organism, 39.5% of 114 tyrosinase positive isolates were pathogens, whereas in a soil from Oostelijk Flevoland 24.4% (of 119) and from Groningen 0% (of 64).

Since the pathogenicity test is too laborious for routine research different methods were tried in an attempt to find a quick and yet reliable test.

2.2.1 Identification by morphology

Visual characteristics such as colour of mycelium and spores, colour of the substrate and type of colony cannot be used, nor the way in which the spore chains are spiralled because, even in the same colony, the spirals at the edge of the colony are often different from spirals in the centre because of age and spiralling also differs with the medium used.

Because of the smallness of the spores their morphology had to be studied with the electron microscope. More than 20 pathogens, causing various types of scab and six non-pathogens were studied and photographed. Of the non-pathogenic isolates four had smooth spores as did pathogens, but two had echinulate spores. The shape and size of smooth spores showed considerable variation and it was not possible to distinguish between pathogens and non-pathogens on the basis of spore morphology; neither was it possible to correlate spore morphology with the type of scab produced (Fig. 3).

2.2.2 Identification with an actinophage

The possibility of recognizing pathogenic isolates with an actinophage was mentioned by Newbould (1953), Newbould & Garrard (1954) and Welch et al. (1955).

Using the method of Robinson & Corke (1959) an actinophage was isolated from soil heavily infested with the scab organism, but this actinophage lysed pathogenic and some non-pathogenic isolates, and therefore could not be used for purposes of identification.

2.2.3 *Identification by physiology and biochemistry*

Taylor & Decker (1947) reported a good correlation between the ability to produce lesions on tubers and the production of a dark brown ring of surface growth on separated milk, and Hoffmann (1959) peptonisation and browning of skimmed milk agar, but neither could be confirmed using a number of our isolates of known pathogenicity.

In collaboration with Drs. C. Kliffen (biochemist at IPO) I looked for physiological characters which could be used in distinguishing:

group I. actinomycetes, causing normal scab
group II. actinomycetes, causing superficial scab
group III. actinomycetes, causing russet scab
group IV. actinomycetes, which were tyrosinase positive non-pathogens and could not be separated from the foregoing groups by other means (see IPO, Annual Rep. 1964–1966).

In the first series of experiments we used different carbon sources in the nutrient media and three representatives of the groups I, III and IV, two of group II and three non-pathogenic, tyrosinase negative isolates.

In two basal media different carbon sources were added, viz.

To basal medium 1 (containing 0.1% K_2HPO_4, 0.1% Na-*l*-asparaginate, 1% glycerine and 1.5% ion agar) peptone was added in quantities varying from 0–0.4%. The pH has been adjusted to 7.

To basal medium 2 (containing 0.2 g $MgSO_4$, 0.2 g KCl, 1 g $NH_4H_2PO_4$ and 15 g ion agar per litre), adjusted to pH 7, 1% of one of the following compounds was added: glucose, trehalose, sorbose, xylose, inuline, galactose, melibiosehydrate, inositol, lactose, sorbitol, fructose-6-phosphate, maltose, maltosehydrate, salicine, dulcitol, adonitol, arabinose, raffinose, aesculine, mannitol, saccharose, Na-succinate, Na-acetate; or glycine was added in quantities varying from 0.1–5%.

The nutrient agar in Petri dishes was inoculated with the various isolates and incubated for seven days at 28° C, when growth and sporulation, colour of mycelium and spores and colour of the substrate were recorded. No striking differences were noted. However, of the three isolates in group IV two produced a dark colour on the aesculine medium and one also produced grey spores on glucose (on all other media it was either white-spored or sterile), whereas the third isolate also produced grey spores on glucose, but was the only one to do so on inuline. The colour changes on the aesculine medium were caused by one or more compounds with an absorption maximum at 420 nm. Five isolates per group (I–IV) were inoculated on to solid and liquid media, containing different concentrations of aesculine and the colour changes were found to decrease as the concentration of aesculine increased. However, no distinction, either between pathogens and non-pathogens, nor between groups could be made.

In the series of experiments the nitrogen source of basal medium 2 was varied by addition of:

a. different amino-acids: *l*-serine, *l*-cysteine, *l*-arginine, *dl*-α-alinine, *l*-glutamine, *l*-tryptophane, *l*-asparagine, *l*-threonine, *l*-leucine and *l*-cytine in a concentration of 1 g/l
b. potato albuminoids (sterilized hot, or cold by passing through a Seitz-filter)
c. extracts of young potato tubers (sterilized cold)
d. exudates of young potato tubers (sterilized cold)
e. nucleic-acid derivates (DNA, RNA and thiouracil, sterilized cold).
The pH was adjusted to 7 with KOH, after the nitrogen source had been added.

Five isolates of each group were cultured and the growth and sporulation differed greatly, but the variation was not correlated with the pathogenicity of the isolates.

Extracts of young tubers of the variety Bintje were fractionated with the aid of ion exchangers into liquid with or without either kations or anions or without both, filtered through a Seitz-filter and added to the basal medium 2. Two pathogens and two non-pathogens were inoculated and variation in growth and sporulation did occur, but was not correlated with pathogenicity.

Two pathogenic and one non-pathogenic isolates were grown in a potato-glucose solution with 0.7% peptone and the absorption spectra in the filtrate determined, but no differences were noted.

2.2.4 Identification by serology

Serological recognition of pathogens and non-pathogens has been attempted (Vruggink & Maat, 1968) with some success. Isolates reacting negatively serologically proved to be non-pathogenic and among isolates reacting positively a variable proportion of non-pathogens were found. The proportion depended on the origin of the soil sample and they could only be distinguished from true pathogens by using a pathogenicity test.

Serology has been used to study soil populations and only isolates serologically positive needed to be tested for pathogenicity, which decreased the amount of screening work.

2.3 Discussion and conclusions

Opinions differ between taxonomists as to the precise classification of scab-causing actinomycetes because they cannot agree on which of the various characters are the most important for determination of the species. For example, the type strain IMRU 3018 of *Streptomyces scabies* is described by Waksman (1961) as having sporophores much branched, wavy or slightly curved, occasionally forming spirals; spores cylindrical, sub-globose and echinulate (illustrated). Tyrosinase reaction is strong. Recently, Shirling & Gottlieb (1968b) have shown the spores of IMRU 3018 to be angular, smooth, and smaller than described by Waksman, also that melanoid pigments are not formed in peptone-yeast-iron agar, tyrosine agar

or tryptone-yeast broth. However, the absence of melanoid pigments or positive tyrosinase reaction may be caused by the long period in culture of the type strain or through the production of tyrosinase deficient mutants (Gregory & Vaisey, 1956).

Krassilnikov (Waksman, 1961, p. 89) describes *Actinomyces scabies* as having monopodially branched sporophores, spiral shaped, produced on hyphae of aerial mycelium, whereas Shinobu (Waksman, 1961, p. 101) describes *Streptomyces scabies* with long or short, loose or compact sporophores in open or closed spirals and Nomi (Waksman, 1961, p. 105) aerial mycelium somewhat flexuous or wavy, without long hyphae or spirals. In our experience, spiralling is present in nearly all pathogenic isolates except isolate no. S 29 and S 48. Morphologically S 29 has much in common with *Streptomyces resistomycificus* Lindenbein, and S 48 with *Streptomyces griseus* Waksman et Henrici (Shirling & Gottlieb, 1968a and b). However, both isolates S 29 and S 48 could be placed in *S. scabies* following Waksman's description, provided that Shirling and Gottlieb are right about the smooth spores of type strain IMRU 3018. However, in general we agree with Corbaz (1964) when he describes *S. scabies* as follows: 'Mycelium aérien gris cendré, le plus souvent clair; abondant, fortement ramifié, (d'où un aspect laineux); type de l'embranchement: monopodial; spirales nombreuses, longues, régulières. Spores lisses. Formation de mélanine.' (Type culture 135.64 C.B.S.).

Most of our scab isolates complied with this description. Many non-pathogenic isolates meet the description too and cannot be distinguished serologically from the pathogens (Vruggink & Maat, 1968), and therefore have to be included among *S. scabies* (as advised by Waksman, 1961). For the same reasons our isolates causing russet scab have to be included in the species, and in fact some russet scab isolates did cause superficial scab on Eigenheimer.

A russet scab organism, described by Harrison (1962) and also isolated by Mygind (1965) in Denmark was tyrosinase negative and not identical with *S. scabies,* and Harrison suggested it should be placed somewhere between this species, *S. tenuis* and *S. marginatus*. This organism has been found in the Netherlands by Wiersema (pers. comm.), but not by me, because of the method of isolation followed. Mygind also showed this tyrosinase negative isolate to attack the same limited range of varieties in Denmark as did our tyrosinase positive isolates in the Netherlands.

The possibility that other *Streptomyces* species cause scab is known from older as well from more recent papers. Wollenweber (1920) distinguished six species and Millard & Burr (1926) worked with 24 isolates of which 12 were pathogenic and belonged to 11 different species. More recently Corbaz (1964) found in isolations from scabby tubers that 70.7% belonged to *S. scabies* (which he considers the most virulent species), 12.1% to *Streptomyces griseus* Waksman et Henrici, and 13.9% to *Streptomyces aureofaciens* Duggar, both tyrosinase negative. He also found *Streptomyces flaveolus* (Waksman) Waksman et Henrici capable of causing scab. The 'acid tolerant *Streptomyces* species', which causes scab in soils with a low pH (Bonde & McIntyre, 1968) is not identical with *S. scabies.*

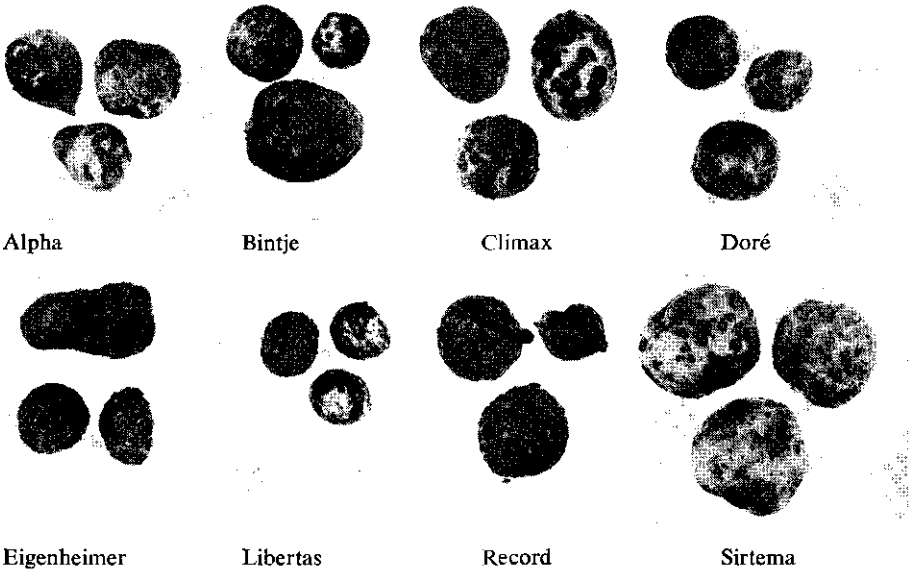

Fig. 4. Reaction of eight potato varieties to infection by a virulent normal scab strain (S 80), showing Sirtema with most resistance.

We could not distinguish between pathogenic and non-pathogenic isolates but recently Knösel (1970) found, when checking some of our and other isolates, a high pectinacid transeliminase activity only in pathogenic isolates. Since the scab pathogens first attack the pectin of the cell walls and only later penetrate into the cells of the tuber, it is reasonable to suppose that the presence of high concentrations of pectin-destroying enzymes should correlate with pathogenicity. This needs further research.

Physiologic specialisation does occur among isolates of *S. scabies* but I have made little study of this aspect. In the Netherlands the order of susceptibility of the potato varieties shows little variation from year to year and from region to region (Internal Rep. Institute for Research on Varieties of Field Crops (Instituut voor Rassenonderzoek van Landbouwgewassen, IVRO, Wageningen)), as found by Emilson & Gustafsson (1953) in Sweden. Susceptible potato varieties seem attacked everywhere in the world where common scab occurs, while the more resistant ones remain more or less unaffected. Thus I conclude that physiologic specialisation is of secondary importance with at most small, local variations.

However, the degree of virulence of local strains is important. I found that superficial scab isolates were generally less virulent than the normal scab isolates as shown by smaller surface area affected (figs 4 and 5) (Chapter 4). Some maintain that the occurrence of superficial scab on tubers means a certain degree of resistance of the potato variety (Leach et al., 1939; Emilsson & Gustafsson, 1953). I found this scab type on both very susceptible and on rather resistant varieties but that this depended on the virulence of the isolate.

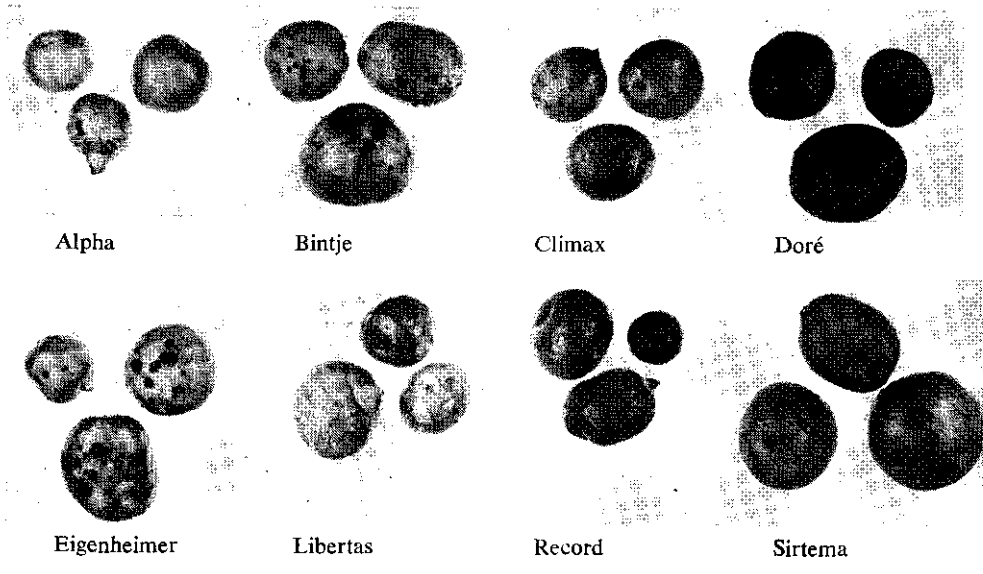

Fig. 5. Reaction of eight potato varieties to infection by a superficial scab strain (S 15), showing only Bintje, Doré and Eigenheimer affected.

The scab type (with exception of russet scab) depends therefore mainly on the resistance of the potato variety and on the virulence of the pathogen. Russet scab is different in that varietal resistance is based on a simple monofactorial principle (pers. comm. Wiersema), which accounts for its restricted host range. Because only a few potato varieties are attacked in only a few regions, russet scab is considered of little importance.

Summarizing, the following conclusions can be drawn:

1. Most of our pathogenic isolates belonged to *S. scabies*, as described by Corbaz (1964). Other *Streptomyces* species may cause common scab but to a much lesser extent and virulence of such strains is generally less.
2. Non-pathogenic *S. scabies* strains do exist and are morphologically and serologically indistinguishable from pathogenic strains.
3. Our russet scab strains belonged to *S. scabies*. The taxonomic position of the russet scab organism of Wiersema (pers. comm.), Harrison (1962) and Mygind (1965) is not clear.
4. Future recognition of pathogens among actinomycetes from soil may be simplified when more is known about the enzyme activity of pathogenic and non-pathogenic isolates.
5. Physiological specialisation among *S. scabies* does exist, but is mainly of local importance. The virulence of strains is more important locally and largely determines the type of scab on the potato variety grown.

3 Anatomy of scab types

When considering the infection of potato tubers by the scab causing organism (usually *Streptomyces scabies*), three major factors are of importance. Firstly how does the infection occur, secondly how does the infection develop and finally what conditions influence the incidence of the disease?

Study of the initial stages of infection is difficult because of the small size of actinomycetes. Lutman (1913) suggested that scab lesions may originate anywhere on the tuber surface but most often at lenticels. Fellows (1926) states: 'Whenever it was possible to distinguish the point of infection it was found in a lenticel or stoma, except when infection occurred near an eye, in which case it was always in the region where the protective layer was epidermis and stomata were present in the vicinity.' Jones (1931) concluded that young lenticels are the usual points of infection and this is now generally accepted. Infection through wounds can occur (Thaxter, 1892), as caused by insects (MacMillan & Schaal, 1929; Schaal, 1934).

