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Pathology and control of soil-borne fungal pathogens of potato

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Summary

Several soil-borne fungal pathogens continue to cause problems in potato production worldwide. The reasons for these problems are illustrated by reference to the pathogens *Verticillium dahliae*, *Rhizoctonia solani*, *Spongospora subterranea* and a group normally considered to be tuber-borne, including *Colletotrichum coccodes*, *Helminthosporium solani* and *Fusarium* species. Generally, the long-term persistence of survival structures, the difficulties in reducing inoculum and lack of good sources of resistance hinder attempts to improve control of soil-borne fungal pathogens. Post-harvest fungicide treatment of seed or ware potatoes does not entirely alleviate storage problems. In the foreseeable future there is no alternative to the use of integrated measures from the time of planting seed to movement from storage. Key research areas that arise as a means of better controlling most of these pathogens are: the role of intraspecific variation in pathogenesis and ecology, problems of detecting and quantifying inoculum, and the need for improved methods for biological control.

Introduction

Diseases are one of the most important causes of yield and tuber quality losses in potato production worldwide (Hooker, 1981; Oerke et al., 1994) (Table 1). Similar lists can be compiled for the principal weeds and arthropod pests. Members from all major pathogen groups affect the crop and all plant organs are affected during the production cycle. Agronomic factors including rotation, planting material, cultivar selection, soil management and tillage, irrigation, pesticide application, haulm destruction and harvesting, crop residues and volunteers, and storage all have a profound influence on the incidence and severity of diseases. There can be strong interactions with other pest organisms in causing damage and loss. A number of soil-borne fungal pathogens may pose particular problems in potato production because of their long term persistence, the difficulties of controlling inoculum and the lack of good sources of resistance. A comprehensive list of pathogens with a soil-borne phase important in Europe is given in Table 2.

The main pathogens considered in this paper are the cosmopolitan species *Verticillium dahliae* and *Rhizoctonia solani*; a group including *Colletotrichum*

Table 1. The principal pathogenic agents causing loss in potato (after Hooker, 1981; Oerke et al., 1994).

Pathogen	Disease/ Commonname	Distribution
(a) fungi		
Alternaria solani	Early blight	Worldwide
Erysiphe cichoracearum	Powdery mildew	L. America, Europe, Near-East
Fusarium spp.	Fusarium dry rot	Worldwide
Macrophomina phaseolina	Charcoal rot	Worldwide where T >28 °C
Phoma fo eata	Gangrene	N. America, Europe, Asia, Oceania
Phytophthora infestans	Late blight	Worldwide
Rhizoctonia solani	Black scurf/ stem canker	Worldwide
Spongospora subterranea	Powdery scab	Worldwide
Synchytrium endobioticum	Wart	Africa, Asia, America, Europe
Verticillium spp.	Verticillium wilt	Worldwide
(b) bacteria		
Erwinia caroto ora ssp. atroseptica	Black leg, soft rot	Worldwide
Pseudomonas solanacearum	Bacterial wilt, brown rot	Asia, Africa, S. America (probably worldwide)
Cla ibacter michiganense ar. sepedonicum	Ring rot	Worldwide
Streptomyces scabies	Common scab	Worldwide
(c) viruses		
PLRV Potato leafroll virus		Worldwide
PVY^{o} Potato virus Y^{o}		Worldwide
PVN^{n} Potato virus Y^{n}		Europe, USSR
PVA Potato virus A		Worldwide
PVX Potato virus X		Worldwide
PVM Potato virus M		E. Europe
(d) nematodes		
Globodera rostochiensis	Golden nematode	Worldwide
Globodera pallida	White potato cyst nematode	N.W. Europe, S. America
Meloidogyne chitwoodi	Root knot nematode	Worldwide?
Meloidogyne incognita	idem	Europe, America, Africa, Asia
Meloidogyna hapla	idem	Europe, America
Meloidogyna ja anica	idem	Africa, Asia, S. America
Nacobbus aberrans	False root-knot nematode	America, India, USSR, N.W. Europe
Pratylenchus penetrans	Lesion nematode	N. America, Europe
Pratylenchus spp.	Lesion nematode	Worldwide

coccodes in which inoculum is also seed tuber-borne; and the biotrophic plasmodiophorid pathogen *Spongospora subterranea*. Rather than attempt to provide a comprehensive review we shall selectively emphasise more recent work on these pathogens. Recently there has been much research done on *V. dahliae* emphasising in particular intraspecific variation, detection methodology and cultural

Table 2. List of soil-borne fungal pathogens on potato (after Smith et al., 1988). Pathogens of main importance in Europe on potato are marked '*'.

*	*Colletotrichum coccodes*	
	Fusarium eumartii	(= *Nectria haematococca* var.)
	Fusarium ja anicum	(= *Nectria haematococca* var.)
	Fusarium oxysporum f.sp. *tuberosi*	
	Fusarium solani	(= *Nectria haematococca* vars.)
	Gibberella cyanogena	(= *Fusarium sulphureum*)
	Gibberella pulicaris	(= *Fusarium sambucinum*)
	Helicobasidium brebissonii	(= *Rhizoctonia crocorum*)
*	*Helminthosporium solani*	
	Macrophomina phaseolina	
	Phoma eupyrena	
	Phoma exigua	
*	*Phoma fo eata*	
	Phytophthora cryptogea	
	Phytophthora drechsleri	
	Phytophthora erythroseptica	
*	*Phytophthora infestans*	
	Polyscytalum pustulans	
	Pythium ultimum	
*	*Rhizoctonia solani*	(= *Thanatephorus cucumeris*)
	Sclerotium rolfsii	(= *Corticium rolfsii*)
*	*Spongospora subterranea* f.sp. *subterranea*	
*	*Synchytrium endobioticum*	
	Verticillium albo-atrum	
*	*Verticillium dahliae*	

methods of control. For *R. solani*, recent work has stressed inter-isolate interaction and processes associated with hyphal compatibilities at the molecular level. The teleomorph (sexual stage) of *R. solani* has been considered to be important on potato in some countries and on other crops. For seed tuber-borne pathogens such as *C. coccodes* there is accumulating evidence that soil-borne inoculum is important in some cultivations, and may cause increasing problems in storage where fungicide usage and fungicide resistance problems are also increasing. The biotrophic fungal pathogen *S. subterranea* presents a different range of problems in terms of planting material, chemical treatments and resistance breeding.

Verticillium dahliae

V. dahliae is a cosmopolitan wilt pathogen on many dicotyledonous plant species. Economically the most important hosts are potato and cotton, but in many other crops the disease is significant, e.g. on strawberry, oil seed rape, rose and ash. For potato, *V. dahliae* is the major component in the potato early dying syndrome (Powelson & Rowe, 1993). The pathogen may survive nonhost periods for numerous years in the form of microsclerotia, which are largely produced on senescing shoot tissue. The key-issue of the last few years has been to describe intraspecific variation in *V. dahliae* (Rowe, 1995).

Intraspecific ariation

Intraspecific variation in *V. dahliae* has been considered the exception rather than the rule, in contrast to the situation in *Fusarium oxysporum*, where many special forms and races are distinguished. Adaptation of strains of *V. dahliae* to hosts is, in comparison to *Fusarium oxysporum*, a rare phenomenon which has been reported only from cotton (*Gossypium hirsutum*), the Cruciferae, peppermint (*Mentha* x *piperata*), Brussels sprouts (*Brassica oleracea* var. *botrytis*) and horseradish (*Armoracia rusticana*) (Table 3). Host adaptation of *V. dahliae* appears not to be a rigid character since, for example, several peppermint isolates which were initially nonpathogenic to tomato became pathogenic after one or more passages through tomato plants (Fordyce & Green, 1963). Likewise, diploid strains of *V. dahliae* from cruciferous hosts appear to be able to cause disease in noncruciferous plant species and haploid isolates from noncruciferous hosts generally can cause disease in cruciferous species (Subbarao et al., 1995). The general lack of specificity in *V. dahliae* has been confirmed by showing that single isolates of *V. dahliae* can infect many hosts (Subbarao et al., 1995), including the roots of monocotyledonous plants like barley, onion, tulip and wheat (Malik & Milton, 1980).

