Effects of crop rotation on the incidence of soil-borne pathogens and the consequences for potato production

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Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. H. C. van der Plas,
in het openbaar te verdedigen
op donderdag 14 december 1989
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen.

STELLINGEN

1. Verschillen tussen rassen in vatbaarheid of tolerantie voor een bodempathogeen kunnen benut worden om oorzaken van vruchtwisselingseffecten op te sporen.

   -Dit proefschrift.

2. De mening, zoals onder andere verwoord in het NRLO-rapport nr. 89/17, dat *Rhizoctonia solani* een persistent niet specifiek pathogeen is, is onjuist.

   -Dit proefschrift.

3. Hoewel *Colletotrichum coccodes* veel voorkomt in aardappelgewassen kunnen negatieve vruchtwisselingseffecten zelden mede aan deze schimmel worden toegeschreven.

   -Dit proefschrift.

4. Een snellere en intensievere beworteling van een aardappelplant vergroten de kans dat deze wordt geïnfecteerd door de schimmel *Verticillium dahliae*.

   -Dit proefschrift.

5. Verruiming van de vruchtwisseling heeft meer gevolgen voor het teeltsysteem dan alleen het beheersen van bodempathogenen.

6. De belangrijkste oorzaak van lage opbrengsten van rogge geteeld in een hoge frequentie is het verhevigd optreden van de halmdoder (*Gaeumannomyces graminis*).

   -Scholte, K. & L.J.P. Kupers. Netherlands Journal of Agricultural Science 25 (1977): 255-262, 26 (1978): 250-266 en 32 (1984): 229-235.

7. In de vruchtwisselingsliteratuur wordt de term 'zelfonverdraagzaam' ten onrechte gebruikt wanneer bedoeld wordt dat een plantesoort als gevolg van het optreden van bodempathogenen teeltfrequentiegevoelig is.

8. Het positieve havereffect op de opbrengst van wintertarwe en zomergerst, zoals gesignaleerd door Grootenhuis e.a., moet worden toegeschreven aan de slechte waardplantgeschiktheid van haver voor de halmdoder (*Gaeumannomyces graminis*).

-Grootenhuis, J.A., J.K. Mulder en H. Schuller. Instituut voor Bodemvruchtbaarheid Haren-Gr. Rapport 4-79: 89 pp.

9. Dat weinig haver werd verbouwd op de Drentse essen in de periode 1650 - 1900 moet deels worden toegeschreven aan een heftig optreden van het havercysteaaltje (*Heterodera avenae*).

-J. Bieleman: Boeren op het Drentse zand 1600-1910. Landbouwuniversiteit, Wageningen en HES Uitgevers B.V., Utrecht (1987): 835 pp.

10. Ook bij gelijke stengeldichtheid kan de sortering van de aardappelopbrengst worden beïnvloed zonder dat het opbrengstniveau wordt veranderd.

11. Rasverschillen in fysiologische verouderingssnelheid van aardappelpootgoed kunnen met een eenvoudige toetsmethode worden opgespoord en dienen als raseigenschap in de Beschrijvende Rassenlijst voor Landbouwgewassen te worden vermeld.

12. Bij de huidige stand van de patrijs dient de jacht op deze vogelsoort te worden verboden.

13. Het doelbewust uitdunnen van populaties van wildsoorten, die een grote bedreiging vormen voor het op een redelijk niveau handhaven van andere inheemse diersoorten, is een verdedigbare beheersmaatregel.

Proefschrift van K. Scholte
Effects of crop rotation on the incidence of soil-borne pathogens and the consequences for potato production.
Wageningen, 14 december 1989

WOORD VOORAF

Dit proefschrift zou nimmer tot stand zijn gekomen als het mij ontbroken zou hebben aan deskundige en enthousiaste hulp van anderen.

In de eerste plaats ben ik zeer veel dank verschuldigd aan mijn promotoren Prof. Ir. L.J.P. Kupers en Prof. Dr. Ir. P.C. Struik. Prof. Kupers is de grote stimulator geweest om op de vakgroep Landbouwplantenteelt en Graslandkunde onderzoek te gaan verrichten op het gebied van de vruchtwisseling en hij heeft mij de ruimte gegeven dit onderzoek uit te voeren. Tijdens de onderzoeksfase heeft zijn enthousiasme zeer stimulerend en zijn diepzinnig inzicht zeer verhelderend gewerkt. Prof. Struik heeft mij aangespoord tot het schrijven van dit proefschrift. Beiden ben ik zeer erkentelijk voor het kritisch doornemen van de manuscripten en voor suggesties ten aanzien van veranderingen. Ook Dr. Ir. J. Vos dank ik voor de aanbevelingen na het doornemen van manuscripten.