I have examined many microtome sections of young tubers but have been unable to demonstrate early lenticel infection. However, when symptoms are visible to the unaided eye, the site of infection has always been a lenticel.

The anatomy of the potato scab lesion has received little attention. Lutman (1913) reported seeing dark stained cells in brown spots on the skin of scabby potatoes and threadlike filaments of the parasite in very young scab lesions, which he assumed produced the disease. Fellows (1926) found that the blackening extended along the middle lamellae of dark stained cells, and where adjacent cells met the walls were separated and the space filled with a dark-brown liquid. No mycelium was present which suggests the actinomycete can affect cells at a considerable distance in advance of the mycelium. Mycelium was found however in dead corky cells near the surface of lesions and starch grains were present in invaded cells. Jones (1931) had difficulty in finding mycelium in infested tissue and found none in the tissues surrounding the lesion. Lutman (1941) however considered the tuber tissue systemically infected and states: 'Regardless of scab the cell walls of all tubers were infested with *Actinomyces* filaments. Clean tubers from various local sources, among them specimen from fields never known to produce scab, and clean tubers obtained in the market from other states were alike infested.' ... 'The *Actinomyces* filaments extend from the cork and cork cambium and can be followed into the body of the tuber.' However, he did not succeed in isolating the causal organism and therefore his argument is not very convincing.

Because of these different opinions a study was made of the anatomy of scab

infection. Three types of scab (already mentioned in the previous chapter) were examined separately, partly because Leach et al. (1939) and Emilsson & Gustafsson (1953) considered that the differences in lesion type are caused by differences in the susceptibility of potato varieties and partly in order to look for a correlation between the degree of varietal resistance and the anatomy of the tuber.

Elevated scab types were included with normal scab for Jones (1931), when comparing his pitted and tumulus types, said: 'Excepting the differences in number of wound cork barriers and of the amount of fungal mycelia present, there is no other structural feature by which the two kinds of scab may be distinguished from one another.' As most elevated scab types have only one wound cork barrier they can be considered less serious forms of normal scab.

3.1 Scab types

The visual characteristics of the three scab types were studied on one potato variety Bintje. They were deliberately chosen to show that the type of scab lesion depends on the degree of virulence of the pathogen and the susceptibility (or resistance) of the host.

Normal scab This type embraces all those lesion types where the tuber skin is destroyed and the underlying tissues more or less deeply cracked through tuber growth. The extension of cracks into the surrounding skin gives the 'scab' a star-shaped appearance; if lesions coalesce the star-shape is lost. Even when the 'scab' becomes deep, pitted or elevated by cell division of the underlying healthy tissue to produce tumulus or elevated scab, this is considered 'normal' scab. Raised scab is unusual in Bintje but is more common in other varieties such as Patrones.

Superficial scab This is characterised principally by the shallow depth of penetration and consequently tensions caused by tuber growth are less and the skin remains more or less intact. Small cracks may occur but the scab spots remain roundish and not star-shaped, otherwise the differences between 'superficial' and 'normal' scab are merely one of degree.

Under comparable conditions the extents of the infection on the tuber surface is less than with normal scab.

Russet scab This scab type was only studied on Bintje and differs from the others in that it is superficial with shallow cracks and ridges arranged in square or pentagonal patterns similar to drought cracks in clay soil. Often large areas of the tuber surface are affected when the separate spots fuse.

Economically russet scab on the tuber cannot be considered very serious, because of its superficial nature. Russeting may be a quite normal varietal characteristic, for example 'Russet Burbank', an American variety. However this scab type, unlike the other two, may attack the entire root system which becomes light brown, in

contrast to the white roots of healthy plants, and the cortex is destroyed. The other two scab types may cause local lesions on stolons, underground stems and, only if the attack is severe, on roots.

3.2 Materials and methods

Diseased tubers for anatomical study of the different scab types were obtained from the field- and pot-grown plants of the varieties Bintje, Eigenheimer or Sirtema. Occasionally sections were cut by hand from fresh material, but generally with a microtome, using FAA-fixed (formaldehyde-acetic acid-alcohol) and paraffin embedded material. Sections were stained in different ways, either using Harris and Heidenhain haematoxylin and Flemming's triple stain (Johansen, 1940), or cotton blue and safranin (Lepik, 1928), or toluidine-blue (Shoemaker & Riddell, 1954). In hand sections the deposition of suberin during wound barrier formation was detected by Sudan IV.

Actinomycete mycelium does not readily stain and of the methods tried the haematoxylin dyes have given the best and most consistent results.

3.3 Anatomy of normal scab

In general my findings agree with previous workers. Depending on the severity of the attack, so one, two or even three wound barriers can be seen. When three are formed the first two may only be a few cell layers thick and in the centre of the lesion difficult to see because of tissue disruption (Fig. 6). Beneath the last and innermost barrier, which generally consists of many cell layers, a starch-free zone of parenchyma is found, and above it enlarged parenchyma cells are often observed. Near the lesion surface the original parenchyma may be present with some cells still containing starch grains, but this has become isolated from the inner tissues by

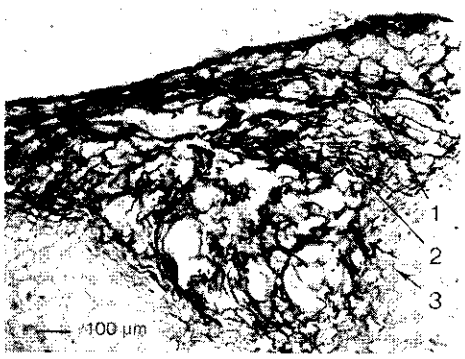

Fig. 6. Section taken near the centre of a normal scab lesion on Eigenheimer showing the first (1), second (2) and third (3) wound barriers.

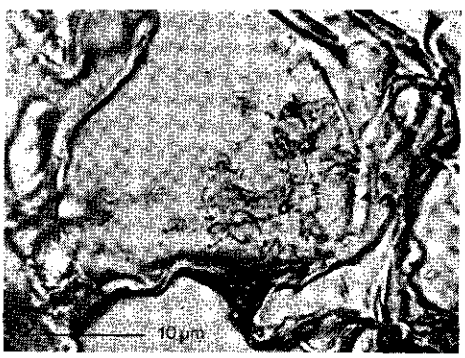

Fig. 7. Sporulation of Streptomyces mycelium within a parenchyma cell near the tuber surface of Eigenheimer.

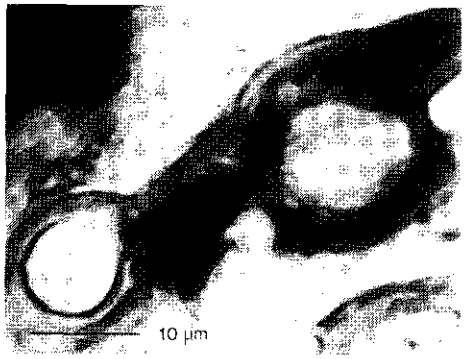

Fig. 8. Swollen brown cell walls with small black spots indicating the presence of mycelium (Eigenheimer).

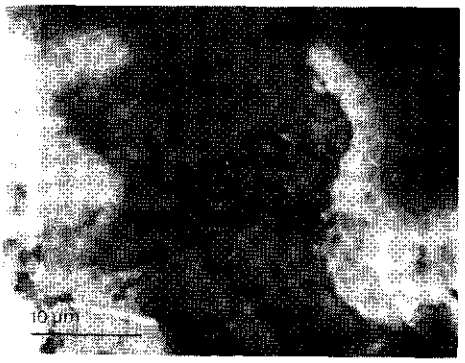

Fig. 9. Mycelium on or in part of a swollen cell wall.

the wound barriers. It is in this region that the remains of the first barriers, recognised by cells with thick brownish walls and compressed appearance, may be seen. The cell walls of the original tuber skin, when still present, also are considerably thickened, while mycelium in these cells is sparse. Abundant mycelium may be seen in the centre of the lesion in the parenchyma cells of the original cortex or on the lesion surface (Fig. 7). Mycelium is also present between the cell walls of the

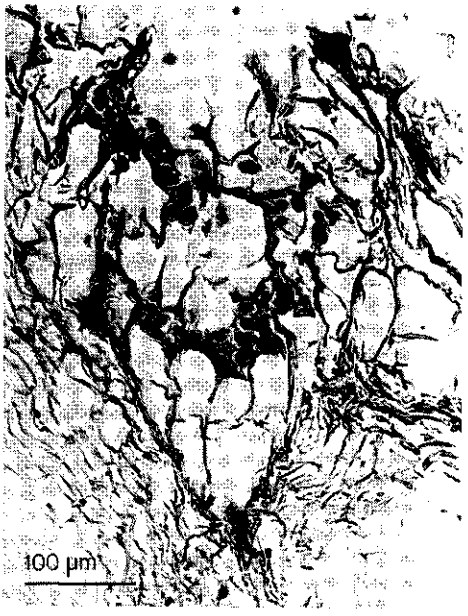

Fig. 10. Section of the centre of a normal scab lesion showing the thick-walled cells containing starch grains (Sirtema).

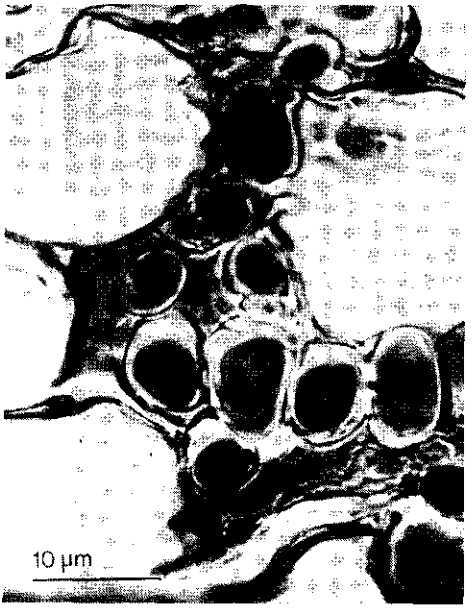

Fig. 11. A thick-walled cell with the starch grains embedded in cell wall material (Sirtema).

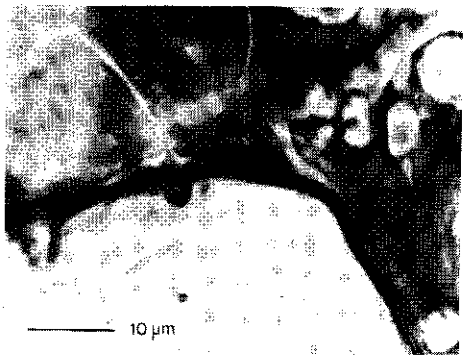

Fig. 12. A lignituber-like swelling on the cell wall of a starch-filled cell (Eigenheimer).

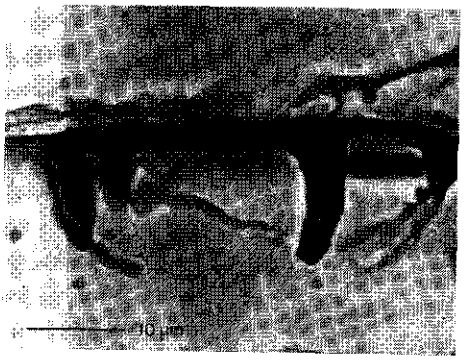

Fig. 13. Lignituber-like swellings on a parenchyma cell wall (Eigenheimer).

brownish cells of the barriers and the original skin, although it is difficult to demonstrate because of the brown material, unless the cell wall is parallel or nearly parallel to the plane of sectioning (figs 8 and 9). Similarly the presence of mycelium can be seen on normal parenchyma cell walls of the cortex and under the first wound barrier. However, it is difficult to decide if the mycelium is on or inside the cell wall. Because it does not sporulate, as often happens when mycelium is found inside the cell, it most probably is inside the cell wall.

Parenchyma cells with starch grains in an infected area have thickened and distorted walls so that the cells resemble intercellular spaces. In the centre of the lesion many of these cells are often found together (figs 10 and 11). Again with difficulty, mycelium can be found in between the brownish cell wall layers of the swollen cells. Where the infection has penetrated most deeply into the tuber tissues, isolated or grouped starch-filled cells often indicated the direction of mycelial growth. As the enclosed starch grains appeared intact, they were therefore unlikely to have been a food source, although the existence of lignituber-like swellings (Fellows, 1928) on the cell walls was evidence for presence of the parasite (Fig. 12). Such swellings, caused by mycelium of *S. scabies*, have not been reported in the literature but were found fairly often in scab lesions on Eigenheimer. Mycelium originating from a 'lignituber' showed all the characteristics of an actinomycete. 'Lignitubers' were also found on unthickened cell walls of the parenchyma between the epidermis and the first barrier, projecting mostly to one side. No mycelium could be detected in the adjacent cell (Fig. 13). Apparently, during an attack, the mycelium grows first between the cell-wall layers and only reaches the still living cell through the lignituber.

3.4 Anatomy of superficial scab

There appears to be a gradual transition from the less serious 'normal' to the more serious 'superficial' scab type and there is a stage where the types are not

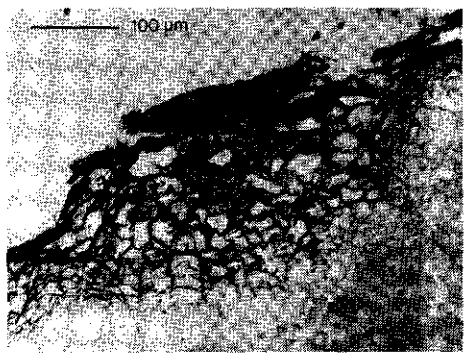

Fig. 14. Section of a superficial scab lesion (Sirtema).

readily distinguishable. If the skin over a lesion remains intact, or only slightly ruptured, then this is considered 'superficial' scab. In section, the lesion shows extensive invasion of the outer cell wall layers of the tuber skin with only shallow penetration of the tissues at the lesion centre. The walls of the skin cells, as well as those showing starch inclusions, are thickened. Unthickened parenchymatic cells are few in the lesion, because of the superficial nature of the infection. Only one barrier is formed, consisting of 8–12 cell layers directly under the centre and fewer towards the edge of the lesion. The parenchyma cells under the barrier have no starch (Fig. 14).

Mycelium can sometimes be seen in cells, but because of the structure and discolorisation of the thickened cell walls, growth between walls has not been seen, although is considered very likely.

3.5 Anatomy of russet scab

Sections (of Bintje only) confirm the superficial nature of russet scab. The pentagonal cracks are nearly always in places where the wound barrier has formed most deeply in the tissue. As the tuber grows, tensions crack the parenchyma outside the barrier and the primary skin and there these layers curl up to form the ridges on either side of the crack (Fig. 15).

Between the cracks the wound barrier is only a few cells below the original skin

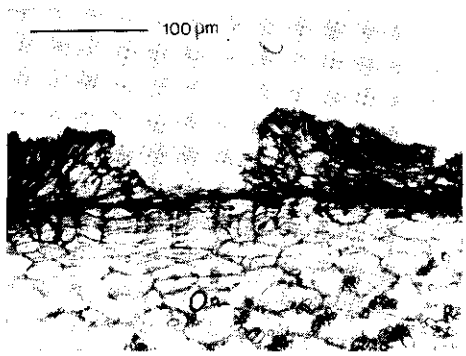

Fig. 15. Section of a russet scab lesion showing the ridges on either side of a crack (Bintje).

and consists of many layers of thin-walled suberised cells. Towards the edge of the lesion the wound barrier and skin merge. The dead parenchyma outside the barrier and between the cracks, originally situated directly under the skin, showed remnants of nuclei, indicating that the process of 'cutting off' happened quickly and effectively. In the centre of the lesion, cells with thickened walls and some mycelium were seen. However, the host seems to react so rapidly to the attack, that actinomycete mycelium has little chance of penetrating very far into the tuber tissues.

Cells of the primary skin, when present, often show the thickening which is characteristic of the presence of mycelium. Apparently growth of the mycelium is favoured by this layer, which may explain the quick expansion of lesions over the surface of the tuber.

3.6 Conclusions

Earlier workers described many types of scab lesions, but these can readily be decreased to three standard scab types, viz. normal, superficial and russet. My studies of scab lesion anatomy have suggested that the differences between superficial and normal scab depend entirely on the virulence of the isolate, the degree of susceptibility of the host and on the conditions under which infection takes place. All isolates have been tested on the one very scab-susceptible variety Bintje under standarised conditions and therefore virulence of the isolate can be said to have caused the differences in symptom expression.