Recently, vegetative compatibility analysis, and molecular analyses of restriction fragment length polymorphisms (RFLP) and the internal transcribed spacers (ITS) regions in genes encoding ribosomal RNA, have shed more light on intraspecific variability in *V. dahliae*.

Puhalla & Hummel (1983) recognized 15 vegetative compatibility groups (VCG) using UV-induced mutants lacking melanin in the microsclerotia. Using *nit*-mutants, Joaquim & Rowe (1990) recognized only four VCG, numbered 1 to 4. Isolates that belonged to the same VCG recognized by Puhalla & Hummel (1983) were all assigned to the same VCG as recognized by Joaquim & Rowe (1990). Heale (1988) stated that pairing melanin deficient mutants would require relatively many hyphal fusions to obtain a visible heterokaryotic reaction. In contrast, rare hyphal fusions using *nit*-mutants result in visible wild-type growth. The frequency of hyphal fusions needed to observe a heterokaryotic reaction may well explain the larger number of VCG recognized by Puhalla & Hummel (1983).

Table 3. Hosts from which host-adapted strains of *Verticillium dahliae* have been reported.

Host taxon	Reference	Remarks
Brussels sprouts	Isaac, 1957	Isolates from Brussels sprouts were nonpathogenic to 12 plant species and weakly pathogenic to potato and tomato.
Cotton	Ashworth, 1983	Leaf-defoliating and leaf-nondefoliating strain[1].
Cruciferae	Stark, 1961; Horiuchi et al., 1990	Diploid strains (= *V. dahliae* var. *longisporum*). Also reported on *Beta ulgaris*
Horseradish	Eastburn & Chang, 1994	-
Peppermint	Horner, 1954	-
Tomato	Schaible et al., 1951	Related to the presence of the *Ve* resistance gene.

[1] Other races have been reported from China and USSR (cited in Daayf et al., 1995).

In a subsequent study, Joaquim & Rowe (1991) subdivided VCG 4 on the basis of weak cross-responses into VCG 4A and 4B. The subdivision of VCG 4 could not be confirmed by Daayf et al. (1995). In a more comprehensive study, it appeared that VCG 3 was not different from VCG 4 and one new VCG, number 5, was discovered (Strausbaugh et al., 1992). In repeated experiments, isolates were never assigned to more than one VCG, indicating stability of the VCG system of *V. dahliae* (Strausbaugh et al., 1992). In a subsequent study, Strausbaugh (1993) recognized six subgroups of VCG 4A (4A1–4A6), two subgroups of VCG 4B (4B1 and 4B2) and one 4A/B1 group, based on pairings with a range of different mutually compatible tester strains. Distinguishing these subgroups and the value of naming them may become irrelevant when larger populations are studied, which may establish a continuum rather than well-defined subgroups (Strausbaugh, 1993). Recently, three isolates of *V. dahliae*, from potato, tomato and strawberry, appeared to be incompatible with the tester strains of Strausbaugh et al. (1993), and they were assigned to the new VCG 2X (Subbarao et al., 1995). The VCG and some of their characteristics including their known geographic distributions are summarized in Table 4.

Table 4. Summary of recognized VCG of *Verticillium dahliae* and some of their characteristics.

VCG	Remarks	Reference
1[1]	Most isolates from woody ornamentals.	Chen, 1994
	All cotton-defoliating strains.	Daayf et al., 1995
	Not pathogenic to tomato.	Daayf et al., 1995
	Distribution probably limited (Mexico, USA).	Bell, 1992
	Solanaceous isolates rare.	Joaquim & Rowe,1991; Strausbaugh et al., 1992
2	No synergistic interaction with *Pratylenchus penetrans*.	Botseas & Rowe, 1994
	All cotton-nondefoliating strains.	Daayf et al., 1995
	Solanaceous isolates common.	Joaquim & Rowe, 1991
	Reported from Africa, America, Australia, Asia and Europe.	
2X	So far, reported only from three isolates, from U.S.A.	Subbarao et al., 1995
4	Most common VCG for solanaceous isolates.	
	Not reported from cotton.	
	Reported from America, Europe.	
4A[2]	Relatively more virulent strains on potato in root-dip experiments.	Joaquim & Rowe, 1991
	Synergistic interaction with *Pratylenchus penetrans*.	Botseas & Rowe, 1994
4B	Relatively less virulent strains on potato in root-dip experiments.	Joaquim & Rowe, 1991
	No synergistic interaction with *Pratylenchus penetrans*	Botseas & Rowe, 1994
5	So far, only reported from one isolate, from U.S.A.	Strausbaugh, 1993

[1] Bell (1992) mentioned subdivision of VCG 1, 2 and 4 in subgroups 1A and 1B, 2A and 2B and 3A and 3B, respectively.
[2] Subdivision based on weak cross-reponses (Joaquim & Rowe, 1991).

All 25 strains isolated from potato stems (assigned to VCG 2, 4A or 4B) appeared to be pathogenic to potato in at least one of two pathogenicity experiments, although individual isolates of VCG 4A and 4B were not always significantly different (Joaquim & Rowe, 1991). In potato root-dip experiments, VCG 4A was significantly more virulent than VCG 2 and 4B (Joaquim & Rowe, 1991). However, using soil artificially infested with microsclerotia, a significant difference in virulence between VCG 4A and 4B was found only if the soil was co-infested with the root-lesion nematode *Pratylenchus penetrans* (Botseas & Rowe, 1994). This difference between VCG 4A and 4B may well explain the conflicting results on the effect of root infecting nematodes on verticillium wilt (Botseas & Rowe, 1994). The pathogenicity experiments of Strausbaugh (1993) with potato plants were in line with those of Botseas & Rowe (1994), except that not all VCG 4A isolates were significantly more virulent than those of VCG 4B and VCG 4A/B.

Using RFLP analysis, five distinct RFLP groups were recognized for *V. dahliae* (coded A, B, I, D and M) (Table 5). The host-adapted isolates from peppermint were classified in a separate RFLP group (M) and three out of four classes of host-adapted isolates from Japan could be assigned to RFLP B, I and D, respectively (Carder & Barbara, 1994). The sequences of the ITS regions of the rRNA genes of the *Verticillium* species showed that the species and RFLP groups differed six nucleotides or less. RFLP groups A, B and I could not be distinguished by ITS analysis, in spite of the quite distinct RFLP patterns (Okoli et al., 1993). Based on the small differences in ITS sequences of the *Verticillium* species and RFLP groups, Morton et al. (1995) speculated that the diploid isolates of *V. dahliae* may be more closely related to *V. alboatrum* than to haploid isolates of *V. dahliae*. It has been suggested that diploid *V. dahliae* (= *V. dahliae* var. *longisporum*) might be considered a separate species (Okoli et al., 1994). Unfortunately, RFLP groups of *V. dahliae* have not been related to VCG. However, using RAPD analysis Li et al. (1994) characterized VCG 1 as a distinct group, but strains of VCG 2 and 4 appeared to be not distinct.

Table 5. RFLP group names and characteristics of *Verticillium alboatrum* and *V. dahliae*, according to Morton et al. (1995).

Species: RFLP group name	Remarks
Verticillium alboatrum	
L	isolates from lucerne = VCG 1
NL	hosts other than lucerne = VCG 2
Verticillium dahliae	
A	not host-associated
B	not host-associated
I	not host-associated, intermediate between A and B
D	diploid isolates, largely from Cruciferae
M	isolates from peppermint

In contrast to *V. dahliae*, intraspecific characterization in *V. alboatrum* seems to be more simple, since strain origin (either from lucerne, L, or not, NL) coincided with RFLP analysis (Carder & Barbara, 1991) and VCG (L = VCG 01 and NL = VCG 02) (Correll et al., 1988). Rather recently, a new subgroup ('group 2') of *V. alboatrum* was reported by both ITS analysis (Robb et al., 1993) and RFLP analysis (Morton et al., 1995). The ITS and RFLP of 'group 2' appear to be more closely related to *V. tricorpus* than to *V. alboatrum* 'group 1'. The ecological significance of *V. alboatrum* 'group 2', which has been isolated from potato in Canada and The Netherlands and from hop in UK, has yet to be determined.