Het onderzoek zou heel wat bescheidener van omvang zijn geweest als niet doctoraal studenten en stagiairs in zo'n ruime mate hadden bijgedragen als het geval is geweest. Zonder ook maar enigszins te kort te willen doen aan bijdragen van studenten en stagiairs aan vruchtwisselingsonderzoek anders dan in dit proefschrift is vermeld, beperk ik mij tot het noemen van die namen welke direct van betekenis zijn geweest voor de inhoud van dit proefschrift. Mijn dank gaat daarom uit naar Frans Annot, Lammert Bastiaans, Wim de Boo, Simon Bosselaar, Meeuwie Dortmond, Hanneke Elema, Katja Gehem, Harm Groeneweg, Harry Hansma, Lothar Hoekstra, Henk Jansen, Han Kavelaars, Johan Klompe, Metske Lootsma, Luc Mangnus, Rien Nijboer, Ton Ploeg, Nico Schutter, Annelies Sleutel, Werner Smeelen, Aad Spaans, Chris de Visser en Rob de Vries.

Voor de aanleg, uitvoering en verzorging van veldproeven ben ik zeer veel dank verschuldigd aan de medewerkers van het proefbedrijf van de vakgroep onder leiding van Ing. L.A. Mol. Eénmaal een fout gemaakt in een vruchtwisselingsproef kan voor jaren fataal zijn. Gelukkig heeft deze situatie zich niet voorgedaan. Dat is niet in de laatste plaats te danken aan de inzet en toewijding van dhr. L. Haalstra, die niet alleen bij de uitvoering van proeven een zeer belangrijke bijdrage heeft geleverd, maar ook bij het verzamelen en verwerken van gegevens.

Dhr. J.C.M van der Pal bedank ik voor zijn grote inzet en toewijding, ook in vele weekenden, bij de uitvoering van de pot- en containerproeven. Ook de medewerkers van het proefbedrijf de Ir. A.P. Minderhoudhoeve ben ik zeer erkentelijk voor de uitvoering van de vruchtwisselingsproef op dit bedrijf.

Ten aanzien van de planteziektenkundige aspecten bij het onderzoek heb ik vruchtbaar kunnen samenwerken met onderzoekers van andere onderzoeksinstellingen. Zeer intensief en plezierig is gedurende de gehele onderzoeksperiode de samenwerking met Ing. J.J. s'Jacob van de vakgroep Nematologie geweest. De nematodenanalyses zijn volledig onder zijn leiding uitgevoerd. Met Mw. J.W. Veenbaas-Rijks en Dr. Ir. R.E. Labruyère van het Instituut voor Planteziektenkundig Onderzoek (IPO) heb ik zeer aangenaam mogen samenwerken, waardoor met name de betekenis van netschurft als vruchtwisselingsziekte kon worden benadrukt. Mijn contacten met Drs G.J. Bollen van de vakgroep Fytopathologie hebben in hoge mate bijgedragen tot de resultaten van het onderzoek. Bovendien verschafte hij inoculum van de schimmel *Verticillium dahliae* voor potproeven en maakte hij het mogelijk dat de bereiding van selectieve media voor schimmels op het laboratorium van Fytopathologie kon plaatsvinden. Daarom wil ik ook de medewerkers van deze vakgroep, die studenten bijgestaan hebben bij de bereiding van deze media, bedanken voor hun diensten. Drs G. Jager en dhr. H. Velvis van het Instituut voor Bodemvruchtbaarheid (IB) verschaften inoculum van de schimmel *Rhizoctonia solani* en adviseerden bij opsporingsmethoden van de antagonist *Verticillium biguttatum*. Met Ing. O. Hoekstra en Ir. J. Lamers van het Proefstation voor de Akkerbouw en de Groenteteelt in de Vollegrond (PAGV) werd veelvuldig overleg gevoerd en bovendien stelden ze grond, afkomstig van 'hun' vruchtwisselingsproefvelden, beschikbaar voor potproeven.

Mw. J. Burrough-Boesch heeft zeer zorgvuldig de Engelse teksten gecorrigeerd. De heren G.C. Beekhof en H.H.W. van Lent verzorgden met grote accuratesse de tekeningen en dhr. K. Wind de afbeelding van het omslag.