Russet scab type does differ in symptom expression and anatomy, and in attacking the root system. In all of the three scab types the main pathway of the mycelium seems to be intercellular. Only in the older and peripheral regions of lesions has mycelium been found inside cells, where it may sporulate abundantly. Invaded cells may be alive, with sometimes (Eigenheimer) lignituber-like structures, or dead. Towards the interior of the lesion the mycelium progresses in cell walls, but is very difficult to find because it stains poorly when masked by the brownish cell wall material. However, it can be seen in the very minute intercellular spaces between the thick cell walls, especially when these lie in the plane of sectioning. The presence of mycelium in the cell walls has also been demonstrated by Fellows (1926) and Jones (1931).

4 Influence of external conditions on scab

The influence of external conditions on the severity of symptoms was also considered important particularly temperature, soil moisture and pH (the latter in pure cutlture only). Schaal (1940b) found differences in pH-tolerance between various strains of the scab organism, and Bonde & McIntyre (1968) describe an 'acid-tolerant *Streptomyces* species'. The field work done on the influence of soil pH by the Institute for Soil Fertility (Instituut voor Bodemvruchtbaarheid, IB, Groningen) is not recorded here.

4.1 Temperature

The influence of temperature on the infection of Bintje tubers by *Streptomyces* strains from the three scab types, has been assessed using Wisconsin tanks. Four isolates from each lesion type were used in artificially infected sterile soil and the optimum temperature for infection for each isolate determined. Wisconsin tanks

Table 1. Percentage of surface of Bintje tubers with scab caused by four isolates each of three scab types at different soil temperatures.

No of isolate	Soil temperature (°C)			
	12	16	20	24
Normal				
S 80	1.2	4.1	4.5	3.2
S 47	16.5	41.7	44.1	43.0
S 60	24.4	24.3	51.2	50.1
S 35	3.4	5.4	12.6	10.1
Superficial				
S 21	0.03	0.7	2.3	1.6
S 29	0.1	0.4	0.9	0.2
S 37	1.6	3.8	5.6	2.0
S 105	1.8	5.5	12.4	8.2
Russet				
N 78	49.6	70.1	55.8	22.5
S 13	26.6	34.1	22.2	15.0
N 66	27.1	22.1	24.8	16.3
S 89a	47.7	48.7	37.3	25.9

were kept at about 12, 16, 20 and 24° C. Although the temperature of the air in the greenhouse was adjusted to 18° C, small fluctuations could not be avoided, so that the temperature of the 12° C tank could rise during the day, whereas the 24° C tank could not always be maintained at that temperature during the night. Temperatures of the 16 and 20° C tanks could be kept constant.

From Table 1 the optimum temperature for infection for all isolates of superficial and normal scab is about 20° C, whereas for russet scab nearer 16° C.

4.2 Soil moisture

In the field both normal and superficial, but not russet scab are affected by high soil moisture conditions during the time of tuber formation (Section 8.1.2, experiments PAW 1057 and PAW 1059 in 1966, and Labruyère, 1965). As further proof of these observations, six lots of sterile soil in pots were infested with six different isolates (two from each of the three scab types) and the soil adjusted to three different moisture regimes.

Table 2 shows that, although superficial scab covered a smaller percentage of the surface area than normal, development of both types was inversely related to the moisture content of the soil. Russet scab did not show such a reaction and tended to be most severe at the higher moisture contents.

4.3 Soil acidity

Observations made on different farms near Stiens (province of Friesland) showed that scabbed tubers could be found in fields with acid soil which indicated the

Table 2. Percentage of surface of Bintje tubers with scab caused by two isolates each of three scab types at different soil moisture contents.

No of isolate	Moisture content (% by weight)[1]		
	50	37.5	25
Normal			
S 23	0.7	5.1	30.3
S 80	7.0	16.9	41.7
Superficial			
S 29	0.1	0.7	5.4
S 97	0.0	1.2	7.8
Russet			
S 13	12.7	19.9	10.9
S 128	34.5	30.3	23.8

1. The potsoil, very rich in humus, and at field capacity contained 55% water by weight.

presence of acid tolerant strains. At a pH below 4.5 only superficial scab occurred on tubers and above pH 5 only normal scab. Between pH 4.5 and 5 both scab types could be found on the same tuber. Apparently the pH-range of strains causing both scab types overlap between pH 4.5 and 5.

In the province of Groningen superficial scab is both common and severe, but in practice has been found to become less severe when the soil is limed. At Hornhuizen in 1968 an almost scab-free yield was obtained, although the soil had been heavily limed (100 tons/ha Kencica, a calciumcarbonate/calciumsilicate fertilizer with 5% K_2O), whereas in the untreated plots of an adjacent irrigation experiment there were no scab-free tubers and on average 25% of the surface area of tubers was affected.

Attemps have been made to assess the pH-ranges of three isolates each, of normal, superficial and russet scab and also an atypical type of superficial scab (the isolates of which form red pigment in pure culture on certain nutrient media). Emerson's medium with 0.1 g yeast extract (Waksman, 1961, p. 331) was used as basal medium, and this was adjusted with citric acid-phosphate buffer to give a range from pH 4.5 to 8.0, at intervals of 0.5. (Above pH 7 the isolates did not grow on this medium, presumably because of the high disodium-hydrogenphosphate content in the buffer, and therefore the upper part of the pH-range was buffered by Tris and HCl.) After sterilisation the pH was rechecked and the range proved to be pH 4.3 to 8.0.

Flat medicine bottles (100 ml) containing 40 ml of the variously adjusted pH nutrient solutions were then inoculated and placed in a shaking machine at a temperature of 24–28° C. After a fortnight the liquid was filtered off and the mycelium dried and weighed. The pH of the filtrate was again measured.

In all bottles in which the inoculum had grown well the pH had risen to between

Fig. 16. Eigenheimer with white roots and normal scab on the tubers (left) and Bintje with brown roots and russet scab on the tubers (right) harvested from the same field.

pH 7 and pH 9, regardless of the initial pH-value. The alkalinity was probably caused by ammonia released during the breakdown of proteins which could be smelt when the bottles were open.

Since the pH had deviated so far from the starting point, the weight of mycelium produced could not be used as a measure of growth. Therefore we could only record the initial pH-value at which isolates began to grow and at which they grew well. Two of the three normal scab isolates grew well between pH 6 and pH 7.5 and the third between pH 5.3 and pH 7.5. Isolates from both types of superficial scab could grow from pH 4.8 to pH 7.5–8 and one showed some growth at pH 4.3

The optimum pH for the russet scab isolates was between pH 6.5 and pH 7, most started to grow below pH 5, but one did not grow below pH 5.7.

A further pot experiment with Friesland soil adjusted to pH's 4, 6 and 7.5 with sulphuric acid and lime, confirmed a lower pH-optimum for the development of superficial than for normal scab.

4.4 Conclusions

Russet scab isolates differed from the other two scab types not only in symptom expression and the range of varieties attacked, but also in reaction to temperature and moisture; only the pH-range was similar.

Russet scab can cause a general infection of the root system, whereas the other two cause local lesions on the roots only when the attack is severe (Section 3.1). A general infection may lead to yield losses, as shown in a pot experiment in which the average yield of Bintje plants was decreased from 1080 g with a normal and 1370 g with a superficial to 900 and 650 g respectively with two russet scab isolates. The same effect was shown in a field experiment with Bintje and Eigenheimer (Fig. 16). At harvest, russet scab affected on average 52% of the tuber surface of Bintje and the mean yield of 21 replicates of plots of six plants was 3790 g (of which 3120 g were tubers $>$ 35 mm) and normal scab 16% of Eigenheimer tubers and the yield was 4890 g (of which 3100 g $>$ 35 mm). Although the comparison is between the yield of two different potato varieties, Bintje normally has 5–10% higher yield than Eigenheimer. Here the yield of Bintje was about 25% less than Eigenheimer and the characteristic brown root symptoms were found only on Bintje.

Although the russet scab isolates used in these experiments were morphologically identical with *Streptomyces scabies* (Section 2.3) they differ from the other scab isolates in many physiological respects.

5 Review of control methods

As most of the commonly used potato varieties lack resistance the research for control of common scab can be directed in: chemical control (tuber disinfection, soil disinfection, systemic chemicals) and control of the environment (regulating the pH, antagonism, soil moisture).

5.1 Tuber disinfection

The disinfection of seed potatoes, although recommended in the past, can give quite contradictory results. Schaal (1946) concluded from his research: 'None of the seed or soil treatments appear to have value for the control of scab in the alkaline soils of northern Colorado.'

Seed potato disinfection is still practised, but it serves mainly for the control of other seed-borne diseases like *Rhizoctonia solani* or bacterial diseases which may be spread by seed tuber cutting. In my experiments on control of Rhizoctonia in new polders I found that the occurrence of scab was independent of the seed treatment with organic mercury compounds and that the soil infestation was not checked by the use of disinfected seed.

The soil is generally accepted as the main source of infection, while infection by seed tubers is only of importance on newly cultivated land, e.g. new polders or irrigated desert soils.

In most agricultural soils, *S. scabies* is a normal soil inhabitant in biological balance with the other members of the microflora, but the role it plays depends largely on environmental conditions. Because most arable land in the Netherlands has a *S. scabies* population, further research on seed tuber disinfection was considered unnecessary.

5.2 Soil disinfection

A number of mercury compounds have been effectively used as soil disinfectants by many workers, but the relatively high costs and danger to operators have prevented general use. Many other chemicals have been tested, but most have proved effective only in pot tests or under particular field conditions. Only PCNB (pentachloronitrobenzene) or quintozene, first used by Meijers (1935) in the Netherlands and later by Gram (1944) in Denmark has become widely accepted for scab control; for work in the Netherlands see van Emden & Labruyère (1958).

We have tried PCNB, formaldehyde (better known as a seed potato disinfectant) and a few other chemicals, which were selected, either because of favourable reports in literature or promising results in pot trials.

5.3 Systemic chemicals

If systemic chemicals could be used to control scab they would have the advantage that they could be applied shortly before or during the period when infection of the tubers takes place. To test this we have used the antibiotic streptomycin and the fertilizer $MnSO_4$, which has systemic properties and has shown fungicidal action against *S. scabies* in vitro. Manganese sulphate has been applied as a foliar spray and other manganese compounds as soil disinfectants in field experiments carried out in collaboration with the extension service.

5.4 Regulating the pH

Even before the causal agent of scab was discovered it was known that an alkaline soil increased the disease. Thaxter (1892) noted that the use of calcareous material resulted in severe scab, while Staes (1895) dissuaded the use of such materials in potato cultivation. Van Hall (1902) recommended sulphur and acidifying fertilizers as a method for scab control. Much attention has been given to the use of sulphur mainly in the USA (Martin, 1920, 1921 and 1922; Vaughan, 1921; Leach & Rose, 1924; Duff & Welch, 1927; Larson et al., 1938; MacLeod & Hurst, 1939; Muncie et al., 1944; Oswald & Wright, 1950; Vlitos & Hooker, 1951) and in the Netherlands Huisman (1933) and van Emden & Labruyère (1958).

Increasing pH above the scab range by heavy liming was suggested by Menzies (1950) as a means of scab control. When tried in the province of Groningen 100 tons/ha gave practically no scab and commercial applications were sometimes used for scab control by he farmers (Internal Rep. Dutch Potato Scab Committee).

Making a soil more alkaline or more acid has disadvantages in that it may decrease potato yields or crops of the normal rotation grown subsequently may be adversely affected. The scab organism may also adapt to the new pH-level (Schaal, 1940b; van Emden & Labruyère, 1958; Bonde & McIntyre, 1968). In the Netherlands scab has been found on very acid soils and therefore pH as a means of scab control has not been included in the research programme, but has formed part of the work done by the Institute for Soil Fertility.

5.5 Antagonism

Because *S. scabies* is a soil inhabitant, the environmental microflora will influence the organism as well as its relationship to its host plant and therefore reports of antagonism are not surprising (Sanford, 1926; Dippenaar, 1933; Wieringa & Wiebols, 1936; Orellana, 1947; Menzies, 1957b, 1959).

During our scab surveys differences in occurrence of scab have been noted between fields or parts of fields, which could not be explained by chemical or physical differences in soil characteristics, or by differences in crop rotation. The possibility that such differences were caused by antagonism has been investigated and the addition of antibiotic agents and green manure to the soil has been tried as a control measure against scab.

5.6 Soil moisture

The influence of soil moisture on scab (Sanford, 1923, 1924 and 1926) and the discovery that tubers are only susceptible during the early stages of their development (Sanford, 1923 and 1924; Fellows, 1926; Jones, 1931; Dippenaar 1933; Hooker & Page, 1960) lead Noll (1940) to suggest the possibility of scab control by overhead irrigation. However, this work was done with pot experiments and whether such findings were true under field conditions remained unknown, although it was well known that more scab occurred after dry than wet summers (Large & Honey, 1955).

After 1950 many field experiments on the practicability of overhead irrigation in Netherland agriculture were carried out by the Research and Advisory Institute for Field Crop and Grassland Husbandry (Proefstation voor Akker- en Weidebouw, PAW, Wageningen; nowadays called Research Station for Arable Farming, Proefstation voor de Akkerbouw, PA) and the work showed that potatoes nearly always responded positively to irrigation when given in the second part of the growing season, but no effect on scab was noticed. After Lewis (1962b) reported that a high soil moisture level maintained until shortly after the development of young tubers suppressed scab, we decided to use overhead irrigation for scab control in large scale field experiments. Some of the results obtained have already been published (Labruyère, 1965, 1966 and 1968; Baars, 1968; Annual Rep. IPO and Extension Services Noord-Friesland and Noord-Groningen, 1964–1968), but Section 8.1 deals with all te irrigation experiments carried out from 1963 to 1968.

6 Chemical control

Pentachloronitrobenzene (PCNB, quintozene) has been used by workers in many potato producing countries, e.g. Great Britain (Rosser, 1960), France (Guntz & Coppenet, 1957; Hervé et al., 1968), Germany (Dingler et al., 1960), the Netherlands (Meijers, 1935; van Emden & Labruyère, 1958), Denmark (Gram, 1944; Stapel & Lindegaard, 1962), Norway (Hansen, 1967), Sweden (Gustafsson, 1962), Switserland (Anom., 1957), USA (Potter et al., 1959) and USSR (Popkova et al., 1964); although long, this is still an incomplete list.

In the USA ureaformaldehyde was tried (Bartz & Berger, 1958; Anom., 1958; Fleischfresser, 1959; Schultz et al., 1960; Busch, 1961; Weinhold et al., 1964), because in soil it slowly disintegrades into urea and the active material formaldehyde. Formaldehyde was used as a seed tuber disinfectant by Melhus (1918), Porter (1921) and Wiant (1931) and as a soil treatment against scab (Meyer, 1940; Shuvalova, 1962).

Manganese has been applied to soil (McGregor & Wilson, 1964) and to the plant (Mortvedt et al., 1961 and 1963).

Ark (1947) found *S. scabies* highly sensitive to streptomycin and so this antibiotic was tested for scab control by applying to soil or to leaves.

6.1 Materials and methods

Most experiments were done in the field, but pots were used if further information on a particular chemical was wanted. The field experiments were mostly conducted by the local extension service under our supervision, and were usually carried out on farmers fields used for seed production and known to be infested. In most cases they were situated on calcareous sandy loams of the young polders; experiments with formaldehyde were done mainly on sandy soils and on ware crops. Scab assessment of tubers after harvest was always done by experienced personal of IPO.

The research programme has been aimed mainly at the problem of scab control on seed potatoes and therefore the field experiments have been treated and harvested as seed potato crops, unless otherwise stated.

For scab assessment samples of about 100 seed size tubers (± 5 kg) between 35 and 45 mm were taken from every plot in the experiment. The tubers were examined individually and classified according to the percentage of tuber surface area covered by scab lesions. In the early experiments Scale 1 was used (Table 3).

Table 3. Classification in Scale 1 and Scale 2 of tubers according to percentage of surface with scab.

Class	Surface with scab (%)	Class mean (%)
Scale 1		
1	scab free	0
2	0 – 10	5
3	10 – 30	20
4	30 – 60	45
5	60 –100	80
Scale 2		
2a	0 – 1	0.5
2b	1 – 5	3
2c	5 – 10	7.5

The mean surface area affected of a sample was found by dividing the sum of the products of the weights of the tubers in each class (g_x) and the class means (m_x) by the total weight of the sample (G). (Mean surface area affected = $g_x m_x/G$)

In the above system tubers which are only slightly affected or even with one lesion are classified in class 2 (average 5%), giving an exaggerated rating for the sample. Therefore in recent years class 2 was subdivided (Table 3).