The relevance of intraspecific groupings in *V. dahliae* is potentially great. In breeding programmes, the appropriate VCG should be used. Specificity of subgroups has been confirmed for the peppermint isolates (Morton et al., 1995; RFLP group M), the cruciferous isolates (Morton et al., 1995; RFLP group D), the tomato isolates (Daayf et al., 1995) and in part also for the cotton isolates (Daayf et al., 1995) and the Japanese isolates (Carder & Barbara, 1994), but not for the Brussels sprout isolates and the cauliflower isolates (Koike et al., 1994). The recognition of host adaptation and characterization by RFLP analysis contradicts the observation that host specificity of subgroups is not absolute (Strausbaugh et al., 1992; Subbarao et al., 1995) and that host adaptation can be altered (Fordyce & Green, 1963). This apparent discrepancy may be explained by differences in the inoculation procedure. By using root dip inoculation, disease pressure may be unrealistically high, resulting in disease even in resistant or partially resistant plant species. More quantitative field and laboratory research on the distribution of VCG, their host range and ecology is necessary to be able to answer the question to what extent VCG are associated with the variation in effects of *V. dahliae* observed in the field. Finally, more attention has to be paid to the relations between VCG and RFLP groups of *V. dahliae*.

Control

Control of *V. dahliae* has focused on breeding for resistance, cultural measures and avoidance. Only the most recent developments are dealt with here.

Resistance. Conventional screening of germplasm has not led to commercial potato cultivars which are resistant or tolerant to *V. dahliae*. Several reasons can be put forward. Synergistic interactions of *V. dahliae* with root infecting nematodes occur and effects of *V. dahliae* alone may not be apparent. Wheeler et al. (1994) observed a synergistic interaction between *V. dahliae* and the root infecting nematode *Pratylenchus penetrans* in only one out of three years. In all years, however, Wheeler et al. (1994) were able to separate the effect of *V. dahliae* alone from the effects of *P. penetrans* and the interaction; they concluded therefore that *P. penetrans* could be deleted from screening programs. Resistance effects may also be masked when indirect effects play a significant role. For example, Subba-Rao & Bailey (1961) showed an association between the presence of an antagonistic fungal microflora in the rhizosphere of tomato seedlings and their resistance to *V. dahliae*. Davis et al. (1985) reported reduced yield loss of the susceptible Russet Burbank if cropped the

year after a resistant line was grown, and attributed this to increased numbers of antagonistic bacteria in the rhizosphere (Azad et al., 1987). McLean (1955), albeit showing great differences in susceptibility to *V. dahliae* among more than 100 cultivars of potato, observed that results depended on environmental conditions. Screening programmes under controlled conditions therefore produce less variable results, but how these relate to the field situation is of major concern. Simple screening procedures have been suggested using toxin extracts of *V. dahliae*, but Mohan et al. (1990) found, using an excised leaf bioassay, no correlation between the necrosis effects of crude toxin extract and symptom expression and yield loss in greenhouse and field experiments. Research dealing with the nature of resistance to *V. dahliae* may achieve rapid bioassays, but it remains to be established whether resistance occurs during one single part of the infection process. Tsror & Nachmias (1995) grafted susceptible scions of potato on resistant roots which were planted in soil which was infested with microsclerotia of *V. dahliae*, and vice versa. The production of conidia in the stems above the grafting point was 75% higher if the roots were susceptible. However, when stem segments were directly dipped in a conidial suspension of *V. dahliae*, the production of conidia was correlated with tolerance to *V. dahliae*. Tsror & Nachmias (1995) concluded that the root system plays a dominant role in the defense mechanism to verticillium wilt in potato, but that other mechanisms located in the stem are also active. Production of microsclerotia on the root surface seems to be uncorrelated with resistance, since production was higher on nonhosts than on hosts (Levy & Isaac, 1976). Vaughn & Lulai (1991) concluded from their work with potato tuber discs that several resistance mechanisms, both biochemical (insensitivity to toxins and hypersensitivity) and mechanical (localization of the pathogen), are active at the same time. Therefore, bioassays which use only part of the plant to screen for resistance carry the risk of giving unreliable results. Although first screening may be carried out with some types of bioassay, prolonged screening in the field is indispensable. A key factor is to understand the relations between resistance to *V. dahliae*, environmental conditions and dynamics of *V. dahliae* in the plant. Resistant plants have been obtained using protoplast fusions of *Solanum* species resistant to *V. dahliae* with potato (Jadari et al., 1992), but a major drawback is the inability to backcross sexually with potato.

Cultural measures. Among cultural measures, the most reliable method to control *V. dahliae* is soil solarization (Katan et al., 1976). However, this method is successful only in regions with a warm climate. Although elimination of *V. dahliae* is not complete, disease incidence and yield loss can be reduced drastically by soil solarization (Lazarovits et al., 1991; Melero-Vara et al., 1995). In some areas, the long period of time required for soil solarization to be effective is problematic. Morgan et al. (1991) studied the effect of polyethylene mulching during tomato cultivation. It appeared that reduction in soil inoculum density of *V. dahliae* and increase in yield were significant compared with the nonmulched control and not significant compared with mulching without planting tomatoes. Unfortunately, the authors did not present soil temperatures. The combination of soil solarization with other techniques may

increase the efficacy of control. For example, Tjamos & Fravel (1995) reported a synergistic interaction between sublethal heating and the heat-tolerant *Talaromyces fla us* on *V. dahliae* and Fravel (1996) reported a similar interaction of *T. fla us* with sublethal rates of metham sodium. Recently, the principles of solarization and green amendments have been introduced in countries with a cool climate. Blok et al. (1995) mulched fields with gas-impermeable plastic after ploughing in fresh organic matter (grass or cabbage). After 15 weeks, microsclerotia of *V. dahliae* were killed as, in addition, were several other plant pathogenic fungi and nematodes. The effect could not be attributed to lethal temperatures and it was hypothesized that fermentation of fresh organic matter under anaerobic conditions leads to production of lethal toxins and inactivation of microsclerotia.

If potatoes are cropped in a 4-year rotation, yield is not significantly different from that in fields where potatoes are grown for the first time (Bollen et al., 1989). Generally, however, potatoes are grown in rather narrow rotations. The use of nonhosts of *V. dahliae* to induce germination of microsclerotia and thus giving a reduction of soil inoculum density has not proved successful (Mol et al., 1996). However, certain hosts such as Sudangrass (*Sorghum ulgare* var. *sudanense*) did reduce soil inoculum density and yield loss in potato (Davis et al., 1996). It was suggested that the effect was related to an increase in nonpathogenic *Fusarium* species.

It has been shown that the fertilization regime influences verticillium wilt (Pennypacker, 1989). Elmer & Ferrandino (1994) reported that ammonium sulphate reduced verticillium wilt of eggplant in soils with low inoculum densities and attributed this to increased manganese levels in the rhizosphere as a consequence of rhizosphere acidification due to ammonium sulphate. Manganese has repeatedly been linked to suppression of verticillium wilt (cited in Elmer & Ferrandino, 1994). Davis et al. (1994) showed that yield loss in potato due to verticillium wilt can be affected strongly by the balance of nitrogen and phosphorus fertilization. Depending on the particular regime, wilt incidence ranged from 62% to 0%.