Niet in de laatste plaats gaat mijn dank ook uit naar mijn gezin. Mijn vrouw Djoeke stond toe dat veel van mijn 'vrije' tijd in de avonduren en de weekends opging aan het schrijven van dit proefschrift. Bovendien zorgde zij ervoor dat ik mij steeds op tijd kon ontspannen. Mijn kinderen Karin en Marcel hebben vaardig een aantal manuscripten getypt.

Veel nuttige contacten zijn er geweest met talloze anderen welke niet met name zijn genoemd, maar die via discussies in werkgroepen en daarbuiten mij van nuttige adviezen hebben voorzien. Hen wil ik hiervoor hartelijk danken.

Het LEB-Fonds ben ik erkentelijk voor de subsidie die werd verleend voor het drukken van dit proefschrift.

In vruchtwisselingsproeven worden effecten van rotaties pas merkbaar nadat de rotaties meerdere cycli hebben doorlopen. Daarom is vruchtwisselingsonderzoek altijd langdurig onderzoek. Bovendien zijn de niveaus van effecten sterk jaarafhankelijk door verschillen in weersgesteldheid. De

groei en ontwikkeling van gewassen en van bodemorganismen is sterk afhankelijk van temperatuur(fluctuaties) en neerslag (bodemvochtgehalte). De groei van gewassen en het optreden van ziekten en plagen moest derhalve jaarlijks consequent worden vervolgd. Daarom ben ik dankbaar dat zovelen bereid zijn geweest met volle overgave aan dit onderzoek mede te werken.

ABSTRACT

Scholte, K., 1989. Effects of crop rotation on the incidence of soil-borne pathogens and the consequences for potato production. Doctoral thesis, Wageningen, X + 143 pp., Eng. and Dutch summ.

This thesis describes the effects of various rotations on the growth pattern, yield and quality of potato and on the incidence of soil-borne pathogens, other than potato cyst nematodes (*Globodera* spp.), associated with potato. These rotations differed in the frequency of potato and in the crops with which the potato crop was rotated.

The effects of the rotations depended greatly on the soil type. Lower yields of potato in short rotations were mainly caused by *Streptomyces* spp. (causing netted scab), *Rhizoctonia solani*, *Verticillium dahliae* and, on sandy soil, also by root-knot nematodes (*Meloidogyne hapla* and *M.chitwoodi*). Rotation effects were indirectly influenced by the root-lesion nematodes *Pratylenchus thornei* and *P.neglectus*, and under special conditions, also by *Colletotrichum coccodes*. The susceptibility and tolerance of potato cultivars to these pathogens and synergistic interactions between the various pathogens largely determined the final yield depressions in the short rotations.

Keywords: aldicarb, antagonism, black scurf, *Colletotrichum coccodes*, common scab, cropping frequency, crop rotation, ethoprophos, *Fusarium tabacinum*, girth scab, granular nematicides, *Meloidogyne hapla*, *M.chitwoodi*, netted scab, oxamyl, *Pratylenchus neglectus*, *P.thornei*, *Rhizoctonia solani*, russet scab, *Solanum tuberosum*, soil-borne pathogens, stem canker, *Streptomyces scabies*, synergism, *Verticillium dahliae*, *V.biguttatum*

Reference to the contents of Chapters 2 to 10 should be made by citing the original publications.

NOTE

The papers included in this thesis have been published in, are in press by, or have been submitted to Potato Research. However, as presented in this thesis they differ from the original papers in four ways:

1. the German and French translations of summaries, tables and figures have been omitted;

2. the acknowledgements are now given in the 'Preface' (Woord vooraf);

3. the 'References' of the individual papers have been amalgamated into one list;

4. The 'keywords' of the individual papers have been combined into one list at the end of the 'Abstract'.

I thank the editorial board of Potato Research for its permission to include these papers in this thesis.

CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

High cropping frequencies increase problems with soil-borne diseases and pests. In many crops, cyst nematodes have become a problem: e.g. *Globodera rostochiensis* and *G.pallida* attack potato, *Heterodera schachtii and H.trifolii* f.sp. *betae* attack sugar beet and *Heterodera avenae* attacks cereals. Other soil-borne pathogens also cause problems. To prevent large-scale damage from these pathogens, various measures are taken to reduce soil infestation.

In the Netherlands the cropping frequency of potato is regulated by law, in order to control the cyst nematodes. The frequency of cultivation of potato on the same field is limited to only once in every four years and from 1997 onwards will be limited to only once in every five years. However, farmers are allowed to grow potato more frequently on the same field if nematode-resistant cultivars are grown and/or the soil is disinfected with nematicides. Therefore, rotations with 33 % and even 50 % potato are not uncommon in the Netherlands. However, in many cases when pesticides are frequently applied to the soil their efficacy declines because the soil microflora becomes adapted to them resulting in an accelerated transformation (Smelt et al., 1987 and 1989). Moreover, the extensive use of chemicals in agriculture is becoming increasingly unpopular among consumers, partly because of the proven or suspected effects on the environment. In many cases frequent cropping of resistant cultivars makes it more likely that the pathogen will break through the resistance.