In pot experiments the same method was followed using fewer tubers than in the field experiments.

Statistical treatment has been applied whenever possible and use has been made of both the percentage scabby tubers (unless most of the samples had only scabby tubers) and of the percentage of surface area covered with scab lesions. In both cases for the analysis of variance, the arcsin transformation has been used. In tables means of the transformed values are written as percentages. Yields were treated statistically only when sufficiently accurate data were available.

6.2 Results with PCNB

In 1958, PCNB was applied in April, to a soil on a farm in the Noordoostpolder at Kraggenburg at two rates. One ha was treated with 100 kg powder containing 60% active material and was planted with Sirtema and one ha with 50 kg powder which was planted half with Sirtema and half with Bintje. The powder was mixed with moist sand, added to the potassium fertilizer, scattered over the ploughed land, harrowed into the top soil and planted two weeks later at the end of April. After a month, a marked retardation of Sirtema plants in the area treated with 100 kg was noted; with 50 kg the retardation was slight in Sirtema but more pronounced in Bintje. At harvest in late July samples were taken at eight places in each treatment and compared with samples from adjacent untreated areas. The percentage of scabby tubers and of surface area covered with lesions were assessed on Bintje,

Table 4. Effect of application of PCNB on percentage scabby tubers and percentage of tuber surface with scab of Bintje and Sirtema (Kraggenburg, 1958).

PCNB (kg/ha)	Scabby tubers (%)[1]	Surface with scab (%)
Bintje		
0	97.4	7.1
50	69.7	3.6
Sirtema		
0	64.7	—
50	43.2	—
0	83.4	—
100	51.7	—

1. % means from transformed data.

whereas on Sirtema only the percentage of scabby tubers have been recorded because of the small surface area affected on this resistant variety (Table 4).

Differences in scabbiness were significant in all three cases, but differences in yield were slight and not significant for Sirtema (with 100 kg there was a 2% loss in yield, with 50 kg 3%). No yield figures are given for Bintje because the treated area was planted with larger seed and at a greater planting distance then the adjacent untreated field, but there was evidence that the yield loss was greater than in Sirtema.

In 1959 the experiment was repeated on the same farm but now, in view of the danger of decreased yield, 50 and 33.3 kg/ha (30 and 20 kg active substance) were applied. Scab was assessed on Bintje only. The early development of the Bintje plants was slower than Sirtema where only a slight retardation was noticed in the area treated with 50 kg powder. Figures for yield of both varieties and for scab on Bintje are given in Table 5.

Table 5. Effect of application of PCNB on percentage of Bintje tuber surface with scab and yield of Bintje and Sirtema (Kraggenburg, 1959).

PCNB (kg/ha)	Surface with scab (%)	Yield (% of untreated)	Proportion of seed size tubers (%)
Bintje			
0	21	100	73
33.3	7	95	69
50	7	69	75
Sirtema			
0	—	100	39
33.3	—	81	50
50	—	92	46

Scale 1 was used for scab assessment, and therefore the rating of 7% surface area affected for Bintje was probably between 1 and 2% too high. PCNB controlled scab but decreased yield especially of Bintje. Tubers of Sirtema were generally smaller, and in Bintje fewer.

In 1959 a combined seed-tuber and soil-disinfection experiment was made at West-Brabant, in which seed treatments with organo-mercury compounds, formaldehyde vapour and untreated were combined with soil treatments with 0 or 50 kg PCNB (60%) per ha. The results are given in Table 6.

Although the data could not be treated statistically, because replicate samples had been mixed and subsampled, PCNB was again shown to decrease both scab and tuber yields. In 1960 a similar experiment gave a similar result. PCNB was also found to delay the expression of virus diseases making seed certification difficult.

In 1960 PCNB (60%) was used on seven farms in the province Noord-Holland, mostly at a rate of 50 kg/ha and on varieties Ackersegen, Bintje, Libertas and Meerlander. Mostly a reasonable control of scab was obtained, only on one farm did

Table 6. Percentage scabby tubers and tuber surface with scab of Bintje after tuber and soil disinfection with PCNB (West-Brabant, 1959).

Treatment		Scabby tubers (%)	Surface with scab (%)	Yield (% of untreated)
PCNB (kg/ha)	seed tuber			
0	org.merc.comp.	100	14.1	99
0	form. vapour	100	12.5	98
0	none	100	26.4	100
50	org.merc.comp.	80.6	4.0	93
50	form. vapour	83.8	5.0	98
50	none	71.9	3.6	95

Table 7. Percentage of tuber surface with scab and yield of Libertas after application of formaldehyde (40%) (Groesbeek, 1961).

Formaldehyde (l/ha)	Surface with scab (%)	Yield per plot (kg)	Yield (% of untreated)
0	60.0**	28.3	100
200	31.5[1]	29.3	103.5
400	19.5	29.8	105.3
800	15.0	30.1	106.4

**. The untreated is significantly different (1% level) from the others.
1. The 200-litre treatment is significantly different from the 800-litre (1% level) and from the 400-litre treatment (5% level).

PCNB fail to control a very light attack. Yields from two farms showed that the use of PCNB resulted in nearly 15% yield loss with Ackersegen and nearly 7% with Meerlander. In the same year PCNB was applied to soil at Groesbeek before a ware crop at rates of 25 and 50 kg/ha, but no significant influence either on yield or on scabbiness was noted.

Further experiments between 1961 and 1964 confirmed that PCNB will control scab and Rhizoctonia to some extent, but will delay virus symptoms by 7–10 days and decrease yield. The yield loss depends on the season, the locality, the rate of application of PCNB, the susceptibility of the variety to the chemical and whether soil and organo-mercury seed treatments are combined. The latter is especially important in the lighter sandy loams.

6.3 Results with formaldehyde

On the sandy soils surrounding Groesbeek, although potatoes are grown for ware, crops are often too scabby for human consumption and can only be sold as fodder. PCNB cannot be advised partly because of the danger of off-flavour and partly for economic reasons (PCNB is rather expensive). Therefore in 1960 we compared the application of 100 and 200 l formaldehyde per ha with PCNB with no significant effect, so in 1961 the rates were increased to 200, 400 and 800 l/ha (the last quantity being at the margin of being economically justified). Formaldehyde was applied by watering a solution of the 40% commercial product (rates are given in litres of the commercial product) over the top soil immediately before planting with the variety Libertas. Results are given in Table 7.

There were no significant yield differences but plant growth was stimulated by formaldehyde. In the same year formaldehyde was used at 500 l/ha on a sandy loam in Friesland without affecting scab, yield was increased 2.5%, but again not significantly.

In 1962 four experiments were made at Groesbeek at rates of 250, 500 and 750 l/ha and with the variety Libertas. The results are given in Table 8.

A combined analysis has been done on the yield data of the first three experiments but not of the scab data. No significant differences were found.

Formaldehyde at 800 l/ha in Friesland and Groningen in 1962 gave non-significant increase in yield but a slight reduction in scab on Bintje.

6.4 Results with streptomycin

Streptomycin inhibited growth of *S. scabies* in vitro and therefore in single pot trials in 1960 it was either applied to soil at a rate of 125 mg per plant or sprayed on foliage at a rate of 50 mg per plant on three occasions or at 25 mg per plant on five occasions. Foliar application appeared promising and so more elaborate pot experiments were carried out in the glasshouse at IPO. Bintje plants were sprayed five times at weekly intervals with varying quantities of streptomycin during the

Table 8. Percentage of tuber surface with scab and yield of Libertas after application of formaldehyde in four experiments (Groesbeek, 1962).

Formaldehyde (l/ha)	Field experiment No.			
	1310	1342	1343	1344
Percentage of tuber surface with scab				
A 0	12.0	13.0	7.8	8.1
B 250	14.8	6.7	2.8	3.8
C 500	8.7	7.6	3.9	4.5
D 750	8.4	5.5	3.7	4.2
Residual variance	15.61	2.49	3.52	6.49
Significant differences	none	A>B,C,D**	A>B,C,D*	none
Yield (kg per plot)				
A 0	37.3	31.9	28.0	34.4
B 250	41.9	36.6	27.0	34.2
C 500	40.3	36.6	27.0	34.2
D 750	49.7	36.7	30.2	34.0
Residual variance	0.75	0.33	0.58	1.98
Significant differences	none	A<B,C,D**	none	none

**. A is significantly different (1% level) from the others.
* . A is significantly different (5% level) from the others.

time of tuber development. Most results were negative. In field experiments in Friesland and Noord-Holland streptomycin sprayed during tuberisation failed to control scab on Bintje.

Research carried out at the laboratory of the 'Koninklijke Nederlandsche Gist- en Spiritusfabriek' at Delft showed, that streptomycin sprayed on leaves was transported through the plant to the stolons and young tubers, but remained restricted to the vascular ring in the young tubers and could not be detected outside this ring.

6.5 Results with other chemicals

Orthophenylphenol at a rate of 75 and 150 l/ha, zineb and ferbam at 20 and 40 kg/ha were tried but no scab control was obtained. Harmsen (Internal Rep. Dutch Potato Scab Committee) showed that *S. scabies* is inhibited in vitro by manganese. Some inhibition was shown when 0.05 mg/ml manganese sulphate was added to a nutrient agar, it was very obvious at 0.8 mg, and at 1.6 mg no growth occurred. Sensitivety to MnO was less, requiring 1.6 and 2.0 mg/ml to produce noticeable inhibition.

A survey carried out by the extension service of Noord-Groningen indicated that scab incidence was negatively correlated with the concentration of reduceable manganese in soil.

From 1965 to 1968 the Institute for Soil Fertility helped in analysing the manganese content of both soil and crop samples from a number of field and pot experiments, conducted on behalf of the Dutch Potato Scab Committee. In these trials manganese was given at varying rates and in different forms. Eighty to 400 kg/ha manganese sulphate or equivalent amounts of manganese oxide applied before planting or 12 kg/ha of manganese sulphate sprayed one, two or three times during growth, had no significant effect on scab in field experiments carried out by the extension service in Noord-Groningen. Pot and small plot experiments at the Institute for Soil Fertility with rates to 500 kg/ha gave no scab control. Soil and crop analyses from these experiments and from experiments with irrigation, crop rotation and liming, failed to demonstrate a correlation between manganese and the occurrence of scab. In view of these negative results, research on manganese was stopped.

6.6 Conclusions

None of the chemicals, except for PCNB, were sufficiently active to control scab when applied at economic dosages. The failure of streptomycin was not because of the occurrence of streptomycin-resistant scab strains as found by Weber & Menzies (1962), but the result of the inability of streptomycin to reach the skin of young tubers. Although systemic fungicides could be applied at a time when the tubers are susceptible the results with streptomycin are not encouraging.

The role of manganese in the scab problem appeared to be very complex. Although application of manganese to the soil resulted in higher manganese levels in the tuber skin, no consistent correlation was found between manganese content of the skin and sabbiness (Internal Rep. Institute for Soil Fertility). Other factors, for example pH, Ca-content and organic matter appeared to influence the results with manganese. However, the value of manganese in scab control is rather doubtful.

Use of formaldehyde nearly always increased yield but scab control, especially on clay soils, has not been promising. The cost of an application is uneconomical (750 l is about Dfl 500 per ha).

PCNB generally controlled scab but decreased yield on average by 6–7% in seed crops (calculated from a large number of experiments in the Netherlands). This figure can vary considerably from year to year, from place to place and from variety to variety, and may even amount to a 30% reduction (Bintje, Kraggenburg, 1959).

Yield reduction by PCNB is most obvious in seed crops. When the crop is grown and harvested as ware (Groesbeek, 1960) the effect is lost because the longer growing period enables the potato plant to overcome the slowed early growth. Menzies (1957a) also found with 50 lbs/acre some delay in emergence, but no effect on yield when the crop was harvested after haulm senescence.

When judging the value of a fungicide the degree of disease control and the effect on yield are important, but subsidiary effects may also play an important

role. With PCNB these subsidiary effects include on the credit side control of *Rhizoctonia solani* (van Emden et al., 1966) and of silver scurf (Mooi, 1968) but on the debit side, PCNB slows the expression of virus symptoms by 7–10 days which then delays field inspection for seed certification, and can give an off-flavour in tubers for eating. Many crops are sold partly for seed where flavour is of no consequence, but the larger tubers are mostly sold for ware and the off-flavour becomes important. PCNB applied at 50 kg/ha (60%) nearly always resulted in off-flavour, but at rates lower than this occasionally.

Despite these disadvantages PCNB is becoming more widely used in seed potato growing. It should be used with caution and farmers wishing to use the chemical for the first time should apply it on strips of land using increasing dosages so that the best rate can be calculated. The danger of off-flavour renders this chemical unfit for use on a ware crop in the Netherlands.

7 Antagonism and control

Sanford (1926) found that bacteria could sometimes inhibit the growth of *S. scabies* in nutrient media without increasing the acidity of the substrate. Also the effect of green manure in controlling scab could not always be attributed to acidity, but could have been caused by the multiplication of antagonistic organisms. Sanford concluded: 'It is quite possible that the same degrees of compatibility between organisms and the same toxicity demonstrated on artificial media may also occur naturally in the soil. This is a problem of the biological balance in the soil and therefore may be of particular importance in determining the pathogenicity of *A. scabies*.'

Dippenaar (1933) attributed the decrease in scab incidence in moist soils to bacteria which predominate over the fungal and actinomycete flora in such soils. Wieringa & Wiebols (1936) isolated a 'phage' able to lyse *S. scabies* and some other actonomycetes. Daines (1937) found *S. scabies* susceptible to the antibiotic activity of *Trichoderma*. Orellana (1947) mentioned a number of actinomycetes and bacteria, which inhibited growth of the scab organism and Menzies (1957b and 1959) describes a 'scab suppressing factor' of microbial origin.

These publications all indicate the interrelationship of *S. scabies* and other members of the microflora and point to the possibility of control of scab by antagonists. We have found repeatedly large differences in the distribution of scab between fields or parts of one field, which could not be explained by differences in chemical or physical characteristics of the soils. When different fields show the effect it may be explained by different crop rotations, but not when parts of the same field show a variable scab distribution. We have studied the microflora of a few such fields to find antagonistic organisms, to isolate and to culture them. Such isolates have been used in pot and field experiments in an attempt to control scab.

Antagonism may also be involved when green or organic manures are incorporated into soil or when certain crop rotations are followed. Stewart (1897) found green rye gave good control but Millard & Taylor (1927) showed that control by green manure only occurred when non-pathogenic actinomycetes were also present. In the Netherlands, Huisman (1933) and Meijers (1935) also claimed control and the latter found that rapeseed and especially soya bean meal gave promising results, but the costs were too high for practical application. Soya beans as green manure have also been used (Weinhold et al., 1964; Weinhold & Bowman, 1965), and *Bacillus subtilis* was considered the main antagonist; it showed even more antibiotic activity when grown on soya bean than on barley extract.

So we investigated the influence of some crop rotations and green manure crops on scab incidence. When antagonists were used in field experiments, a green manure crop was incorporated into soil with them.

7.1 Materials and methods

Antagonism Many actinomycetes, obtained from soil dilution plates were tested against each other for antagonism using the cross-streak method of Patrick (1954), but because of bacterial contamination the potato dextrose agar was replaced by chitin agar.

Later, antagonists were obtained more simply using plates from the soil dilution series (on which the actinomycetes and bacteria had been counted, see Section 8.2.1) by spraying them with a suspension of a pathogenic isolate. The plates were then incubated for 3–4 days at 28° C and clear zones around colonies indicated antibiotic activity, the degree of which could be estimated from the diameter of the zone. Actinomycete colonies with strong activity were then isolated (Fig. 17).