A oidance. Avoidance relies on good detection techniques and on reliable risk assessments. Although several methods to detect inoculum in soil have been published (Harris et al., 1993), considerable variation among research workers exists. In an international project aiming to compare detection techniques, 12 experienced laboratories analyzed 15 soils. Controls for effects of transport were included. The results of the mean values obtained for the 15 soils ranged from 0.5 up to 244 microsclerotia per gram of dry-weight soil (Termorshuizen, 1995). In an attempt to optimize detection assays, Wheeler & Rowe (1995) showed that many factors influence recovery of *V. dahliae* from soil, such as soil drying time, gravel content, soil pH, petri dish type (glass or plastic) and amount of soil on the agar plate. Reliable methods to determine infection of plants by *V. dahliae* using PCR (Hu et al., 1993) and monoclonal antibodies (Van der Koppel & Schots, 1995; Plasencia et al., 1996) are not available to quantify soil inoculum due to inhibition of the polymerase enzyme (in PCR) or cross reaction (of monoclonal antibodies). Using traditional

plating methods to estimate disease incidence, it should be kept in mind that isolation procedure can affect the result strongly. Platt & Bollen (1995) found that a polypectate medium was superior to potato dextrose agar for isolation of *V. dahliae* from potato sections, but that the situation was reversed for *V. alboatrum* and *V. tricorpus*.

Harris & Yang (1996) have developed a warning system for strawberry which predicted correctly in 53 cases that precautions had to be undertaken (e.g. soil fumigation), in seven cases it was predicted incorrectly that precautions had to be undertaken, and in five cases it was predicted incorrectly that precaution need not be undertaken. However, the warning system was cultivar-dependent. In addition, it should be noted that the absence of a relation between initial inoculum density and disease incidence has also been reported (e.g. Bejarano-Alcázar et al., 1995; reviewed by Termorshuizen & Mol, 1995).

Future prospects

The available information about intraspecific variation of *V. dahliae* does not lead to new control strategies. However, resistance programmes can be designed more efficiently by using the appropriate VCG. Presently the effects of green amendments are studied by several groups but a limitation is that, generally, large scale applications are expensive. Likewise biocontrol research has not yet led to commercially available products. Although large programmes have been carried out to screen for potential biocontrol agents for those pathogens which form larger sclerotia, this has not been performed for *V. dahliae*.

Rhizoctonia solani

The soil-borne fungus *R. solani* is a widespread pathogen in potato cropping systems that attacks stems and stolons (stem/stolon canker) and forms sclerotia on the tuber surfaces (black scurf) during plant senescence near harvest. The disease is recognized as a significant problem by growers world-wide and economic losses due to the disease vary in severity and predictability ranging from acceptance to levels that demand control of the disease. This is because *R. solani* prunes stolons, resulting in the production of unmarketable tubers, an alteration in the target size and number of tubers and the development of disfigured tubers (Hide et al., 1973; Carling et al., 1989; Banville, 1989); the formation of tuber-borne sclerotia decreases tuber saleability and in seed crops, downgrades seed quality (Jager et al., 1991).

Ecology and epidemiology

Rhizoctonia disease of potato occurs wherever potato is grown, and has been reported as most severe in the temperate zones. The etiology of *R. solani* in respect to the host plant is as follows; the fungus colonizes the below-ground potato plant surface from a food base (e.g. colonized crop residue) in response to root exudates. It expands on the root/stolon system to form an extensive hyphal network of anastomosing hyphae. During the colonization phase the host plant remains

symptomless as long as infection structures are not formed. The early steps of infection are initiated by differentiation of hyphal tip cells in t-shaped branches that evolve in appressorium-like structures, so-called infection cushions, on susceptible stems or stolons. Thin infection hyphae arise from these firmly attached structures that penetrate the underlying plant tissue (Hofman & Jongebloed, 1988). Infection cushions are believed to be prerequisites for developing stem and stolon lesions (Keijer et al., 1996) and serve as additional food bases for further colonization of the below-ground plant. Close to the time of harvest, sclerotia are produced on progeny tubers. It appears that tuber exudates stimulate black scurf development (Dijst, 1990) by remobilising the mycelial resources into sclerotia (Christias & Lockwood, 1973).

R. solani survives as tuber-borne sclerotia or as clusters of persistent thick-walled cells associated with crop residues or detached in the bare soil. Like most soil-borne diseases *R. solani* disease occurs patchily (Gilligan et al., 1996; Jeger, 1990) and the population density in heavily diseased patches, measured by a wet sieving method, amounted to around 100 infection entities per kg of soil (Van den Boogert, 1989). The importance of seed tuber-borne inoculum has been reported by several workers (e.g. Carling et al., 1989; Mulder & Roosjen, 1984). On the exported seed stock the pathogen can be transmitted worldwide. Because of its accessibility for control agents, tuber-borne *R. solani* is relatively easy to control compared with soil-borne inoculum.

Besides seed transmission, the pathogen is disseminated by basidiospore dispersal. Air-borne dissemination may occur following sporulation. Under moist and warm conditions *R. solani* fruits at the base of aerial stems to produce a primitive basidiocarp (hymenium) with basidiospores. These may become air-borne and subsequently disseminated but it is extremely difficult to germinate these field-grown basidiospores in vitro. Their significance for dissemination is further questioned because their formation coincides with canopy closure which decreases the chance of dispersal by wind.

Population structure

R. solani is a species complex composed of morphologically similar fungi which are quite variable in karyotype (Keijer et al., 1996), cultural appearance and growth characteristics (Parmeter, 1970) and pathogenicity (Sneh et al., 1991). Field isolates have been divided into anastomosis groups (AG) based on the ability of their hyphae to fuse in vitro. To date, 12 anastomosis groups are recognized, including the bridging group (Sheh et al., 1991; Carling et al., 1994). The resulting division is widely used and valuable, since it accommodates part of the observed diversity between isolates (Anderson, 1982). For example, AG-2, the crucifer group, is extremely variable on a wide range of crop plants, whereas AG-3 is the major incitant of black scurf disease and the sole cause of stem canker of potato (Bandy et al., 1988). Potato, however, is not the exclusive host of AG-3 and representatives of other AG, including AG-5 (Jager & Velvis, 1989) and AG-8 (Hide & Firmager, 1990) colonize the potato root and stolon system. Although isolates within an AG are more similar than between AG, distinct subgroups exist within AG. Based on variation in isozyme pattern, three

Table 6. Average disease response (0-8 scale) of 3 potato cultivars grown in artificially infested soil by 3 different *Rhizoctonia solani* isolates (AG-3) under laboratory conditions.

Isolates of *R. solani* AG-3	Disease response of potato cultivars P_{1-3}		
	P_1	P_2	P_3
3R03	3.2	6.7	2.2
3R09	5.4	4.8	6.4
3R41	1.9	2.9	5.1

$LSD_{5\%} = 2.1$.

subgroups have been identified within AG-3 (Laroche et al., 1992), indicating its heterogeneity at the iso-enzyme level. In pathogenicity tests (Table 6) it became evident that AG-3 isolates differ in virulence depending on the potato cultivar tested, indicating physiological specialization. From these and microscopic observations on anastomosis it is assumed by Van den Boogert that field populations of AG-3 consist of vegetative compatibility groups (VCG) each with their unique genetic background. Isolates belonging to the same VCG form hyphal connections allowing nuclear of extra-chromosomal gene flow. Isolates that cannot form such hyphal connections with one another, due to lysis of the contacting hyphal tips (Vilgalys & Cubeta, 1994), belong to different VCG. Different VCG cannot exchange genetic information and potentially diverge into physiologically specialized subgroups as illustrated for AG-3. Isolates from the same potato plants were assigned to one and the same VCG and those isolated from neighbouring plants to different VCG (Van den Boogert, pers. comm.). Apparently, each rhizoctonia-infected plant harbours its own VCG and at a field level numerous VCG can be expected. It is suggested that the sexual cycle plays an essential role in generating novel VCG. Indeed, the existence of hymenia have frequently been confirmed at the stem base of potato plants, indicating the potential for generation of genetic variation. Understanding of the population structure, including the mechanisms of genetic variation, is of essential importance for breeding programmes and novel control strategies. The questions to answer are to what extent VCG conserve pathogenicity, how stable they are and what the sources are of new VCG.