The cultivation of crops in long-term rotations seems to be one of the most effective and accepted measures of controlling soil-borne diseases. However, the limited number of arable crops that can be grown on a large scale, the increased size of farms, specialization, mechanization and economic pressure mean the demise of rotations with such a low cropping frequency that they can provide optimal growing conditions for each crop. Moreover, crop rotation does not always control soil-borne pathogens, because some of these pathogens have a wide host crop range or survive in the soil for many years.

So, using really long-term rotations to prevent the incidence of soil-borne pathogens does not seem to be realistic. The control of these pathogens by crop rotation should be integrated with the use of resistant cultivars, an efficient and limited use of pesticides and, perhaps in the future, by biological control using antagonists of the pathogen. Other cultural practices should also be included in the programme, such as a well-balanced cropping sequence within a rotation, disease-tolerant cultivars, soil cultivation and weed control, but also hygienic measures, organic manure, catch crops and adequate irrigation.

To be able to apply all these factors in a well-integrated control and management programme, the behaviour of plant pathogens in soils and their effects on plant growth must be well understood. Therefore, in 1979 a research programme was started to investigate the effects of crop rotation on crop growth and yield of potato and certain other crops and, because much research had already been done on cyst nematodes, on the long-term development of soil-borne pathogens other than these notorious nematodes. With this aim, three different crop rotation experiments were laid out in 1979. Because soil texture may affect the occurrence of pathogens, one experiment was carried out on a light, coarse sandy soil with potato, sugar beet, silage maize and barley as test crops, one on a richer sandy soil with silage maize as test crop, and one on a marine clay soil with potato as test crop. In each of these experiments the test crops were grown continuously on the same plots and/or in 1:2 rotations (the test crop every second year) and these rotations (for convenience, continuous cropping is designated as a rotation) were compared with a control rotation, in which the test crop was grown only every fourth or fifth year on the same plot.

Besides these three crop rotation experiments, other field experiments were carried out with the aim of studying relations between specific soil-borne pathogens and the plant growth of the test crops. Pot and container experiments were also carried out to detect soil pathogens, to study the effects of soil pathogens on plant growth and to study the interactions between different soil-borne pathogens and between such pathogens and other factors. For these experiments, soil was inoculated with cultures of well-determined pathogens or soil was taken from the three crop rotation experiments, from other crop rotation experiments in the Netherlands and from farmers' fields and treated with selective pesticides or grown with a number of cultivars that differed in resistance to diseases.

This thesis deals solely with the effects of crop rotation on growth and yield of potato and on pathogens associated with the potato.

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CHAPTER 2

POTATO GROWING IN SHORT ROTATIONS AND THE EFFECT OF *STREPTOMYCES* SPP., *COLLETOTRICHUM COCCODES*, *FUSARIUM TABACINUM* AND *VERTICILLIUM DAHLIAE* ON PLANT GROWTH AND TUBER YIELD

K. Scholte, J.W. Veenbaas-Rijks and R.E. Labruyère

Summary

The yield of potatoes decreased as the frequency of growing this crop in a rotation increased, even in the absence of well-known soil pathogens e.g. *Globodera* spp. Soil disinfection with methylbromide or pasteurization at 60 °C with steam for 30 minutes eliminated the rotation effect on yield, suggesting that it was caused by a complex of microbial pathogens. Organisms thought to belong to the complex were *C.coccodes*, *F.tabacinum*, *V.dahliae* and *Streptomyces* isolates causing russet (netted) scab. Their effects on growth and yield were studied in non-sterilized soil that had never carried a potato crop before. *V.dahliae* decreases the yield of susceptible potato cultivars, *C.coccodes* may cause damage only late in the growing season in weakened plants. In the highly susceptible cv. Amethyst yield loss by *V.dahliae* was almost doubled in the presence of *C.coccodes*. *F.tabacinum* did not influence growth and tuber yield neither singly nor in combination with other pathogens. The *Streptomyces* isolates cause extensive root damage and yield loss in susceptible potato cultivars.