Another way of obtaining antagonists was to take 75 to 100 colonies at random from the dilution plates and to transfer and culture them in small Petri dishes. When colonies had developed agar discs were transferred to large Petri dishes (about ten per dish) containing potato dextrose agar which had been seeded with a spore suspension of a pathogenic scab isolate. After 3–4 days incubation at 28° C the diameter of the inhibition zones (if present) could be measured and those cultures showing most activity were noted, and the corresponding isolate in the small

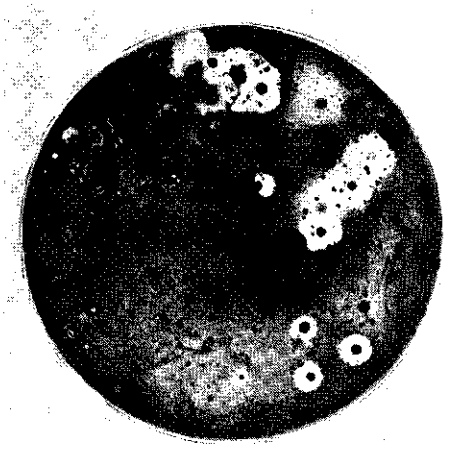

Fig. 17. Inhibition zones around some of the colonies on a dilution plate sprayed with *S. scabies* spores after incubation.

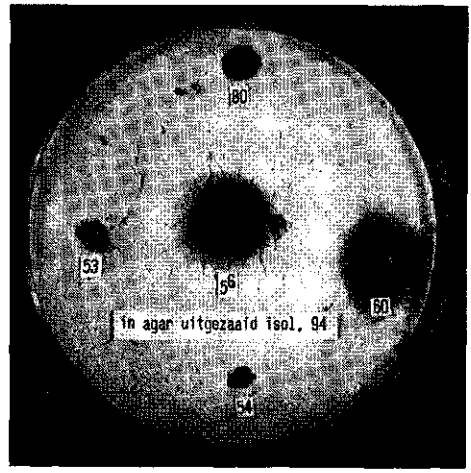

Fig. 18. Three antagonistic actinomycetes (isolate 5G showing the most inhibition) and two actinomycetes showing no antagonism. Plate seeded with the normal scab isolate S 94.

Petri dish was saved for further use (Fig. 18).

Antagonists for pot experiments were cultured in Petri dishes with Perlite as for the pathogenicity test (Section 2.1). When large quantities of inoculum were needed for field experiments the multiplication was done by the 'Koninklijke Nederlandsche Gist- en Spiritusfabriek'. A minimum of 0.5 l/10 m² of a concentrated mycelial suspension was, after dilution with water, sprinkled over the green manure crop immediately before incorporating this into the top soil.

Crop rotation Two long term experiments with three triannual rotations were compared. The layout was such that each phase of the rotation occurred each year in duplicate. Potato plots were sampled by harvesting eight or ten groups of plants with six adjacent plants in a group. Scab has been expressed as an average of these eight or ten observations, and the figures for both duplicates are given because replicate plots could be far apart.

7.2 Results with antagonists

In 1960 an isolate 5G with specific and strong activity against *S. scabies* was obtained from soil. When mixed in equal quantities with a pathogenic scab isolate in sterilized soil the scabbiness of the tubers grown was much less when compared with tubers from sterilized soil with *S. scabies* only (Fig. 19).

In 1961 a preliminary field experiment on a sandy soil at Groesbeek was made with this antagonist. On duplicate plots of 16 m², 40 kg of mowed ryegrass sprinkled with 2 or 4 l of a concentrated mycelial suspension of isolate 5G, was incorporated into the soil before planting with the variety Libertas. The results are given in Table 9.

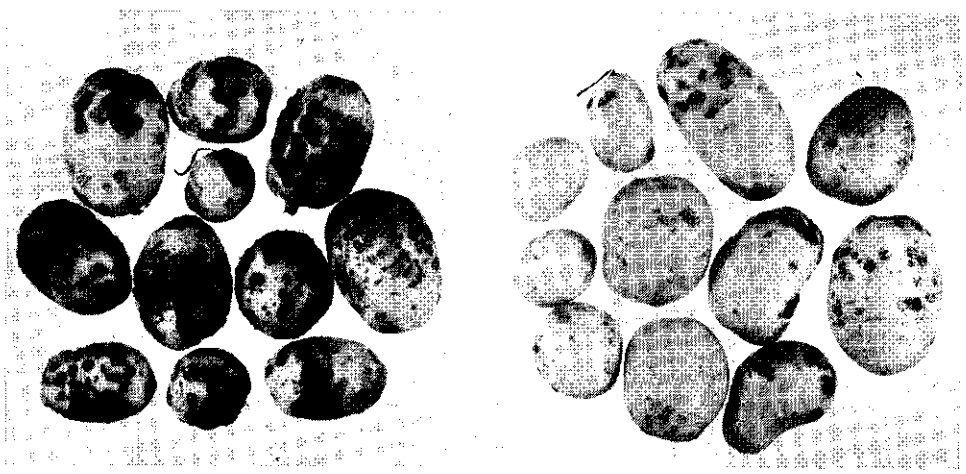

Fig. 19. Bintje tubers grown in a sterile soil with *S. scabies* only (right) and with *S. scabies* plus an antagonist (left).

Table 9. Percentage of tuber surface with scab and yield of Libertas after the addition of grass inoculated with antagonist 5G.

Treatment	Surface with scab (%)	Yield of 24 plants (kg)
none	49.4	30.2
grass	36.1	32.5
grass + 2 l 5G	44.4	27.9
grass + 4 l 5G	38.0	29.6

The differences are small and not significant. An experiment at Den Andel on a sandy loam with green rye as substrate was planted with Bintje. The percentage of surface area covered with scab for the treatments as in Table 9 were respectively 22.8, 20,2, 19.9 and 19.1. Here also the differences were small and not significant.

In the new polder Oostelijk Flevoland, part of a field experiment on the spread of the scab organism and *Rhizoctonia solani* in virgin soil, was used for a study of antagonists. The substrate was green winter wheat and the rhizomes of reed (the pioneer crop in new polders). The antagonists used were 5G and isolates 'Aroes' and 'Sibil' obtained from the laboratory of the 'Koninklijke Nederlandsche Gist- en Spiritusfabriek' at Delft. There were two blocks of four plots 10 rows by 4 m, two plots in each block were untreated, two plots in one block received 5G and two plots in the other either 'Aroes' or 'Sibil'. Table 10 gives the average results of five samples.

Treatments were ineffective and in one plot treated with 5G, much scab was recorded, mainly of the russet type. The following year when the same plots were planted with potatoes russet scab was even more serious on the 5G plots than before, whereas the main part of the field showed only slight normal scab.

In 1962, 5G and three isolates from the laboratory at Delft were used at IPO. Winterrye preceding the potato crop was used as green manure and substrate for the antagonists. Plots were treated, either with each of the antagonists (400 ml per plot of 30 plants), or with all four together (100 ml per antagonist) and planted with Bintje. At harvest no scab free tubers were found. The results are given in Table 11.

Differences were not significant as variation between the five replicates was considerable, probably because of uneven moisture in the sandy soil. The drier areas were low in yield and high in scab.

The results from experiments with green manures inoculated with antagonists were always disappointing and the treatment uneconomic.

Native antagonism was found to play a role in a field in which scab increased from one end to the other. In 1964 tuber and soil samples were taken at the same time from each of five plots arranged along the disease gradient. Eighty actinomycetes were isolated from each at random and tested for antagonism against a super-

ficial and a russet scab isolate (which were predominant in this field). The number of antagonists among the total number of actinomycetes tested and the total area of all the inhibition zones are given in Table 12.

Table 10. Percentage scabby tubers and percentage tuber surface with scab of Bintje after addition of wheat, reed rhizomes and antagonists in young polder soil.

Treatment	Scabby tubers (%)	Surface with scab (%)
Reed	89.6	2.4
Reed	86.9	1.8
Reed + wheat + 5G	80.7	1.7
Reed + wheat + 5G	97.3	7.6
Reed	74.7	1.3
Reed	76.7	1.4
Reed + wheat + Aroes	84.6	1.3
Reed + wheat + Sibil	83.7	1.8

Table 11. Percentage of tuber surface with scab and yield of Bintje after addition of rye and antagonists (Wageningen).

Treatment	Surface with scab (%)	Yield of 18 plants (kg)
Rye	19.1	12.8
Rye + 5G	15.8	12.2
Rye + Epinal 159	13.5	11.7
Rye + Metz 347	29.8	11.9
Rye + Quinhon Pt 21	21.3	12.0
Rye + antagonists	18.3	13.1

Table 12. Scab on tubers and antagonism against local strains of *S. scabies* in a commercial field with a pronounced disease gradient.

	Plot No					
	1	2	3	4	5	6
Scab (% cover)	0.4	7.0	14.4	22.2	27.8	44.9
Superficial scab antagonists	27	19	21	21	20	16
Total inhibition (cm^2)	22.63	1.59	1.90	1.86	1.70	4.96
Mean inhibition/antagonist	0.84	0.08	0.09	0.09	0.08	0.28
Russet scab antagonists	22	19	31	29	16	27
Total inhibition (cm^2)	16.06	4.21	4.56	6.43	2.12	10.10
Mean inhibition/antagonist	0.73	0.22	0.15	0.22	0.13	0.37

Table 13. Percentage of Bintje tuber surface with scab on plots with a pronounced disease gradient to which local antagonists were added.

Plot	Tuber size (mm)	Surface with scab (%)	
		untreated	treated
1	28–35	2.6	2.4
3	28–35	5.4	5.3
5	28–35	16.8	14.9
1	35–45	3.3	2.9
3	35–45	6.2	6.3
5	35–45	16.1	14.5

Tubers from Plot 1 had negligible scab, and many antagonists isolated from soil showed a strong inhibitory effect on the two scab strains. Samples from the other plots lacked such correlation.

A number of the strongest antagonists were cultured and used in 1965 to inoculate half of Plots 1, 3 and 5 (Table 12), which again were planted with potatoes. At harvest scab was assessed on tubers 28–35 mm and 35–45 mm diameter (see Table 13).

Scab increased from Plots 1 to 5 but the influence of local antagonists was negligible. Scab figures for both tuber sizes were the same. Soil samples were again taken from the untreated parts of the different plots and about 120 actinomycetes were isolated. Their antagonistic ability was measured against a russet scab isolate and although no significant difference was shown in the number of antagonists, the degree of inhibition differed greatly between the different plots. An inhibiton zone $>$ 4 mm was shown by 13 isolates from Plot 1, 3 isolates from Plot 3 and 2 isolates from Plot 5.

In 1966 the test varieties Bintje (susceptible for all three scab types) and Eigenheimer (susceptible for normal and superficial scab) were planted on the different plots to see which scab type was most prominent. On Plots 1, 3 and 5, russet scab covered respectively 7.4, 27.9 and 29.4% of the surface of Bintje tubers and superficial scab 1.7, 2.4 and 0.8%; whereas on Eigenheimer superficial scab affected respectively 2.4, 5.9 and 2.0%. The russet scab organism was therefore dominant in this soil.

In 1967 no correlation could be found between the antagonism of actinomycetes and the occurrence of scab on fields which differed in scabbiness.

7.3 Results of crop rotation experiments

From 1963 to 1969 the incidence of scab was studied at two sites after three different crop rotations, namely:

Table 14. Percentage of Bintje tuber surface with scab after three different crops in two experiments located in Tzummarum and Eenrum.

	Preceding crop	Surface with scab (%)			
		Tzummarum		Eenrum	
		plot 1	plot 2	plot 1	plot 2
1963	Before the experiment	9.8	11.9	2.7	2.3
1964	ley	29.4	20.4	7.0	9.0
	cereals	30.5	23.0	12.0	8.8
	sugar beet	33.9	17.5	7.1	9.6
1965	ley	4.7	5.8	0.3	0.5
	cereals	9.9	6.5	0.6	0.8
	sugar beet	5.1	3.4	1.3	0.7
1966	ley	14.5	16.3	2.3	1.7
	cereals	18.3	21.0	3.0	2.4
	sugar beet	14.0	24.5	2.1	2.0
1967	ley	49.8	39.3	4.6	4.9
	cereals	46.9	41.0	4.3	6.4
	sugar beet	47.9	34.1	4.2	7.5
1968	ley	19.7	15.2	9.6	10.0
	cereals	25.9	18.2	11.0	8.2
	sugar beet	16.2	14.5	4.7	7.1
1969	ley	25.4	24.5	7.8	8.4
	cereals	27.6	29.0	10.7	8.1
	sugar beet	29.6	32.0	11.6	8.2

1. cereals (wheat or barley), ley, potatoes
2. cereals, cereals, potatoes
3. cereals, sugar beet and potatoes.

A ley was expected to increase superficial scab ('greideschurft') and frequent cereals the amount of scab, through the drying of soil in the ridges by the stubble, whereas sugar beet was expected to decrease scab. The results are summarized in Table 14.

Differences were small and inconsistent, but a correlation was found between the occurrence of scab and the amount of rainfall during tuber formation.

When the same crop rotation was repeated there appeared to be no effect on scab. At Tzummarum scab incidence was already high before the experiment began and remained so, but at Eenrum it was low because potatoes were rarely grown and here the increased frequency of potatoes caused an increase in incidence of the disease.

At IPO the influence of green manure crops on scab has been investigated with lupin, Phaseolus beans and soya beans. In the first year soya beans did not grow

Table 15. Percentage of Bintje tuber surface with scab when different green manure crops were added to a sandy soil (Wageningen).

Order of crops			Surface with scab (%)	
1963	1964	1965	1964	1965
lupin	potato	potato	60.9	50.4
lupin	soya bean	potato		44.2
French bean	potato	potato	60.0	49.2
French bean	soya bean	potato		39.2
soya bean	potato	potato	58.0	38.9
soya bean	soya bean	potato		29.7

well so in the second year half the plots were planted with potatoes and the other half with soya beans; both halves were planted with potatoes in the third year. Scab was assessed after the second and third year (see Table 15).

Soya bean in 1963 had no effect on the incidence of scab in 1964, although soya beans in 1964 appeared to decrease scab in 1965. However, it is difficult to prove whether this was an effect of soya bean or of different numbers of potato crops. Thus the beneficial effect of soya beans claimed by Rouatt & Atkinson (1950) could not be confirmed.

7.4 Conclusions

Most organisms antagonistic to *S. scabies* were found among other actinomycetes, viz. between 20 and 50% of all actinomycetes isolated, but only the strongest inhibitors are likely to influence the disease. Such organisms could be found most frequently in soils where scab incidence was low. In experiments with artificially infested sterile soil these isolates checked scab, but in naturally infested soil the results have been disappointing even when an organic substrate was provided. However, even if good control had been achieved the method would be impractical because of the labour costs involved.

Application of green manure alone has had little, or at best a variable effect, probably because the factors involved are not clearly understood. Early workers attributed control to changes in the microflora. However, changes in the moisture status of soils with added green manures may prevent or promote scab, or the increased nitrogen may delay tuberisation (Lapwood & Dyson, 1966) so that the susceptible period for the infection of young tubers may be shifted to different weather conditions either favourable or unfavourable.

The crop rotation experiments showed that the influence of the preceding crop in the rotation on scab incidence is small and is completely overshadowed by the influence of the weather, for example in 1965, a wet year, the average scab for all rotations was low and in 1967, a dry season, the average was high.

8 Overhead irrigation

8.1 Control by overhead irrigation

Dutch seed potato growers wanted scab control urgently because of new and exacting requirements of the export trade and this led us to investigate the possibility of scab control by means of overhead irrigation. The practicability and the economy of overhead irrigation had been studied on many crops by Baars (1962 and 1964), Eldik (1961) and Geneijgen (1962 and 1965). We wanted to know when to start irrigation and for how long, and the minimum number of irrigation required, the amount of water per irrigation and the effect of the quality of water applied (high or low in chlorine).

Most of the irrigation experiments were carried out under field conditions, without covering of the crop against natural rainfall and this has meant in certain years the irrigation regimes could not be carried out completely. However, it was thought better to use this method as these were the conditions under which a farmer would have to plan his irrigations.

8.1.1 Materials and methods

In the field experiments normal irrigation equipment or mobile units specially designed and provided by the Research and Advisory Institute for Field Crop and Grassland Husbandry (PAW) was used (Fig. 20). When using normal equipment unirrigated plots were either covered with polyethylene hoods, 2 × 2.5 m, protecting three rows during irrigation or by blocking off the appropriate number of sprinkler nozzles.

The PAW-irrigation apparatus consisted of a mobile structure, 3.5 × 3.5 m, in which one nozzle centrally placed gave a very uniform distribution of the irrigation water. Side curtains prevented the wind from interfering with water distribution and also caught the excess water which was directed into gutters draining off some distance from the experiment. The quantity of water applied was measured and by arranging the experimental plots in long rows many plots could be watered to the same extent with a few such mobile units, within a reasonable time.

The first irrigation was always applied to bring the upper 10–15 cm of the soil in the ridges to full moisture holding (field) capacity, subsequent irrigations then made up the loss of moisture by evaporation.