Control

Current measures. The key lies in the production and use of *Rhizoctonia*-free seed tubers because of their importance in disseminating the disease and adding to the pool of soil-borne inoculum. Both soil- and tuber-borne inoculum are targets for disease control measures varying from chemical control to preventive measures based on microbial sanitation.

A wide range of synthetic fungicides has been evaluated in both seed tuber and soil treatments and also for post harvest control. Fungicides or fumigants are applied with a wide spectrum of antimicrobial activity, ranging from metham sodium (Powelson &

Rowe, 1993) to compounds that are extremely selective against *R. solani* and *Rhizoctonia*-like binucleate fungi, e.g. pencycuron (Sumner, 1987) and tolelofos-methyl (Hide & Read, 1981). In The Netherlands, a few selective and low persistence fungicides are registered for tuber and soil treatment against *R. solani* in potato, e.g. validamycin (Solacol) and pencycuron (Monceren). Key points in application of synthetic fungicides are 'precision' and 'integration' (Kataria & Gisi, 1996). Precision involves selection, timing and targetting of an appropriate fungicide for a given disease situation, and integration involves compatible combination of fungicides with other disease control measures.

There are several biocontrol systems under development using antagonistic bacteria and fungi, of which the mycoparasite *Verticillium biguttatum* is most likely to establish practical application in potato growing. As mentioned earlier, an integration of measures and their precise targetting may lead to adequate and sustainable control of potato pests and pathogens. In this respect the mechanical vine killing technique 'green crop lifting' (Mulder et al., 1992) offers a unique opportunity to target control agents onto progeny tubers (Jager et al., 1991). The time of green crop lifting coincides with the onset of black scurf development but also under conditions conducive for mycoparasitism by *V. biguttatum*. Application of *Verticillium* conidia in green crop lifting leads to predictable and relevant control of black scurf disease and a appreciable reduction of the viability of tuber-borne sclerotia (Table 7).

Crop residues have a profound influence on the incidence and severity of disease. As shown in Table 8 potato plant residues are extremely important for black scurf development and by spraying these the stimulatory effect can be disregarded including the survival of *R. solani* inoculum. In green crop lifting crop residues are also targets for the control agents. Based on the results achieved in green crop lifting this microbial sanitation of crop residues by *V. biguttatum* has led to a novel application which is now under investigation in a wide range of agricultural crops. Apart from green crop lifting other applications have been worked out for *V. biguttatum*, such as treatment of the seed tubers at planting time (Van den Boogert & Jager, 1984) or as a postharvest measure (Jager & Velvis, 1988). Moreover, its

Table 7. The effect of crop residues on black scurf disease (*Rhizoctonia solani*) and the biocontrol effect by *Verticillium biguttatum* upon crop residues or tuber treatment in a soil-system with natural crop residues, artificially infested field soil and *in itro* grown minitubers.

Fytosanitary measures	Black scurf disease on minitubers (0-100)	
	non-inoculated	*Verticillium*-inoculated
Crop residues	68.5 a	1.6 c
Removal of residues by hand	8.6 b	1.3 c
Verticillium-treated crop residues	0.0 c	0.0 c

Data followed by a different letter are significantly different at $P < 0.01$.

Table 8. Biocontrol of black scurf disease by *Verticillium biguttatum* applied as a pre-harvest treatment in 'Green Crop Lifting' at different locations during 4 successive years. Between brackets vitality index (0-100) of black scurf.

Location	Black scurf disease (index 0-100)			
	Untreated		*Verticillium*-treated	
Rolde (1991)	29	(85)	10*	(7)
De Krim (1991)	23	(54)	2*	(0)
Rolde (1992)	14	(37)	5*	(9)
Munnekezijl (1992)	51	(92)	36*	(26)
Creil (1993)	8	(88)	1	(0)
Creil (1994)	37	(94)	24*	(43)
Munnekezijl (1995)	12	(60)	0*	(0)

* $P<0.01$.

compatibility with a number of synthetic oomycetous and *Rhizoctonia* fungicides, and other biocontrol agents, makes *V. biguttatum* suitable for integration into broad-range disease control against *R. solani* (Van den Boogert et al., 1994).

Other potential control measures including crop rotation and plant breeding have their economic or practical limits. In principle, a wide crop rotation of once potato in 5 years rarely exceeds the threshold for economic damage. However, since seed potato growing is relatively profitable, the generally accepted rotation frequency of one potato crop every three year in The Netherlands remains generally conducive for *Rhizoctonia* diseases (Scholte, 1992). Control by conventional plant breeding has been considered to be important. Differences in susceptibility can be seen (Scholte, 1989) but no resistant cultivars have been identified. In addition, resistance to infection does not necessarily correlate with resistance to black scurf development. The use of resistant cultivars would obviously improve the control of *Rhizoctonia* disease in the field.

Practices that favour rapid shoot emergence will generally aid in diminishing stem canker infections. Mature tissue expresses greater resistance to infection than immature tissue e.g. emerging sprouts and stolons. A recommended practice would be shallow planting in warm soil, conditions that also favour natural or artificially introduced antagonists.

No el measures. The search for novel measures has launched a number of new concepts, including the above mentioned system of green crop lifting. Resources for novel control measures are potentially available in the biotic environment. Field populations of *R. solani* exhibit a continuum between high virulence and hypo- or non-virulence. Hypovirulent isolates may reach considerable proportions (10–30%) of the total *Rhizoctonia* species populations (Ichielevich-Auster et al., 1985). Except for their inability to cause disease symptoms, hypovirulent isolates have similar characteristics to those of the virulent ones, including competitive competence to colonize and occupy the same ecological niche on the plant surface. Biological control of *R. solani* in potato using hypovirulent isolates has been demonstrated

under realistic conditions in soil indicating the usefulness of this biocontrol system in practice. Competition and induced resistance have been advanced as main mechanism by which hypovirulent isolates suppress disease caused by *R. solani* (reviewed by Herr, 1995). Mycovirus-like RNA has been reported to cause a cytoplasmatically controlled degenerative disease of the pathogen (Castanho & Butler, 1978). This condition was characterized by loss of mycelial pigmentation and reduced sclerotium and infection cushion production. Upon hyphal tip isolation, virulent type lacking dsRNA was recovered from a diseased culture. Viruslike dsRNA is very common in many of the AG in *R. solani*, including AG-3 (Tavantzis, 1994). It can either suppress or enhance the virulence of *R. solani*, depending on the genes present in the dsRNA segments of a strain (reviewed by Rubio et al., 1996). Upon elucidating the virulence-modifying genes they may be of use as a novel transmissible factor that can confer virulence to hypo-virulence by spreading through natural populations via anastomosis. Upon mycoparasitism, *V. biguttatum* may facilitate spreading of the mycovirus within the hyphal network by challenging cytoplasmatic streaming as shown in vitro (Van den Boogert & Deacon, 1994).

Germplasm for resistance is hardly available, hence a breeding programme to control the epidemic development of *Rhizoctonia* is not feasible. Therefore, the development of transgenic potato may feature in future disease management approaches. Antifungal proteins with the ability to inhibit growth in vitro are abundantly present in nature but whether they are involved in the defence response of the host plant is not yet known. For the development of transgenic plants resistant to *R. solani* only one approach has been employed thus far, i.e. the expression of genes encoding chitinases and ß1-3 glucanases (Cornelissen & Melchers, 1993). These antifungal proteins are present in both plants and fungi. The single protein hydrolyses cell walls insufficiently to show an effect but in combination a supposed synergistic interaction results in strong antifungal activity (Ponstein et al., 1994). Apparently, a multi-gene construct is necessary to achieve useful resistance against *R. solani* in planta.

Future prospects

For developing new methods of control fundamental research is needed as follows.