Introduction

Growing potatoes at increasing frequencies in a rotation may lead to substantial yield losses even in the absence of pests or pathogens well known to reduce tuber yield, e.g. *Globodera* spp. Hoekstra (1981) reported tuber yield losses of 15 % in a 1:3 (every third year) and 6 % in a 1:4 rotation compared to yield in a 1:6 rotation on marine clay. Lamers (1981) noted 30 % loss by continuous cropping compared to a 1:3 frequency. Scholte (unpublished) found on both sandy soil and marine clay 30 % yield loss of tuber weight when potatoes were grown continuously and 15-20 % when grown in a 1:2 frequency compared to a rotation frequency of 1:5. Roth et al. (1981) analysed the effects of frequency of cropping potatoes in twelve rotations in fields none of which were infested with cyst nematodes. The average yield loss in a 1:4 frequency was 3.2 %, compared to a 1:8 frequency. When 1:3, 1:2, 2:3, 3:4 and 1:1 frequencies were compared to 1:4, yield decreases were 2.4, 7.9, 14.4, 18.0 and 30.2 %, respectively. O'Sullivan (1978) found 27 % and McDole and Dallimore (1978) 14 % yield loss comparing continuous cropping and a 1:2 frequency. Emmond and Ledingham (1972) compared continuous cropping with a 1:3 frequency and found 19 % yield loss.

The percentage yield reductions cited above all refer to total tuber yield, but real losses of marketable product are higher because shortening the rotation also leads to small, poorly shaped tubers.

In preliminary pot experiments an increase in soil pathogens was identified as a possible cause of yield losses of potatoes associated with short rotations. We therefore investigated the pathogenicity of some soil fungi (*Colletotrichum coccodes*, *Fusarium tabacinum* and *Verticillium dahliae*) and actinomycetes (*Streptomyces* spp. causing russet scab, and their interactions, in a series of pot experiments. *C.coccodes*, *V.dahliae* and the *Streptomyces* spp. are known pathogens of the potato plant; *F.tabacinum* was included because this fungus is strongly stimulated by potato growing (van Emden, 1972) and can be isolated in large numbers from potato roots (our observations, unpublished).

Materials and methods

Experiment 1, 1977

For all experiments, soil was taken from the crop rotation field experiment 'De Schreef' in the polder East Flevoland (Hoekstra, 1981) where, since 1962, 14 rotations with different frequencies of a number of agricultural crops are compared in such a way that every crop in a rotation is grown in each year. Rotation and crops grown in 1962 (and then successively in the sequence given) were as follows:

Rotation 1: flax-grass seed-rape seed-spring barley-peas-winter wheat
Rotation 3d: spring barley-grass seed-sugar beet
Rotation 5b: potato-grass seed-sugar beet

For Experiment 1, soil from rotation 1 was collected after the rape seed crop and from rotation 3d and 5b after the sugar beet crop. Each soil was sieved and thoroughly mixed before applying three soil treatments:

C = no treatment;

M = disinfection with methylbromide;

S = sterilization with steam at 100 °C for one hour.

Black plastic pots (5.8 l) were filled with the treated soil and placed in a glasshouse held at 18/10 °C day/night temperature for 13 weeks and then at 24/18 °C for 7 weeks under natural light conditions.

Eight pots of soil x treatment were planted on 21 April with a 13-g singly sprouted tuber, cv. Bintje, previously disinfected with ethylmercurybromide (Aardisan, 4 % a.i.; tubers were immersed for 5 minutes in a 0.3 % solution of the trade product). The following total amounts of nutrients were applied per pot, apportioned over four applications from the planting date to 10 weeks after planting: 3780 mg N, 930 mg P, 4485 mg K, 360 mg Mg and 10 ml of a trace element solution containing 20 g $MnSO_4 . H_2O$, 30 g H_3BO_3, 5 g $ZnSO_4 . 7H_2O$, 1 g $CuSO_4 . 5H_2O$ and 1 g $Na_2MoO_4 . 2H_2O$ per l water. The amounts of the main elements were based on expected dry matter yield of haulm and tubers and their mineral content.

Experiment 2, 1978

Soil was again collected from rotations 3d and 5b after the sugar beet crop, prepared as before, and treatment P (soil pasteurization at 60 °C with steam for 30 minutes) applied as well as treatments C and M.

Black plastic pots (5.8 l) were filled and placed in white enamel pots, which were placed outdoor during the summer months. Cultivar and tuber treatment (10 replicates) were as in Experiment 1, the planting date was 18 April and the total amounts of nutrients applied per pot, added as in Experiment 1, were: 3780 mg N, 775 mg P, 5265 mg K, 360 mg Mg and 10 ml of the trace element solution.