Scab assessments were done on tuber samples as before (Section 6.1). When a

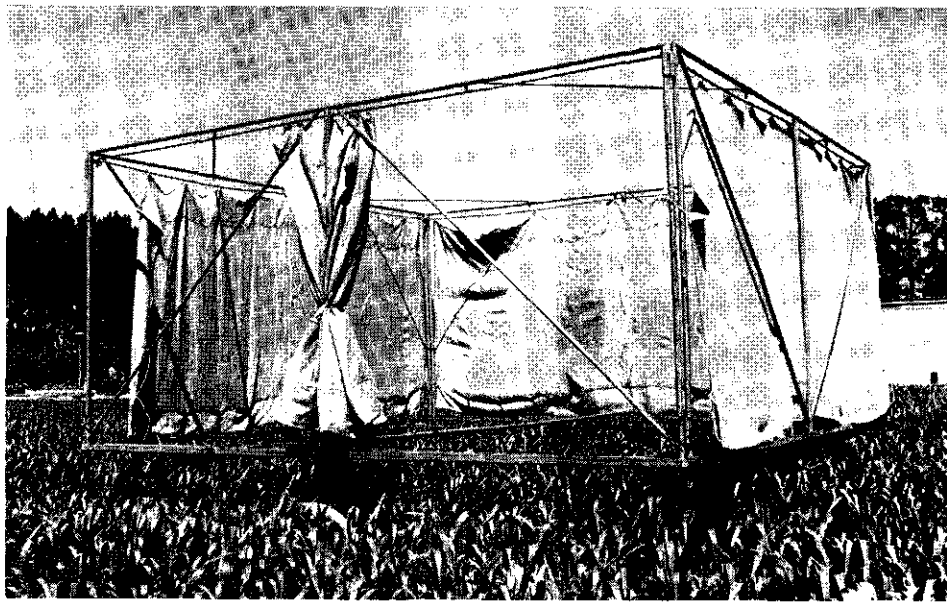

Fig. 20. Mobile irrigation unit of the PAW as used in most of the irrigation experiments.

hood was used a tuber sample from six plants from the middle row of the three under cover, was compared with four samples taken from rows just outside the covered area. Samples from unirrigated areas where the nozzles of sprinklers had been blocked were taken at regular intervals along or perpendicular to the irrigation pipes.

To determine the 'beginning of tuberisation' in order to time the start of irrigation, plants were at first dug at random. However, it was soon obvious that this was unsuitable because of large individual differences between plants, for example, in Bintje on the same date and in the same field some plants had nearly 40 tubers and others none at all. Since 1965 the following procedure has been adopted.

Depending on the area planted and the uniformity of the crop several groups of five plants are lifted at 3–4 days intervals until at least two of the five plants have at least two stolons with tubers (a tuber is defined as a swelling at the end of a stolon, which is at least twice the diameter of the stolon).

Yield data from experiments on farmers fields were less accurate than when the mobile irrigation equipment was used because the seed was handplanted and handlifted so that accurate yield assessments could be made.

8.1.2 Results

Most of the preliminary experiments were done using normal irrigation and polyethylene hoods and although they demonstrated the benefits of irrigation, there were disadvantages both from the irregular distribution of water and from the small

Table 16. Percentage scabby tubers and percentage of tuber surface with scab in field experiments with irrigation.

			Scabby tubers (%)		Surface with scab (%)	
			unirrigated	irrigated	unirrigated	irrigated
Ens[1]	1963	Sirtema	54	40**	—	—
Oudkarspel	1963	Eersteling	68	28**	—	—
Stiens	1964	Bintje	100	76**	5.0	1.0**
Stiens	1964	Sirtema	87	50**	2.4	0.3**
PAW 1057	1964	Bintje	99	74**	5.7	1.7**
Ens[2]	1964	Sirtema	81	66	8.6	2.5
Oudkarspel	1964	Eersteling	70	19**	—	—
Stiens	1965	Bintje	100	80**	3.7	1.2**
PAW 1057	1965	Bintje	49	36	0.9	0.4
Oudkarspel	1965	Eersteling	74	31**	—	—
Stiens	1966	Bintje	100	70**	24.1	3.2**
Hornhuizen	1966	Bintje	92	59**	4.2	1.1**
PAW 1057	1966	Bintje	—	—	15.5	8.4**
Stiens	1967	Bintje	100	46**	18.7	0.5**
Hornhuizen	1967	Bintje	100	27**	41.1	0.2**
PAW 1057	1967	Patrones	54	2**	0.7	0.02**
Stiens	1968	Bintje	93	69**	2.5	1.0**
Hornhuizen	1968	Bintje	100	45**	24.1	0.6**
PAW 1629	1968	Bintje	61	38	2.4	1.1

**: Irrigated is significantly different (1% level) from unirrigated.
1. Unirrigated controls by hoods.
2. Unirrigated controls by blocked nozzles.

areas that could be covered. Also the drainage of water from the hoods during irrigation must have affected part of the covered area so that only a few plants from the middle row could be used for comparisons.

Later experiments were made usually by mobile units and occasionally by the blocked nozzle sprinklers in stationary pipes. Selected results of experiments between 1963 to 1968 are summarized in Table 16 to demonstrate the degree of scab control by overhead irrigation.

When results are expressed as the percentage scabby tubers, scab incidence is overestimated because tubers with only one small scab spot (tubers with 0–1% of the surface covered with scab) are included. Irrigated plots have a higher proportion of these very lightly infested tubers than dry ones, for example, at Hornhuizen in 1967, 27% scabby tubers were recorded on irrigated plots, but all these tubers were within the stringent export grading limits for seed, whereas in unirrigated plots 94% tubers were unfit for export. At Stiens in 1967 only 0.3% of irrigated but 68% of unirrigated tubers were unfit for export.

The experiment at Ens in 1965 failed because of excess rainfall at the start of

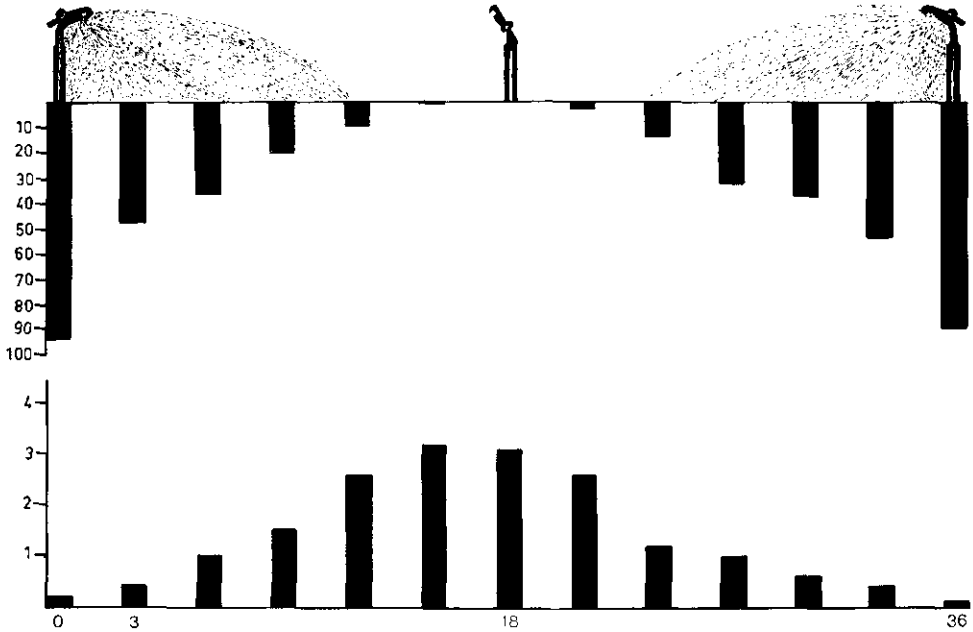

Fig. 21. Correlation between the quantity of irrigation water and scab incidence on Sirtema tubers at Ens 1966. At the top, each column represents the total amount of water (mm) during six irrigation occasions which fell between two open and one closed sprinkler nozzles placed 18 m apart. At the bottom each column represents the average percentage surface area of tubers scabbed, when harvested from the different positions between the nozzles (all figures means of five replicates).

tuber formation (from 25 May till 11 July, 212 mm rain fell). Overhead irrigation was given only twice (3 and 4.5 mm), without any noticeable effect on scab. The percentage scabby tubers averaged 10% and the surface area covered less than 0.2%, exceptionally low for this particular field. Results for 1966, a typical experiment, are shown graphically, each figure is a means of five replicates (Fig. 21).

In this experiment an average of 56.2 mm of water was applied during six irrigations between 18 May and 11 June, and the results (Fig. 21) show that the quantity of water is negatively correlated with the percentage of surface area of tubers covered with scab. The distribution of water was not ideal and too much fell close to the sprinklers. This could cause a decrease in yield through losses of mineral nutrients by drainage. It is therefore essential to ensure that sprinklers are adjusted correctly before use.

The critical period Estimates of the period tubers are susceptible to scab have ranged from ten days to four weeks after they start to form, and therefore the period of high soil moisture necessary to prevent scab infection, can be relatively short. This period during which irrigation will be effective against scab (the critical period) has been assumed to end about four weeks after the start of tuberisation.

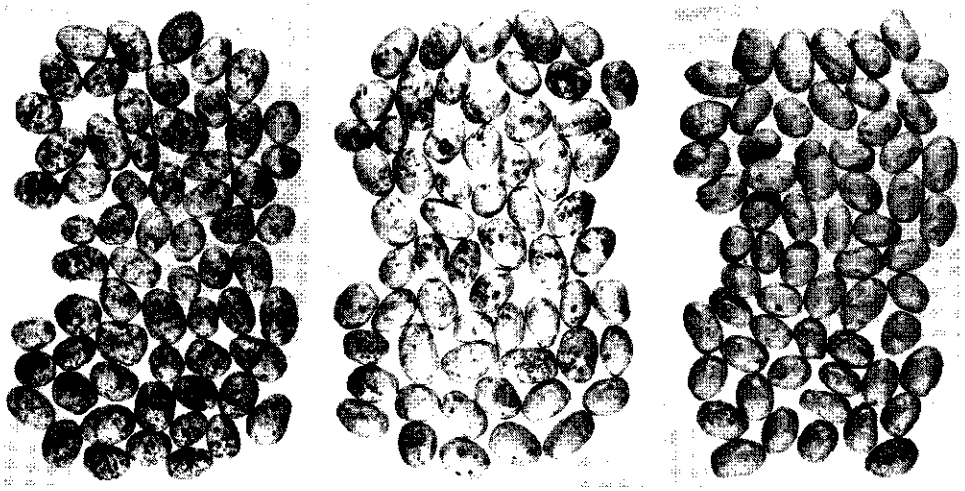

Fig. 22. The incidence of scab on tubers from the experiment at Hornhuizen 1967: unirrigated control (left), irrigation started three weeks after tuberisation (some scab control) (middle) and irrigation from the beginning of tuberisation (a scab-free crop) (right).

To determine the susceptible period accurately the start of tuberisation must be known, but few authors have attempted to define this. The early experiments also showed the importance of knowing when tubers began to form and in 1965 we put forward the definition mentioned in Section 8.1.1. On this basis the dates recorded in experiments before 1965 may differ from the dates based on my definition by a few days.

To test which irrigation was most effective in controlling scab, the data from the various experiments have been collected together in Table 17, and the days before (—) or after (+) the beginning of tuberisation, the total amount of water (mm), the number of irrigations and scab incidence are correlated.

The results show that irrigation before the beginning of tuberisation has no advantage in scab control and in fact tends to decrease yield, and the later irrigation starts, the less effective is the disease control.

At Hornhuizen in 1966 a first irrigation delayed eight days after the beginning of tuberisation was already too late to prevent some scab, but in 1967 a 14 day delay had little more scab than treatments irrigated two weeks earlier. However, a delay of 21 days resulted in a marked increase in disease, although there was still less scab than in unirrigated plots (Fig. 22).

From the results it is obvious that the critical period – that period when irrigation is effective – varies from year to year, because rainfall will affect the period when irrigation is required. The main aim is to ensure that soils do not dry sufficiently to allow scab infection during the four weeks after tuber initiation. Irrigation later than four weeks could increase yields, but generally had little effect on scab incidence.

Table 17. Relation between the period in which the irrigation was given, percentage scabby tubers and percentage of tuber surface with scab.

		Irrigation period[1]		Amount	Number of irrigations	Scabby tubers (%)	Surface with scab (%)
		start	end				
Stiens	1965	— 7	+ 28	60	3	88	1.8
		0	+ 28	60	3	80	1.2
		+ 5	+ 28	60	3	90	1.6
Control						100	3.7
Stiens	1966	— 14	+ 7	80	4	70	3.2
		— 6	+ 14	73	4	69	4.4
		0	+ 14	65	3	70	4.1
		+ 7	+ 14	52.5	2	68	5.0
Control						100	24.1
Hornhuizen	1966	— 18	+ 38	95	8	71	1.4
		— 6	+ 39	62.5	4	65	1.6
		+ 2	+ 39	75	4	59	1.1
		+ 8	+ 39	42	2	75	2.4
Control						92	4.2
Stiens	1967	— 4	+ 32	90	5	46	0.5
		0	+ 32	82	4	43	0.6
		+ 7	+ 32	80	3	57	1.0
		+ 7	+ 32	65	3	53	1.0
Control						100	18.7
Hornhuizen	1967	0	+ 24	110	7	27	0.2
		+ 7	+ 24	85	5	34	0.5
		+ 14	+ 24	80	4	58	0.8
		+ 21	+ 24	40	2	97	7.1
Control						100	41.1
PAW 1057	1967	0	+ 42	95	6	9	0.08
		+ 8	+ 42	90	5	2	0.02
		+ 14	+ 42	80	4	11	0.07
		+ 21	+ 42	75	4	23	0.22
		+ 28	+ 42	70	3	31	0.35
Control						54	0.69
Stiens	1968	+ 19		10	1	74	1.0
		+ 19	+ 28	24	2	69	1.0
		+ 22		8	1	93	2.2
		+ 25		11	1	89	1.9
		+ 32		20	1	86	1.8
		+ 33	+ 40	24	2	89	1.9
Control						93	2.5
Hornhuizen	1968	+ 7		20	1	55	1.0
		+ 7	+ 14	40	2	50	0.8
		+ 14		20	1	98	14.6
Control						100	24.1

1. — and + refer to the number of days before or after the beginning of tuberisation, 0 means that the irrigation started on the day tuberisation started.

Table 18. Influence of small and large amounts of irrigation water given per irrigation occasion on percentage scabby tubers and percentage of tuber surface with scab.

		Irrigation occasion[1]				Water per irrigation (mm)	Total water (mm)	Scabby tubers (%)	Surface with scab (%)
Stiens	1964	0	+ 7	+21	+42	4 × 20	80	76	1.0
		0		+21		2 × 40	80	91	2.2
PAW 1057	1964	0	+ 7	+14	+35	10 + 3 × 15	55	74	1.7
		0		+14		10 + 30	40	79	2.0
PAW 1058	1964	0	+ 7	+14	+35	10 + 3 × 15	55	70	1.6
		0		+14		10 + 30	40	89	2.9
Stiens	1965	0	+19	+28		3 × 20	60	80	1.2
		0		+28		2 × 40	80	99	3.0
		+5	+19	+28		3 × 20	60	90	1.6
		+5		+28		2 × 40	80	99	2.7

1. Days from the beginning of tuber formation.

Amount of water per irrigation For practical reasons it would be easier to irrigate a few times with large quantities of water than to apply smaller amounts more often. Irrigation pipes have to be moved several times during one irrigation, which requires much labour that is not always available when needed (unless stationary equipment is installed). Therefore in some experiments single and double quantities water were applied to see if the number of irrigation occasions could be decreased, and the results are given in Table 18.

The results show that fewer irrigations with more water significantly give less effective control, one disadvantage of much water was that most sandy loam soils could not absorb the water which ran off, resulting in a hard surface crust which, combined with leaching of nutrients, adversely affected yield.