1. Breeding for resistance: Plant breeders need to know the full range of pathogenic variability in field strains to test for disease resistance of potato cultivars or their transgenic progeny. Glucanase chitinases from various origins should be investigated, including novel antifungal proteins, e.g. from the *Rhizoctonia*-specific *V. biguttatum*.
2. Biocontrol using hypovirulent isolates: Hypovirulent isolates compet with virulent isolates for the same infection or nutrient site. Is hypovirulence stable within VCG; can hypovirulence confer into virulent isolates? A strategy of co-inoculation of potato tubers with hypovirulent *R. solani* and *V. biguttatum* may be feasible; hypovirulent *R. solani* are also susceptible for mycoparasitism and co-inoculation may support spread of the obligate mycoparasite along the root/stem system and thus enhance the chance of contact with virulent strains.

3. Biocontrol using dsRNA: How can dsRNA be transmitted between somatically compatible strains (within VCG) and within mycelial networks; is cytoplasm mobilized during sclerotium formation under the influence of the mycoparasite *V. biguttatum* (Van den Boogert & Deacon, 1994)?

Spongospora subterranea

Spongospora subterranea is a member of the Plasmodiophoromycetes, a small class of biotrophic parasites with the most pronounced feature being the plasmodial stage. Four species cause economically important diseases. *Plasmodiophora brassicae* incites club root on Cruciferae. *Polymyxa betae* infects sugar beet and is able to transmit beet necrotic yellow vein virus and *P. graminis* infects members of the Gramineae and is able to transmit wheat soil-borne mosaic virus and barley yellow mosaic virus. For *S. subterranea* two special forms have been identified; *S. subterranea* f. sp. *subterranea* causing powdery scab of potatoes, and f. sp. *nasturtii* causing crook root of watercress. Symptoms on potato tubers are warts and pustules, containing a dusty spore mass. Galls are formed on the roots of both potato and tomato (and some other solanaceous hosts), which vary in both form and size. Under some conditions, cankers form on the tubers of some cultivars. Warts may be formed on the root system in such quantities that the damage leads to wilting.

The impact of powdery scab on the potential value of a potato crop is not easy to assess. The market value of potatoes, especially seed potatoes, is lowered by the presence of powdery scab. Figures concerning rejected (seed) potatoes, destined for export, industry or home consumption are not commonly available, but indicate that 40–60% of a potato crop may be lost to powdery scab. Since resting spores are able to persist in soil for as long as 18 years (Calvert, 1968), and are not influenced by most chemicals, problems are evident, especially in areas where seed potatoes are produced on a large scale and with short rotation period. The presence of powdery scab may force growers to implement crop rotations of at least five years. Recent surveys show that the presence and importance of *S. subterranea* are increasing, not least since most modern cultivars are susceptible. The occurrence of both powdery and common scab (*Streptomyces scabies*) in a potato field is troublesome for potato growers, because irrigation, commonly used to reduce common scab, can increase powdery scab.

Ecology and epidemiology

Life cycle. The life cycle of *S. subterranea* is divided in two phases; the first occurs in the root hairs or root epidermal cells of solanaceous and non-solanaceous plants, the second in roots, stolons or tubers.

Resting spores survive in spore masses, so-called cystosori. Resting spores can germinate and result in primary biflagellate zoospores. After attachment to the surface of the host, these zoospores withdraw their flagellae to form cysts, quickly followed by infection of the host, where plasmodia develop by mitosis. Root hairs as well as roots, stolons and young potato tubers may be infected. Several plasmodia

may develop in one host cell as a result of repeated infections, but usually they coalesce (Kole, 1954). These plasmodia are known as zoosporangial plasmodia, since they eventually form zoosporangia (Ledingham, 1935; Kole, 1954).

The secondary phase in the life cycle of *S. subterranea* is characterized by the development of cystogenic plasmodia, producing the cystosori, in the cortical cells of roots, stolons and tubers in *Solanum* species. Freshly liberated secondary zoospores, released by the zoosporangia in the lumen of the root hairs or in the external environment, swim at random, with the short flagellum in front and the long flagellum trailing behind (Kole, 1954; Kole & Gielink, 1961). Fusion of secondary zoospores of *S. subterranea* has been observed to occur (Cook, 1933; Kole, 1954, 1959). Kole & Gielink (1963) showed that secondary zoospores can infect, after encystment, root hairs, thus giving rise to new generations of zoosporangia - a form of vegetative multiplication. Secondary zoospores infect roots, stolons and tubers of potato or roots of other hosts. The secondary phase is associated with host-cell hyperplasia and hypertrophy, forming gall-like growths on tubers, stolons and roots.

At the end of plasmodial development, the plasmodium changes into a spongy aggregate consisting of numerous resting spores. Resting spores are approximately polygonal in section, hexagonal when closely packed. The spongelike appearance is formed because of cavities in the outer shell and a meshwork of inner channels (Jones, 1978; Lahert & Kavanagh, 1985). The intricate network of inner channels within the cystosorus seen in cross section suggests that all cysts in the inner zone are in contact with external free space (Lahert, 1984; Lahert & Kavanagh, 1985).

Host range. The f. sp. *subterranea* has a wide host range. Zoosporangia are produced in dicotyledons, monocotyledons and gymnosperms. Jones (1970) and Jones & Harrison (1969) found that in some plant families, all species tested were moderate to good hosts (e.g. Solanaceae, Chenopodiaceae, Cruciferae), in others (e.g. Compositae, Umbelliferae) species differed widely in susceptibility, and in a few families (e.g. Gramineae, Caryophyllaceae) species were either poor hosts or did not become infected. However, development of cystosori has not been observed in hosts other than certain *Solanum* species (Janke, 1965; Wenzl, 1985; Würzer, 1965). Susceptibility of different species to infection by *S. subterranea* f. sp. *subterranea* is listed in Jones (1970), Jones (1988) and Jones & Harrison (1969).

The reaction of different *Solanum* species and varieties to infection by *S. subterranea* is well documented by Karling (1968). Several species, indigenous in Mexico and Central and South America were shown to be infected by *S. subterranea*. Moreover, several cultivated species are reported to be infected (Melhus et al., 1916; Würzer, 1965). In addition to this list, Turkensteen (pers. comm.) regularly found powdery scab on tubers of *S. acaule* and *S. curtilobum* in Peru, during the period 1970–1975. These species were reported to possess a high degree of resistance or to be immune, respectively (Karling, 1968). Of all *Solanum* species, *S. tuberosum* is the most important economically, and numerous tests have been made to determine which of its varieties are resistant, immune, or most susceptible.

Modes of dispersal and inoculum sources. The f. sp. *subterranea* originates from the highlands of South America, was introduced with the potato to Europe, and is now worldwide in occurrence (Karling, 1968) by the shipment and importation of infected tubers for food and seed. Several studies (e.g. Ahmad et al., 1991; Blum & Merz, 1993; Hughes, 1980; Nachmias & Krikun, 1988; Soomro et al., 1994; Turkensteen, 1987, 1989) have shown that seed tubers are the main inoculum sources in areas where powdery scab was not previously established. Tsror and co-workers (1993) demonstrated that certified potato seed tubers, imported annually to Israel from western Europe, were always infected by *S. subterranea*. Diriwächter & Parbery (1991) reported that apparently healthy tubers may contain cystosori in lenticels.

It is of particular interest that potato growers sometimes experience problems with powdery scab in regions where potatoes were not grown before (Brereton, 1991) and weed species that serve as hosts for *S. subterranea* may play a role in this context. Weeds which are reasonable hosts of *S. subterranea*, are likely to play a significant role in the persistence of the plasmodiophorid in fields in regions with temperate climates when a continuous supply of roots for zoosporangial generations is available throughout the year. The fact that *S. subterranea* can form functional zoosporangia in *Lolium perenne* is of special interest for the epidemiology of the plasmodiophorid. In the absence of a host, resting spores serve as survival structures, but zoospores and zoosporangia may overwinter in host tissue as well (White, 1954). If hosts other than *Solanum* species are found in which cystosorus formation occurs, these could play a significant role in the persistence of the plasmodiophorid.