Experiment 3, 1981, with Streptomyces spp., C.coccodes and F.tabacinum

In Experiment 2, roots of cv. Bintje growing in soil of rotation 5b showed brownish lesions from which 60 streptomycetes were isolated. From these, 30 were selected on visual characteristics as isolates possibly causing russet scab. Their pathogenicity to the potato plant was tested as described by Labruyère (1971). Ten of the isolates were pathogenic to cv. Bintje and two of the most pathogenic ones, both tyrosinase-positive, were selected and used in Experiments 3 and 4. No attempt has been made to identify these isolates any further and, although Labruyère (1971) states that tyrosinase-positive russet scab isolates may be assigned to *Streptomyces scabies*, the isolates might have belonged to two different species.

These two isolates and two isolates of each fungus were used to inoculate nonsterilized marine clay from 'De Schreef', rotation 3d, where since the reclamation of the polder in 1958 potatoes never had been grown. Inoculum of each organism was added to and mixed thoroughly in the soil in a 1:100 ratio (volume/volume) and check pots consisted of soil with killed inoculum of all three organisms. Each species was used singly or in all combinations and when a given organism was omitted from a treatment and equal volume of a sterilized culture of that organism was added instead. Singly sprouted 14-g tubers, cv. Bintje, disinfected as in Experiment 1, were planted singly on 20 August in 5.8-l black plastic pots (10 per treatment) placed in white enamel pots that remained in the open until 17 September. Then they were transferred to a glasshouse at a fluctuating day temperature (3 h, 18 °C; 6 h, 26 °C and 3 h, 18 °C) and a constant night temperature (12 h, 10 °C). During daytime, additional light was supplied by 400-W high-pressure mercury lamps. The total amounts of nutrients applied per pot, added as in Experiment 1, were: 2353 mg N, 683 mg P, 4173 mg K, 336 mg Mg and 9 ml of the trace element solution.

Experiment 4, 1982, with Streptomyces spp., C.coccodes and V.dahliae

Inoculum of each organism was added to and mixed thoroughly in non-sterilized soil from rotation 3d in a 1:200 ratio (volume/volume). The organisms were used singly and in combinations following the same procedure as in Experiment 3. Singly sprouted 14-g tubers, cvs Bintje, Amethyst and Mirka, disinfected as in Experiment 1, were planted singly on 29 April in 5.8-l black plastic pots (6 per treatment) placed in white enamel pots in the open field. The total amounts of nutrients applied per pot, added as in Experiment 1, were: 3696 mg N, 930 mg P, 5382 mg K, 432 mg Mg and 12 ml of the trace element solution. The relative genotype susceptibility relationships are given in Table 1.

Analyses

In Experiments 1 and 2, total dry matter yield is a summation of dry haulm weight and dry tuber weight. In Experiment 3, during the growing season the height of the plants was recorded periodically and their degree of maturity estimated by counting the numbers of dead leaves. On 21 October, two pots per treatment were harvested for interim observation of the underground plant parts.

For determining the uptake of nutrients in Experiments 1 and 2, haulms

Table 1. The relative susceptibility of Bintje, Amethyst and Mirka to *Streptomyces* spp., *V.dahliae* and *C.coccodes*.

	Streptomyces spp.[a]	*V.dahliae*	*C.coccodes*
Bintje	very susceptible[b]	susceptible[b]	unknown
Amethyst	resistant[b]	very susceptible[b]	unknown
Mirka	resistant[b]	tolerant[c]	unknown

[a] *Steptomyces* spp. standing for the russet (netted) scab isolates.

[b] Derived from pot experiments at the Department of Field Crops and Grassland Science.

[c] Krikun & Orion (1979).

and tubers were dried at 105 °C for 14 h, ground and thoroughly mixed. Subsamples were analysed after digestion in sulphuric acid and hydrogen peroxide. Potassium was determined with a flame photometer and phosphate and nitrogen were measured with a colorimeter.

Inoculum

The *Streptomyces* isolates were cultured in 50-ml lots of potato-glucose-peptone solution (200 g of peeled tubers boiled in 1 l water for 1 h, filtered, and 17 g of glucose and 7 g peptone added) dispensed in 100 ml flat medicine bottles, sterilized at 120 °C for 30 minutes, inoculated with spores and mycelium fragments, and shake-cultured at room temperature (ca 20 °C). Twenty-five ml of culture of each *Streptomyces* isolate was added to 100 g silver sand and the mycelium fragmented by grinding in a mortar. This quantity of mixture was added and thoroughly mixed with the pot soil.