From 1964 to 1966 in the Noordoostpolder experiments were carried out with one irrigation at the beginning of tuberisation in which an excess of water (more than necessary to bring the top soil to field capacity) was applied (experiments PAW 1059). As a soil crust was expected to form on the light sandy loam an extra treatment was included, where the soil crust was broken up after irrigation. Loss of nutrients by leaching was compensated in other treatments by extra fertilizer (20 kg N and 30 kg K_2O per ha). In 1964, 60 mm water was applied, in 1965, when the soil was very wet by natural rainfall, 15 mm and in 1966, 30 mm, and in all irrigation treatments scab was decreased about half that on untreated (based on surface areas scabbed). In the first two years, yield was decreased by the early irrigation, in 1965 by 13%. Hoeing the soil after irrigation in 1965 overcame this effect, but in the other years it did not, probably because of damage to potato roots. The extra fertilizer always increased yield compared with the control.

Table 19. Influence of irrigation on yield (as % yield of the untreated plots).

			First irrigation[1]					
			—2	—1	0	+1	+2	+3
Stiens	1964	Bintje			108	105		98
		Sirtema			107	107		103
Stiens	1965	Bintje		93	105	103		99
Stiens	1966	Bintje	99	103	100	104		
Hornhuizen	1966	Bintje	86	94	105	103		
PAW 1057	1966	Bintje			111	114		
Stiens	1967	Bintje		106	105	102		
Hornhuizen	1967	Bintje			100	109	109	111
PAW 1057	1967	Patrones			103	104	103	110
Stiens	1968	Bintje						106

1. In weeks from the beginning of tuberisation.

Similar significant effects were found on the coarse sands at Ens, where excess water had been fallen near to sprinklers. In 1963 the yield of 20 plants taken near to sprinklers averaged 11.0 kg and farther away 14.8 kg. In later years this effect was prevented by adjustment of the sprinkler nozzles.

Influence on yield Yields (all tubers over 28 mm, unless otherwise stated) from irrigation experiments are summarized in Table 19, where the data are given as percentages of the control. In view of the importance of the time irrigation started the data are arranged roughly according to the number of weeks before or after the beginning of tuberisation.

Irrigation one week before the beginning of tuberisation had no effect on yield, but irrigation at or after the beginning increased yields by an average of 6%. Only when irrigation was delayed three or more weeks the yield effect was gradually lost.

Influence on the number and size of tubers Krijthe (1955) showed that a potato plant forms many more tubers than the number that ultimately achieve a marketable size. To examine the influence of irrigation on the number of well developed tubers, the number of tubers that reached seed potato size or larger, were counted at harvest in several experiments. The data are given in Table 20 as percentages of the number of tubers found in the untreated plots, and are arranged according to the start of the irrigation.

There is some evidence that irrigation causes a larger number of tubers to develop, especially when irrigation starts early. Comparisons with Table 19 show that sometimes the yield gained by irrigation is not as much as the profit gained in number of tubers, e.g. Stiens 1966, PAW 1057, 1967, which means that the grading of the tubers is shifted towards the smaller sizes. This may lead to a greater increase

within the seed potato size bracket than in overall yield. The seed potato grades are financially of the highest value and therefore effects of irrigation on the distribution are of great importance. The shift in the tuber size range caused by irriga-

Table 20. Influence of irrigation on tuber number at harvest (>28 mm) (as % of tuber number of untreated plots).

			First irrigation[1]					
			−2	−1	0	+1	+2	+3
Stiens	1966	Bintje	134	127	136	123		
PAW 1057	1966	Bintje			113	107		
Stiens	1967	Bintje		105	100	105		
PAW 1057	1967	Patrones			120	118	111	104
Stiens	1968	Bintje						100
PAW 1629	1968	Bintje			109	105	101	

1. In weeks from the beginning of tuberisation.

Table 21. Influence of irrigation on yield of tubers in seed potato size (28–45 and 28–55 mm) compared to total yield (all yields as % of yield of untreated plots).

		Number of irrigations	Irrigation-water (mm)	Total yield	Yield	
					28–45 mm	28–55 mm
Stiens	1966	4	80	99	106	
		4	73	103	103	
		3	65	100	102	
		2	52.5	104	95	
PAW 1057	1966	2	30	111	117	118
		1	20	114	114	121
		1	15	110	110	112
Stiens	1967	5	90	106	100	
		4	82	105	111	
		3	80	102	105	
		3	65	100	103	
Hornhuizen	1967	7	110	100	110	
		5	85	109	112	
		4	80	109	113	
		2	40	111	111	
PAW 1057	1967	6	95	103	118	109
		5	90	104	115	110
		4	80	103	106	108
		4	75	110	106	117
		3	70	105	110	107

Table 22. Influence of irrigation, PCNB and both on percentage of tuber surface with scab, percentage scabby tubers and yield (Noord-Holland, 1967: NH-67, Noord-Holland, 1968: NH-68, PAW 1057, 1967: PAW-67).

Irrigation	PCNB	Surface with scab (%)			Scabby tubers (%)	Yield PAW-67 (% of untreated)
		NH-67	NH-68	PAW-67	PAW-67	
—	—	23.4	11.6	0.69	43.5	100
—	+	13.0	13.2	0.25	29.0	69
+	—	11.5	8.0	0.02	2.3	104
+	+	2.3	5.5	0.01	1.9	84

tion is shown in Table 21, where the total yield and the yield of the tubers 28–45 mm or 28–55 mm are given as percentages of the control.

In most cases the profit in the seed potato size bracket caused by irrigation increased more than the total yield.

Irrigation and the use of PCNB In three experiments, irrigation, PCNB and the combination of both were compared and the results are given in Table 22.

In Noord-Holland irrigation gave better control than did PCNB alone, which showed no effect in 1968. In combination there was some additional control in 1967, but not in 1968. In experiment PAW 1057 there was some evidence of a combined effect, but here PCNB caused a significant loss of yield, which could only partially be made up by irrigation.

8.1.3 Discussion and conclusions

Irrigation clearly gives good and even very good control of scab under all kinds of weather conditions and significantly increases yield, unless irrigation is started too early. The yield increase is usually even higher for the seed potato grades than for the total yield. However, irrigation has disadvantages for it may cause a deterioration in soil structure so that mechanical harvesting is made difficult because of clods and adhering soil. This deterioration is especially serious when water contains chlorine. Some of the important seed growing areas are situated near the coast, where in dry weather brackish water tends to accumulate in the ditches. The Research and Advisory Institute for Field Crop and Grassland Husbandry (PAW) has done a number of irrigation experiments with water containing chlorine and we assessed the scab incidence on tubers. Chlorine did not affect scab, but 2 g chlorine per litre decreased yield by injury to leaves and caused a deterioration of the soil structure, which was particularly evident on the heavy clay soils (Internal Rep. PAW).

Irrigation may affect other diseases and although we never had trouble from *Phytophthora infestans* (Late blight), early infection by this fungus could be fa-

voured by irrigation. In the first irrigation experiment at Ens a severe attack of *Alternaria solani* (Early blight) occurred on the leaves near the sprinklers, probably promoted by the excess of irrigation water. With adjustments of the sprinklers and application of a preventive fungicide spray, leaf fungi were never a problem.

In some potato growing areas water supply may cause problems, especially when water, low in chlorine is not available. However, this could be solved by regional water management, especially when reallotments are planned in potato growing areas.

Investigations by PAW show that investment in irrigation equipment is worthwhile, especially when its use is extended to other crops. However, irrigation of the potato crop is laborious and many man hours are needed over a rather short period. The development of semi- or fully-automatic devices is absolutely necessary for the more general use of this method of scab control.

Unfortunately the russet scab organism (Chapter 4, Table 2) does not react to changes in soil moisture, but fortunately it is much less widespread than normal and superficial scab and, also it attacks a few varieties. With careful choice of variety it is possible to grow scab-free crops even when this organism is present.

To minimise labour costs the number of irrigations should be few as possible. There appeared from Table 17 no advantage in irrigating before tuberisation, in fact yield may be decreased, and a delay of seven days after the beginning of tuberisation achieves as good, or nearly so, as irrigations that start earlier. This is because most tubers have reached the susceptible stage by then and therefore postponing irrigation more than seven days will decrease the effectiveness of the control. If the soil is already wet (near field capacity) at the beginning of tuberisation, irrigation can be delayed a few days without risk (see all experiments of 1967, Table 17). If the soil is dry at the beginning of tuberisation (Hornhuizen 1966, Table 17) delay results in less scab control.

The period requiring irrigation varies from year to year depending on the moisture status of the soil at tuber initiation, and on the amount and frequency of rain during the susceptible period, which for Bintje is about four weeks from the start of tuber formation.

In 1968 observations on tuber development were carried out at Stiens by taking samples of ten plants at regular intervals during the growth of the tubers. Tuberisation started on 16 May, but the number of tubers per plant did not reach its maximum until 10 June, and on 24 June about 25% of all tubers were still less than 10 mm in diameter, i.e. they had not yet passed the susceptible stage. Protecting these tubers by irrigation makes little sense because most will never reach the smallest seed size. Krijthe (1955) found that the largest and first initiated tubers were always the fastest growing and the smallest and the last initiated the slowest. Also that some of the smaller tubers are resorbed by the plant so that ultimately only about half the number of tubers that were initiated reach seed size or larger, and that the latter tubers are initiated in the first 2–3 weeks of tuber formation. The last tubers from this group will need protection, and assuming that the limit

for susceptibility lies at 20 mm (Sanford, 1924, mentioned the most susceptible stage as lying below 12 mm; Dippenaar, 1933, 20 mm), for practical purposes, the period during which irrigation will be effective against scab, ends about four weeks after the beginning of tuberisation. Although some later formed tubers may reach seed potato size, their proportion is so insignificant that it is uneconomic to irrigate beyond four weeks.

Recent work on the control of scab in ware crops by irrigation has shown that the critical period (page 46) is about the same as for a seed crop (Lapwood et al., 1970). This is because most of the tuber tissue susceptible to scab infection has been formed within four to five weeks from tuber initiation.

8.1.4 Recommendations for control by irrigation

To control scab by irrigation, one has to determine the beginning of tuberisation as accurately as possible, taking into account individual variation between plants. The beginning is reached normally 5–6 weeks after planting, and is best assessed by digging than by a particular above-ground growth stage. Plants should be dug at regular intervals until two out of five plants show stolons with tubers (Section 8.1.1). When tuberisation has started, the top 10–15 cm soil should be brought up to field capacity within seven days if there is already moisture from rain, but within four days, if the soil is dry. From then on the moisture status of the soil must be known and evaporation losses must be replaced when it reaches about 20 mm. This is only a rough guide and moisture should not be allowed to reach this level on coarse sandy soils, whereas on soils with a high moisture holding capacity it can be greater. At the end of May and beginning of June (the time when tubers start to form) evaporation averages 3 mm per day in cloudy and cool weather, 3.5 mm per day in normal weather and 4.5 mm per day in sunny, warm weather (Baars, 1968). This means irrigating every five days when the weather is dry and sunny. If more than 20 mm natural rainfall occurs, evaporation calculation starts again from the last rainy day. If less than 20 mm rain has fallen, then every 5 mm of rain gives one day postponement of the irrigation. When the 20 mm limit has been reached it is wise not to postpone irrigation, even though rain may be forecast in a day or so, because if scab is allowed to infect, later irrigation will not reverse the infection.

Rain should be measured at the site using a simple rain gauge, rather than depending on meteorological station data, even if this is situated in the neighbourhood, because in showery weather there can be locally considerable differences.

Each irrigation requires the same calculations, and if the whole critical period were to remain dry, this would mean a maximum of five irrigations, but normally 1–3 irrigations will be sufficient. It is essential to realise that omitting the first two irrigations will have a much more serious effect than omitting the later ones.

On well drained sandy and very light sandy loam soils the number of days between irrigations must be reduced and the amount of water applied proportionally decreased.

If these recommendations are followed, scab can be controlled, total yield increased by an average of 6%, and yield of seed potatoes increased even more.

Irrigating before the beginning of tuberisation decreases yield, but the later irrigation starts, although still increasing yield, the poorer the control of scab.

8.2 Influence on microbial population and the scab organism in soil

Sanford (1926) studied the influence of soil moisture on the scab attack and the oxygen requirements of the scab organism and concluded: 'No definite data have been secured relative to oxygen requirements in the soil, or the oxygen applying ability of soils of various types and moisture contents; but it seems quite probable that lack of sufficient oxygen is often an important factor in limiting sporulation, spore germination and vegetative development of the pathogene in the soil. This would then affect the ability of the parasite to cause infection and may help to explain why scab is not so prevalent in wet soils as in drier ones'. He also found that many bacteria have an inhibitory effect on the scab organism in vitro, probably because of acidification of the substrate, although this could occur without change in pH.

Dippenaar (1933) considered the ratio between bacteria and actinomycetes important, for in wet soils this ratio is shifted towards more bacteria.

The growth of *S. scabies* is not retarded by high soil moisture (Sanford, 1926), and Harmsen (Internal Rep. Dutch Potato Scab Committee, 1964) found maximum growth of *S. scabies* at field capacity so long as the soil was well aerated. Harmsen also found that the scab organism would grow at very low oxygen tensions, for example, at 2.5% oxygen the rate of growth on agar media was 70% of that in normal air (20% oxygen), and on a sand medium it remained the same as in normal air and at 0.625% oxygen it was respectively 40% and 10%. A 50% carbon dioxide content in the air (normally 0.03% in air and about 0.5% in soil) resulted in 70% of normal growth. Carbon dioxide was found to increase threefold in soil after irrigation, but the concentration never exceeded 2%, and soil was always sufficiently aerated to support the growth of *S. scabies*.

Of the factors which affect the scab organism in wet soils, viz. decrease in oxygen and consequent increase in CO_2, increase in antagonism, or changes in the microfloral equilibrium unfavourable to the actinomycete, we have studied the last in most detail.

My research (Labruyère, 1965) supported the findings of Harmsen, but I found that the scab attack was largely independent of the type of gas (compressed air, oxygen, carbon dioxide or nitrogen) passed through the soil in which potato plants were growing, but depended mainly on the moisture content. Even when carbon dioxide passed continually at a constant rate, tubers were still scabbed, although plant growth suffered severely from the treatment. With increase in soil moisture content of pots both numbers of actinomycetes and scabbiness of tubers were decreased.

8.2.1 Materials and methods

Soil samples were taken with a 1.5 cm diameter auger from the ridges near potato plants to a depth of 15 cm from plots of the irrigation experiments. At least 40 cores per plot were taken randomly, were bulked either as per plot or per treatment and put in polyethylene bags. When possible, soil samples were processed the next day, but sometimes they had to be stored at low temperature (at first +4° C, later at —20° C). Two 10 g subsamples were weighed and then dried at 110° C for moisture determinations. Soil moisture was expressed as a percentage of the weight of the dried sample.

To determine the number of bacteria and actinomycetes, 100 g samples of soil were suspended in 1 l water and mixed for 2 min in a blender. Coarse particles were allowed to settle briefly, before aliquots were pipetted off for further dilutions. To determine total bacterial numbers, dilutions were made with sterile water and from the final dilution, 5 or 10 ml aliquots were suspended in 10 ml of TBG-medium ('Totaal Bacterie Getal': total bacterial number). The TBG-medium consists of 0.2 g albumin, 0.5 ml 0.1 *N* NaOH, 0.5 g K_2HPO_4, 0.2 g $MgSO_4.7H_2O$, 1.0 g glucose, a trace of $FeCl_3$, 15.0 g agar (or 7.0 g ionagar) and 1000 ml distilled water (Recipe by courtesy of Dr. van Schreven of the 'Dienst Zuiderzeewerken' at Kampen).

To determine the number of actinomycetes the first aliquot from the mixer was diluted with a mixture of water and phenol to give a 0.7% phenol concentration, to eliminate bacteria (Lawrence, 1956). After 10 min a dilution series was made using sterile water: 1 ml aliquots of the final dilution were added to 10 ml Conn's glycerol-asparagine agar (GAA-medium; Conn, 1921), later modified by the addition of 0.05% *l*-tyrosine (GAT-medium), or added to the TCN-medium (Menzies & Dade, 1959), in five or ten replicates.

Table 23. Results of the microbial counts in irrigation experiment Ens, 1963.