The initial inoculum level seems to be a major factor for incidence of powdery scab (Blum & Merz, 1993); however, not all researchers found a clear correlation between higher inoculum levels and increasing disease (e.g. Christ, 1989). Merz (1989) showed that root hair infection increased with a higher density of cystosori in soil. The main source of inoculum for a new potato crop in areas where powdery scab is present seems to be existing soil infestation, considering the general low tolerance of powdery scab on seed potatoes (not more than 1% of tubers with more than five lesions). Kole (1954) and Kole & Gielink (1963) found that planting clean potatoes in infested soil resulted in higher incidence of powdery scab than planting infected potatoes between clean ones in clean soil. Distribution of infested soil is therefore an obvious distribution mode for *S. subterranea.*

Other sources of inoculum may be encountered during the storage of potatoes. De Boer (1983) reported that the dust in potato storage sheds may contain spore balls of *S. subterranea*, thereby acting as an inoculum source.

En ironmental influences. Heavy rainfall and fairly low temperatures as well as damp, poorly-drained and waterlogged soils favour infection and development of the disease. If these conditions are not met, incidence of powdery scab can be high if irrigation is used, as has been shown in the Negev desert in Israel (Nachmias & Krikun, 1988). The effect of high soil water content on the incidence of *S. subterranea* has been studied by Hims (1976); he reported that addition of water in periods with scarce rainfall significantly increased the amount of diseased tubers. Adams and co-

workers (1987) showed that irrigation during the first half of the growing season increased incidence of powdery scab. De Boer and co-workers (1985) and Taylor & Flett (1981) obtained similar results in Australia.

The effect of soil structure and moisture content have also been investigated by several researchers; the results of earlier research are grouped by Karling (1968). Silt-loamy types of soil with poor drainage appear to increase infection, as do soils with large pore spaces, coarse texture and a high water-holding capacity. Mackie & Munro (1986) studied the effect of several cultivation methods on the soil and on the incidence of powdery scab. Powdery scab was more prevalent in soils with 60 to 90% moisture content than in soils with 40% moisture. Kole (1954) found that infection of potato roots and tubers is favoured by moist soil conditions in the early stages of infection and then by a gradual drying of the soil.

Control

Possible control of potato powdery scab is well documented. The use of healthy seed tubers seems to be among the most important control strategies, especially in regions where potatoes have not been grown intensively and powdery scab is not a common disease. However, it must be noted that the plasmodiophorid may be present in low numbers in regions where potatoes are produced without any visible symptoms on potato crops (Blum & Merz, 1993). Therefore, it is important to be able to demonstrate the presence of the plasmodiophorid in soil. Several detection techniques have been described in the literature. In one, tomato seedlings were used as baits for detecting *S. subterranea* in soils (Flett, 1983). The detection level of this technique is high: 10 cystosori per 150 ml soil solution can be detected. Another soil bioassay was described by Brereton (1991), who used a potato microplant bioassay to demonstrate that *S. subterranea* may even be present in soils in which potatoes have never been grown. Techniques have been developed using the enzyme-linked immunosorbent assay (ELISA) to detect cystosori (Harrison & Perry, 1990; Harrison et al., 1993) or zoospores (Wallace et al., 1995) on potato tubers or cystosori in soil (Walsh et al., 1996). If the presence of *S. subterranea* in a soil, destined for potato production, is noted, attention should be given to using the best cultivation techniques and resistant cultivars. In addition to immunosorbent assays for *Spongospora*, Kurppa (1990) developed an ELISA test for detection of potato mop-top virus in potato tubers and soil, using indicator plants as a baiting method.

Cultural methods. The use of bait plants for reducing the numbers of resting spores present in a soil has first been reported by White (1954). The incidence and severity of powdery scab in heavily infested plots could be reduced 79% by cropping *Datura stramonium*. His findings were confirmed by Swiss researchers, Winter & Winiger (1983, 1984). They were able to increase the numbers of powdery scab free seed potatoes by using several bait plants, among others *D. stramonium* and rape seed, *Brassica napus*.

The possibility of soil amendment for reducing incidence and severity of powdery scab has already been studied since the beginning of this century, but the results of these studies were not in agreement (Karling, 1968). The addition of lime as well as

sulphur was believed by some researchers to be effective against the plasmodiophorid, but others reported that the incidence of the disease intensified through addition of conventional lime, chloride of lime, gas lime and calcium cyanamide. Winter & Winiger (1983) studied the effect of lime and lime nitrogen on powdery scab. They found that these compounds increased incidence of powdery scab in some plots, but reduced it in others. Hughes (1980) also found that disease increased with increasing lime gifts, and suggested that lime should be withheld from potato plantings. Cultural measures may reduce incidence of powdery scab. Johnson & Miliczky (1993) suggested that early planting of potatoes in the field resulted in a higher infection by *S. subterranea*, especially when centre pivot irrigation was used, resulting in a high soil moisture.

Chemical and integrated control. Several studies have shown that the cystosori of powdery scab are resistant to most chemical compounds (Bhattacharyya & Raj, 1986; Burnett, 1991; Diriwächter & Gindrat, 1982; Hughes, 1980; Karling, 1968; Lahert et al., 1984; Parker, 1984), including treatment of resting spores with a 0.4% solution of formaldehyde (Diriwächter & Gindrat, 1982). However, on light, sandy soils, chemical control may be possible (Nachmias & Krikun, 1988), possibly due to a better mixing of the chemicals through the soil. Chemical seed tuber treatments may also cause disease reduction in subsequent crops, as shown by Braithwaite and co-workers (1994).

Resistance. It is widely accepted that host plant resistance should be the major method for reducing powdery scab. Initial research concerning resistance of cultivars yielded often contradictory results, mostly because resistance was tested in field experiments, and disease incidence depends largely on environmental influences and initial inoculum, as already has been discussed. However, useful levels of resistance have been reported from various sources (De Boer, 1983, 1991; Black, 1947; Bhattacharyya et al., 1985; Christ, 1987; Eraslan & Turhan, 1989; Jellis & Starling, 1991; Karling, 1968; Kirkham, 1986; Solomon & Wastie, 1988; Wastie et al., 1988; Wastie, 1991). For instance, the cultivars Pirola and King Edward are widely considered to be moderately to highly resistant to powdery scab. Recently, some resistant potato accessions have been identified (Torres et al., 1995). In New Zealand, Genet et al. (1995) reported on a new potato cv. Gladiator with a high resistance to powdery scab.

Field trials are most commonly used for assessing the resistance to powdery scab, although this method has some serious disadvantages, such as the inability to identify sources of heritable resistance, uneven distribution of the plasmodiophorid in the soil and an unpredictable infection rate (Solomon & Wastie, 1988). Assessing resistance under controlled conditions, in greenhouse experiments (De Boer, 1983, 1991; Jellis & Starling, 1991; Makarainen et al., 1994) or in brick-sided beds (Wastie et al., 1988) seems to offer more reliable results, but Solomon & Wastie (1988) express the opinion that more standardized and reliable methods for screening for resistance are needed.

Future prospects

Problems with powdery scab are likely to increase, through build-up of plasmodiophorid populations in soils, export of seed potatoes, use of susceptible varieties, irrigation, and absence of satisfying control methods. The survival of resting spores in soil and of the plasmodiophorid on weeds serves to maintain populations in potato-producing regions, but the contribution of the latter method of survival awaits further research.

There is no information on genetics and genetic variability in populations of *S. subterranea*. For instance, what is the regulation process for plasmodia to become sporangial or cystogenous? The occurrence of mating types of *S. subterranea* is still a mystery. At present, it it not clear if physiological races of this species exist. Recent studies have not been directed towards the question of how heterogeneous are populations of *S. subterranea*? The possibility of variable agressiveness across populations from several localities also remains to be investigated. The way in which the environment triggers resting spores of *S. subterranea* to germinate is unknown. Thus it is hardly possible at present to predict major outbreaks of the pathogen.