Both *C.coccodes* and *F.tabacinum* were grown in Erlenmeyer flasks containing 50 g of a mixture of Trio pot soil (a pot soil containing 60 % organic material manufactured by Trio BV) and 5 % oatmeal. After sterilizing at 120 °C for 1/2 h on two successive days to ensure death of sporeforming bacteria, the flasks were inoculated with spores and mycelium fragments from 10-day old tube cultures of the fungi and incubated at 22 °C for approximately three weeks.

V.dahliae was cultured in 300-ml Erlenmeyer flasks, each containing 100 ml perlite (granules) + 45 ml Czapec Dox solution sterilized at 120 °C for 30 minutes. Inoculum for each flasks was obtained by adding 5 ml of sterile water to a sporulating 10-day old tube culture of *V.dahliae*, the surface of the culture was gently rubbed with a glass rod and then the tube was gently

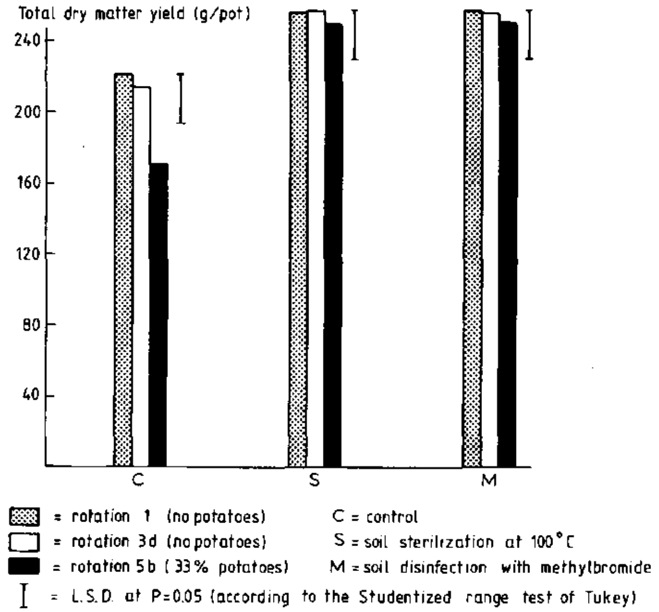

Fig. 1. Total dry matter yield of potato plants as related to rotation and soil treatment. Experiment 1.

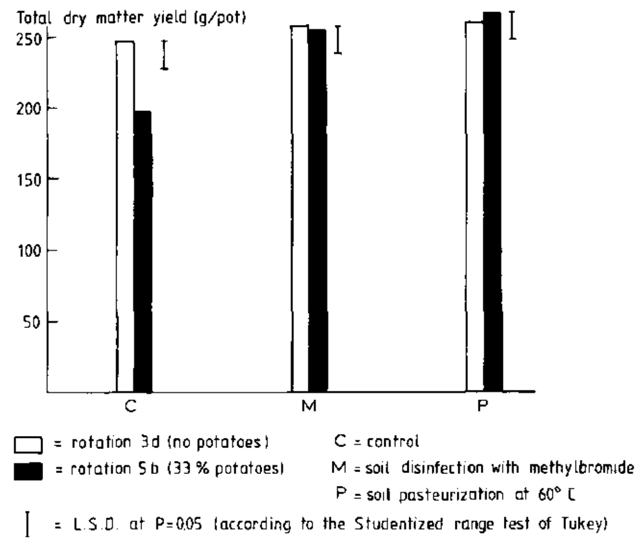

Fig. 2. Total dry matter yield of potato plants as related to rotation and soil treatment. Experiment 2.

shaken to produce a suspension containing numerous spores. The flasks were incubated at 22 °C until the perlite became blackened by numerous microsclerotia and this inoculum was then added in a 1:200 ratio (v/v) to the soil.

When killed inoculum was needed, culture flasks were sterilized at 120 °C for 30 minutes.

Results

Experiments 1 and 2

The production capacity of the untreated soils in rotations 1 and 3d did not differ (Fig. 1); neither soil had been cropped to potatoes. The soil from rotation 5b, which had carried a potato crop once every three years during a 15-year period, had a much lower capacity, but after it had been disinfected with methylbromide or partially sterilized with steam this negative effect disappeared. A similar result was obtained in Experiment 2: the poorer productivity of the soil from rotation 5b, 20 % less than that of the 3d-soil, was restored simply by pasteurization (Fig. 2).

The uptake of nutrients by the plants growing in untreated soil from rotation 5b was not only much less than from the other soils (Fig. 3 and 4) but it was far less than the amount of nutrients given in the fertilizer. However, the uptake was the same as that of the control soil after disinfection, sterilization or pasteurization.