Date	Irrigation	Moisture content (%)	GAA-medium[1]	TCN-medium[1]		On TBG-medium[1]		Ratio total act : tyr+ act	Ratio bact : act
			act ($x10^3$)	total act ($x10^3$)	tyr+ act ($x10^3$)	act ($x10^6$)	bact ($x10^6$)		
21/5	—	12.3	2080	1270	415	27.2		3.1	—
19/6	+	11.2	1790	1465	460	3.3	26.1	3.2	8.0
19/6	—	11.1	2040	1715	420	4.1	29.2	4.1	7.2
9/7	+	11.7	450	1460	395	5.4	33.7	3.7	6.3
9/7	—	11.5	480	1500	435	8.4	48.7	3.4	5.8
9/7	Subirr. ditch	10.3	725	1525	425	9.2	120.1	3.6	13.1

1. act: actinomycetes, tyr+: tyrosinase positive, bact: bacteria

8.2.2 Results

The first irrigation experiment to be systematically sampled was in 1963 at Ens where stationary irrigation equipment was used and unirrigated controls were sheltered plots within the irrigated areas. Soil samples were taken on 21 May before the irrigation had started, from the seven sites which were to be covered. Soil dilutions were made on GAA, TCN and TBG-media. Further samples were taken on 14 June, one week after the last irrigation from the same places and also from adjacent irrigated soil close to the covers. Two soil samples were also collected near a ditch used for subirrigating, where scab was usually slight because of wet soil. The bacterial and actinomycete counts from these samples (Table 23) show that differences between irrigated and unirrigated plots were relatively small. Also that the soil moisture of the plots was similar because of the rapidly draining coarse sand. The small numbers of actinomycetes on the GAA-medium on 9 July probably resulted from a wrongly adjusted pH, because numbers were large on the other media.

Differences in scabbiness were slight (Table 16) and scab was least from tubers near the subirrigation ditch, which also showed the greatest shift in the ratio bacteria to actinomycetes. The soil moisture content near the ditch is unexpectedly low and a weighing error is suspected.

The soil samples taken on 19 June were used to test for antagonism, but from both dry and wet soil, of the 1100 isolates tested per soil, only one colony in four showed inhibition to *S. scabies*, although the zone of inhibition was somewhat greater from wet soil than dry, respectively 0.45 and 0.56 cm^2. Therefore there appeared to be no significant increase in the activity or number of antagonistic actinomycetes by irrigation.

In 1964 soil samples from unirrigated plots (treatment V_0 of experiment PAW 1057) taken on 17 June and 22 July were compared with soil samples of treatment V_2 (of experiment PAW 1057), which had had 10 mm irrigation in late May to bring soil to field capacity and 30 mm in the middle of June. Similarly samples were taken from treatment O_0 of experiment PAW 1059 and treatment O_1 (of experiment PAW 1059), which had had 60 mm water at the beginning of tuberisation. Both experiments in the Noordoostpolder were on the same field and results, which are means of four samples, are shown in Table 24.

Irrigation increased bacteria to actinomycete ratios, with the irrigated soil giving nearly twice as many bacteria per tyrosinase positive actinomycete as unirrigated. There were three reasons for this:

1. there were relatively more tyrosinase positive actinomycetes in the total actinomycete population
2. there were more actinomycetes in dry than in wet soil
3. in three out of four comparisons there were less bacteria in dry than in wet soil.

The moisture content of irrigated plots was greater than that of unirrigated on 22 July, about five weeks after the last irrigation, which suggested the sandy loam

Table 24. Results of the microbial counts in irrigation experiments PAW 1057 and 1059, 1964.

Treatment[1]	Date of sampling	Moisture content (%)	On GAT-medium		On TBG-medium		Ratio total act : tyr+ act	Ratio bact : act
			total act ($x10^3$)	tyr+ act ($x10^3$)	act ($x10^6$)	bact ($x10^6$)		
V_2	17/6	18.4	240	82	24.8	338	2.9	13.6
V_0	17/6	11.5	320	135	34.5	355	2.4	10.3
V_2	22/7	15.2	370	37	28.7	393	10.0	13.7
V_0	22/7	13.4	500	59	41.2	386	8.5	9.4
O_1	17/6	17.6	310	96	28.4	448	3.2	15.8
O_0	17/6	13.7	300	108	31.5	272	2.8	8.6
O_1	22/7	14.5	130	41	39.9	760	3.2	19.0
O_0	22/7	14.0	222	75	40.4	389	3.0	9.6

1. V_2: treated with 10 and 30 mm water, O_1: treated with 60 mm water, V_0 and O_0: untreated

Table 25. Results of the microbial counts of soil water level experiment Oudkarspel, 1964.

Soil water level	Moisture content (%)	On GAT-medium	On TBG-medium	Bacteria ($x10^6$)	Ratio bact : act
		act ($x10^3$)	act ($x10^6$)		
— 30	22.5	420	20.4	347	17
— 45	19.0	350	26.4	387	15
— 60	14.5	580	37.4	285	8
— 75	12.7	900	34.4	249	7
—165	10.6	1410	62.9	832	13

retained water much better than the coarse sandy soil at Ens (Table 23).

A soil water level and irrigation experiment at Oudkarspel (van der Valk, 1961) was sampled once in 1964. The samples were taken from plots on the sandy loam area with water levels of 30, 45, 60, 75 and 165 cm below soil surface and results are given in Table 25.

The number of actinomycetes are greater the lower the soil water level and moisture content, whereas the bacteria show the opposite effect, except at 165 cm (which is probably an error because the effect is not shown in unirrigated plots on the same site (Table 26)).

Counts from the irrigation experiment at Oudkarspel, where soil was irrigated at pF 2.5 or pF 3.5, are given in Table 26.

Irrigation definitely increased bacterial numbers but actinomycete numbers remained the same and so the bacteria to actinomycete ratio increased as soil became wetter. The scab attack in both experiments was slight and few tyrosinase positive

Table 26. Results of the microbial counts of irrigation experiment Oudkarspel, 1964.

Irrigation	Moisture content (%)	On GAT-medium	On TBG-medium		Ratio bact : act
		act ($x10^3$)	act ($x10^6$)	bact ($x10^6$)	
none	10.8	560	47.3	218	4.5
at pF 3.5	13.6	910	47.5	574	12.1
at pF 2.5	17.5	220	42.4	775	18.5

Table 27. Results of the microflora counts of irrigation experiment Stiens, 1965.

Treatment[1]	Moisture content (%)	On GAT-medium		On TBG-medium		Ratio total act : tyr+ act	Ratio bact : act
		total act act ($x10^3$)	tyr+ act ($x10^3$)	act ($x10^6$)	bact ($x10^6$)		
V_0	13.6	9100	680	923	5480	12.9	5.9
V_1T_3	15.6	9170	664	1408	18895	13.7	13.4

1. V_0: untreated, V_1T_3: treated with 60 mm water

Table 28. Numbers of actinomycetes and pathogens from soil of irrigated and nonirrigated parts (Ens, 1966).

Location	Irrigation	On GAT-medium		Pathogens ($x10^3$)
		total act ($x10^3$)	tyr+ act ($x10^3$)	
Pipe I	+	670	67	12
	+	1440	87	22
	—	1450	168	64
	—	2290	120	41
Pipe II	+	1780	78	6
	+	800	36	0
	—	1440	50	4
	—	2090	149	11

actinomycetes were counted on the GAT-medium and so counts are not included in the tables, but still irrigation had a significant effect on the disease (Table 16).

In 1965 plots at Stiens were sampled on 7 July about a week after the previous irrigation and again more bacteria were counted in the moist than in the dry soil (Table 27).

Actinomycete counts were the same for wet and dry soils, using the GAT-medium, but a little higher from moist soil when the TBG-medium was used.

In 1966 tyrosinase positive actinomycetes and the pathogenicity of isolates was

assessed (Section 2.1; Vrugging & Maat, 1968) in irrigated and unirrigated plots at Ens (Table 28).

Table 28 shows that the total number of actinomycetes and the number of tyrosinase positive and pathogenic isolates tend to be lower from irrigated parts of the field.

In 1967 soil samples from the unirrigated plots and from treatment V_1 of PAW 1057, where plots were maintained close to field capacity from the start of tuberisation, were treated as in 1966. The first samples were taken on 22 June, when V_1 had received 50 mm water and the second on 7 July, when 65 mm in total had been applied. The number of pathogens was assessed in the first, but not in the second set of samples and the results are summarized in Table 29.

On 22 June total actinomycete numbers were not different from unirrigated plots, but numbers of tyrosinase positive and pathogenic isolates were fewer in the irrigated. On 7 July both the total and tyrosinase positive actinomycete numbers were now distinctly lower on the irrigated plots.

Table 29. Numbers of actinomycetes and pathogens from soil in irrigated and unirrigated parts (PAW 1057, 1967).

Treatment[1]	On GAT-medium				Pathogens 22 June ($x10^3$)	Scabby tubers (%)
	total act ($x10^3$)		tyr+ act ($x10^3$)			
	22 June	7 July	22 June	7 July		
V_1	960	1030	240	410	14	12.7
	—	1200	220	650	11	7.7
	890	1100	490	460	7	6.0
	920	700	340	340	5	9.6
V_0	890	1440	480	830	20	48.5
	840	2810	490	1340	21	54.5
	940	3110	480	1340	29	57.8
	470	2540	270	1230	4	53.4

1. V_1: treated with 65 mm water in total, V_0: untreated

Table 30. Numbers of actinomycetes from soil (Noord-Holland, 1968).

Treatment		On GAT-medium		Ratio total act : tyr+ act	Surface scabbed (%)
irrigation	PCNB	total act ($x10^6$)	tyr+ act ($x10^3$)		
—	—	12.2	1470	8.3	11.6
—	+	13.9	950	14.6	13.2
+	—	9.0	460	19.6	8.0
+	+	11.7	450	26.0	5.5

The irrigation and PCNB experiment at Noord-Holland in 1968 was sampled but only total actinomycetes and tyrosinase positive ones were counted (Table 30).

Treatments only slightly affected the total actinomycetes, but the tyrosinase positives were decreased by PCNB and more by irrigation. The combined effect of PCNB and irrigation is expressed most clearly in the ratio total actinomycetes to tyrosinase positive actinomycetes. As the irrigation was given only once and sampling took place some time after irrigation, differences were less than would have been expected after a normal irrigation programme.

8.2.3 Discussion and conclusions

The investigations described were mainly of a preliminary nature, but the data obtained from the different experiments from different sites in different years, when considered together, give valuable information on the effect of irrigation on the microflora, in particular the ratio bacteria to actinomycetes and the numbers of *S. scabies* both saprophytic and pathogenic.

Bacterial numbers were always greater in wetter soil, but irrigation appeared not to have much effect on the total actinomycete population. However, the number of tyrosinase positive actinomycetes nearly always decreased and especially the scab pathogens, and therefore wet soils would be less favourable for scab development (tables 28 and 29).

Lewis (1962a) looked at the lenticel microflora of tubers grown in 'moist' and 'dry' soils. He found that the percentage of lenticels, in which 'pigment producing Streptomycetes' (tyrosinase positive actinomycetes on TCN-medium) occurred, decreased under 'moist' conditions and to a lesser degree the total actinomycete population. Also that under dry conditions 34.8% of lenticels had actinomycetes and 8.5% bacteria only, whereas under moist conditions 6.6% had actinomycetes and 49.4% bacteria only. He felt that: 'competition for nutrient could be important in the region of suberized tissues, from which leakage of metabolites would be low; such competitive effects would be exaggerated during isolation in distilled water agar. These antagonistic phenomena might be more important in wet soils where the movement of bacteria in water-films could result in large numbers reaching the lenticels.' However, he did not notice an increase in antibiotic activity after irrigation.

Scab control by irrigation may be the result of a shift in the ratio pathogens to bacteria, which can be caused by a shift in one or more of the ratios pathogens to tyrosinase positive actinomycetes, tyrosinase positive actinomycetes to total actinomycetes or total actinomycetes to bacteria in the soil around the tubers. Water-films on the surface of tubers in wet soil may enable motile bacteria to reach the lenticels before the slower growing mycelium of *S. scabies*.

Lenticels are formed from stomata, during which leakage of metabolites occurs and this chemotrophic stimulus may give bacteria a further advantage.

Under dry conditions there are no water-films to bring bacteria into contact with

lenticels quickly and so *S. scabies* has a better chance of reaching lenticels before bacteria. The organism arriving first can probably maintain its position because the supply of metabolites favours rapid multiplication of the first intruder. Also through growth, metabolites from the lenticel are consumed and the leakage to the surrounding soil decreases and so the chemotrophic attraction to other organisms decreases. Antibiotics may be produced, which may also prevent the establishment of other organisms. Lewis (1962a) concluded: 'the possibility of one group' (meaning actinomycetes, bacteria and fungi) 'occurring in the absence of the other, was always greater than in its presence.' He also found more actinomycetes on the surface of a susceptible than on a less susceptible or resistant variety. De Bruyn (1935) recorded that *S. scabies* grew better in sap extracts of susceptible than resistant varieties. Therefore the possibilities of infection are greater in dry than in wet soil and greater on a susceptible than on a resistant variety, because of the presence of larger numbers of propagules of the pathogen.

Lapwood & Hering (1968 and 1970) demonstrated that the amount of infection by *S. scabies* depends on 'the rate' (tuber) 'internodes form, the number at a susceptible stage when the soil is dry, and on the extension growth of each internode.' ... 'the tissue of each internode remains susceptible for 10 to 15 days, possibly because the transition of stomata to lenticels takes this time.' They induced bands of healthy and diseased tuber surface by interchanging wet and dry periods and found that some of the internodes formed in a wet period may subsequently become scabbed if the soil becomes dry, which suggests that stomata and young lenticels, that have been wet, may still develop scab lesions. Perhaps there is a process within the tuber itself, which determines whether infection of young lenticels is successfull or not. The speed of growth of the scab organism into tissue and the rate of cell division by the meristematic tissue under the young lenticel may be of importance because such a process and especially the latter, might be influenced by moisture conditions in the surrounding soil. However, more research on lenticel development and on young infections of *S. scabies* are needed on the means by which wet soil (or irrigation) prevents scab infections.

Conclusions from the research on scab control

1. Chemical control of scab offers few prospects in the Netherlands. The only chemical applied with some success has been PCNB, and its use is increasing not so much because it might prevent a serious scab attack, but because farmers expect it to control a light attack and also Rhizoctonia. This means that seed potatoes can be sold directly after grading without need for extra sorting when diseased tubers are present. The yield loss from PCNB depends on the weather, potato variety, type of soil, etc., but whatever the loss, the saving in sorting costs seldom makes up for the financial loss from decreased yields.

2. The antibiotic effect of soil organisms affects the occurrence of scab, but introducing such antagonists into an existing microflora is not possible without further farreaching agricultural measures and is nearly always economically unattractive.

3. Crop rotation effects are small and the actual effect of a preceding crop is difficult to judge, because changes in soil moisture at the time of tuberisation may influence the results positively or negatively. Frequent potato growing on the same land is not advisable because of the danger of increasing the scab population.

4. Irrigation was the most effective way of controlling scab, but cannot be used under all circumstances because of shortage of water or water low in chlorine, and because of the labour involved.

5. It appears therefore that at this moment many Dutch seed potato areas cannot be protected; however, not all varieties are of equal susceptibility and varietal choice is another way of controlling scab. Presenting a greater choice of high-grade potato varieties with resistance against common scab to enable farmers to produce scab free crops, where other methods of control are impracticable, remains the difficult task of Dutch potato breeders.

Summary

In the Netherlands common scab of the potato is usually caused by *Streptomyces scabies* (Thaxter) Waksman et Henrici, following Corbaz's description, and rarely by other *Streptomyces* species. Variation in morphological and other characteristics could not be correlated with lesion types and non-pathogenic *S. scabies* strains do exist. Three scab types were described, viz. 'normal', 'superficial' and 'russet'. Studies of scab lesion anatomy and reaction to external conditions suggested that superficial and normal scab isolates mainly differ in virulence. The russet scab type does differ in symptom expression and anatomy, in reaction to temperature and moisture and in attacking the root system, but our isolates do belong to *S. scabies*.

After infection the main pathway of the mycelium seems to be intercellular, and, towards the interior of the lesion the mycelium spreads in cell walls, but is very difficult to find because it stains poorly.

Chemical control of scab offers few prospects in the Netherlands. Only PCNB (pentachloronitrobenzene, quintozene) has been applied with some success, but has the disadvantages of yield loss, delay in the expression of virus symptoms and off-flavour in tubers for eating. Other chemicals were not sufficiently active to control scab when applied at economic rates.

Introduction of antagonists into soil as a measure of scab control proved to be impossible without further far reaching agricultural measures and is economically unattractive. Crop rotations and application of green manures also showed little effect on scab incidence.

Irrigation during four weeks after tuber formation starts, proved to be the most effective way of controlling scab. The effect of irrigation on the microbial population of the soil was investigated and irrigation was shown to shift the ratio of pathogenic actinomycetes to bacteria in an unfavourable way for *S. scabies*.

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