Tuber-borne diseases

Epidemiology and control

As noted in the Introduction many of the pathogens affecting potato tubers are tuber-borne and introduced into the soil through planting diseased seed potatoes. Inoculum present on seed is very amenable to control unlike the situation with soil-borne inoculum which can be dispersed throughout the cultivated soil layer. However, it is becoming apparent that inoculum of some pathogens, originally thought to be predominantly tuber-borne, can equally be introduced into the soil, survive and eventually serve as soil-borne inoculum for future crops. This situation can lead to previously unimportant pathogens increasing in importance and causing economic losses that necessitate control measures to be taken. This seems to be the case with *Colletotrichum coccodes* causing black dot. It now seems likely in the UK that almost all the black dot in crops originates from soil-borne inoculum (Read & Hide, 1988; Read, 1991; Read & Hide, 1995a,b; Read, et al., 1995). Similarly, inoculum of *Polyscytalum pustulans* causing skin spot disease of potatoes spreads from diseased seed tubers and infects stem bases, roots and stolons during a growing season. As infected plants senesce sclerotia develop in decaying plant material and can remain viable in soil for considerable periods of time - up to seven years in undisturbed soil. This soil-borne inoculum can then serve as a source of contamination for subsequent crops (Hide & Ibrahim, 1994).

Fungicides are becoming increasingly used on seed tubers to improve the health of daughter tubers as the importance of disease-free planting material is self-evident (Hide, 1986; Hide, 1994). Thiabendazole applied to seed tubers before planting or to daughter tubers after harvest can control silver scurf (*Helminthosporium solani*) and skin spot (*P. pustulans*) in storage. However, the development of thiabendazole resistance in both fungi is now well documented (Hall & Hide, 1994; Carnegie et al.,

1994) and its use as a fungicide during seed production is now discouraged. It is not known whether this will lead to a decline in the incidence of resistance. Since thiabendazole resistant isolates can be found in potato stores it is clear that resistant isolates would have been added to the soil in the planting of treated seed. However, there is as yet no measure of the longevity of resistant isolates in field soils. A further problem with treating seed potatoes with fungicides (thiabendazole or imazalil) is that if seed tubers are subsequently injured during planting then silver scurf is not significantly reduced compared with non-treated tubers.

It is surprising that little mention is made of *Fusarium* species as soil-borne pathogens of potatoes (e.g. see Vos et al., 1989). A description of thiabendazole resistance in *Fusarium sulphureum* (*Gibberella cyanogena*), an increasingly common cause of dry rot in the UK, is given in Hide et al. (1992). A survey of dry rot in commercial potato stores was done and it was found that most rots were caused by *F. sulphureum*, and slightly fewer by *F. a enaceum* and *F. solani* var. *coeruleum*. Almost 70% of the isolates of *F. sulphureum* were resistant to thiabendazole. In similar stores where the crops had been sprayed with the fungicide during loading into store, all the *F. sulphureum* isolates were resistant. It was assumed that the pre-storage treatment was effective against the sensitive isolates. No resistance to thiabendazole was found in *F. a enaceum* or *F. solani* var. *coeruleum* although, with the latter, apparently one resistant isolate has been found in Germany. One isolate of *F. culmorum* was found to be resistant.

As a result of this survey Read & Hide (unpublished) later sampled 10 commercial crops for inoculum or disease, throughout production from the seed tubers to the stored product. Results showed that:

- No *F. sulphureum* was present on the seed.
- *F. sulphureum*, sensitive and resistant to thiabendazole, was present in the dust and soil obtained from the chitting stores.
- *F. sulphureum*, sensitive and resistant to thiabendazole, was present in isolates obtained from field soil sampled before planting.
- Dry rot in the stored product was caused by *F. sulphureum* sensitive and resistant to thiabendazole.

From these observations it was deduced that *F. sulphureum* dry rot in the commercial crops was caused both by inoculum from the stores, and also by inoculum resident in field soil which contaminated the daughter tubers. Apparently in these crops the procured seed did not carry inoculum. However, as inoculum was found in the dust and dirt of chitting stores, this may not have been the case in earlier years.

In the context of this paper, the observations indicate that thiabendazole resistant *F. sulphureum* survives in field soil and, as with *H. solani* and *P. pustulans*, in the dirt in stores left from previously stored crops. It emphasises the need to clean the stores thoroughly between crops but we do not yet know the most effective means of doing this, nor of how long it persists.

Integrated control

It has been shown that the potato tuber is prone to a range of fungal diseases during

the 18-month cycle of production from planting seed tubers to movement from storage (Hide, 1994). Losses occur due to reduction in tuber yield and quality at the time of harvest, but losses increase progressively during storage due to storage rots and further quality changes attributable to disease (Hide & Horrocks, 1994). Thus control of tuber-borne diseases continues to be important in future strategies for improving potato production. However, it is unlikely that any single measure will provide adequate control against the range of disease problems to be encountered during this extended period of time. Thus virtually by definition integrated control measures will continue to be necessary (Table 9) (Hide, 1992). These will include optimising the integration of chemical treatments of seed with rotation practices (Hide & Read, 1991), within season cultural practices such as irrigation (Hide, 1987; Adams et al., 1987) and harvesting practices known to influence storage diseases (Hide et al., 1994a,b,c). There is also now the option of further integrating cultural methods with biological control using fungal and bacterial antagonists.

Conclusions

Although many of the biological and pathological features of soil-borne plant pathogens are reasonably characterised, there are still many gaps in our knowledge as this review has attempted to highlight. Improved detection methods and a realistic basis for biological control must be established for most of the pathogens considered. It should also be borne in mind that disease situations can dramatically change as shown by the new sexual populations of *Phytophthora infestans* in Europe and elsewhere in potato growing regions of the world, and the apparent ability of *Pseudomonas solanacearum* to survive in temperate climates.

There is a need to base disease management on agronomic practices. In many cases, control of soil-borne pathogens can be achieved by integrated crop management (Van Loon, 1992) and most notably by wide rotations. However, economical constraints limit the possibilities to change current cropping practices. For instance, any move to shift continuous potato cropping in many areas of North America, which contributes dramatically to the problems with soil-borne pathogens and which involves regular chemical soil disinfestation, to rotations with other crops would entail massive costs. However, environmental costs of current agricultural practices should also be taken into account. For this it is necessary to calculate the direct and indirect costs of integrated crop management and the costs of changing the current farming system.

Modelling has long played a role in determining research needs in potato production, especially crop physiological modelling (Haverkort & MacKerron, 1995). There are still few models that have been implemented or directly used in practice. Disease management models, similarly, have rarely been implemented (Butt & Jeger, 1985), although there has now been considerable work on the basic ecology and epidemiology of soil-borne fungal pathogens (Gilligan, 1985, 1990).

Prospects for control of soil-borne fungal pathogens are reviewed in this paper: the most realistic if unsurprising assessment is that no single method of control will lead

Table 9. Significance of main effects and 2-factor interactions in the development of silver scurf and black dot on stored tubers (Hide, 1992).

	Silver scurf			Black dot		
	1987	1988	1989	1987	1988	1989
Seed treatment	***	***	***	ns	***	***
Seed size	***			***		
Seed stock	***	*		ns	ns	
Irrigation		***	**		***	***
Harvest date	*	***	***	***	***	***
Curing conditions	***	***	*	*	***	ns
Seed treatment/						
irrigation		*	***		ns	**
harvest date	ns	***	***	ns	ns	ns
curing	*	***	ns	ns	**	ns
Seed size/						
harvest date	ns			**		
Seed stock/						
seed treatment	**	ns		ns	ns	
harvest date	ns	**		ns	ns	
Irrigation/						
harvest date		*	ns		***	**
curing		*	**		***	ns
Harvest date/						
curing	*	***	*	ns	***	ns

*, **, *** respectively $P < 0.05$, 0.01 and 0.001; ns, not significant.

to major breakthroughs in the next 5 years or so, and that integrated control involving cultural, genetic (resistance breeding), biological and chemical methods, based on a thorough understanding of the crop-pathogen ecosystem, must form the basis for disease management.

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