Experiment 3

The *Streptomyces* isolates caused a 14 % loss in tuber yield and decreased tuber numbers (Table 2), whereas *C.coccodes* and *F.tabacinum* influenced neither yield nor tuber numbers. At the beginning of the growing season, plant height was reduced in the presence of the *Streptomyces* isolates (Table 3) and this was associated with a severe attack on the entire root system (Fig. 5). Infection occurred as soon as the roots started to grow and became manifest by the presence of numerous light brown lesions. Fine rootlets were completely destroyed and stem bases, stolons and young tubers were also affected. During the growing season plants tended to recover so that at the end of the growing season their heights were comparable to those of the controls (Table 3) but their senescence was retarded (Table 4).

F.tabacinum had no effect on plant growth; senescence was retarded but at the end of the experiment root health was not different from that of control plants. Initially, *C.coccodes* had no effect on plant growth and at the in-

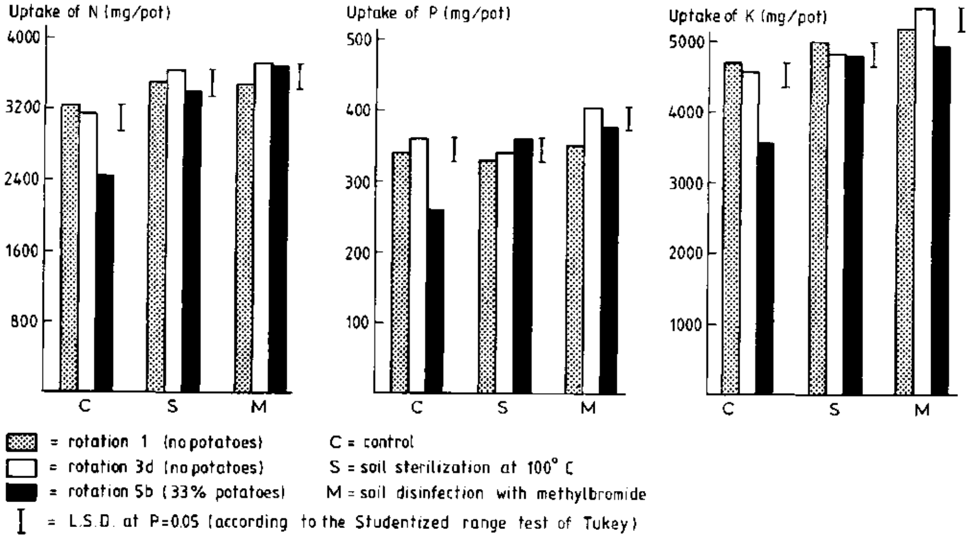

Fig. 3. Uptake of nutrients as related to rotation and soil treatment. Experiment 1.

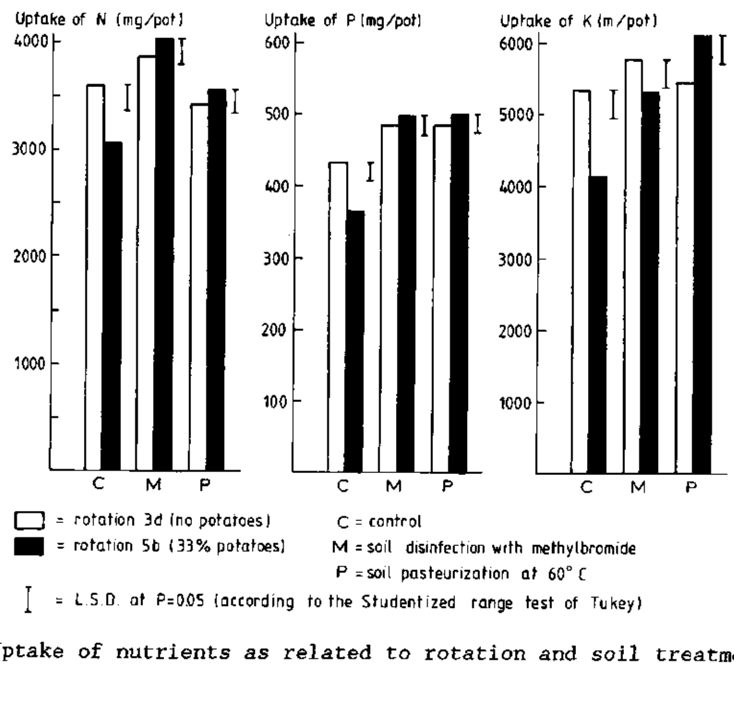

Fig. 4. Uptake of nutrients as related to rotation and soil treatment. Experiment 2.

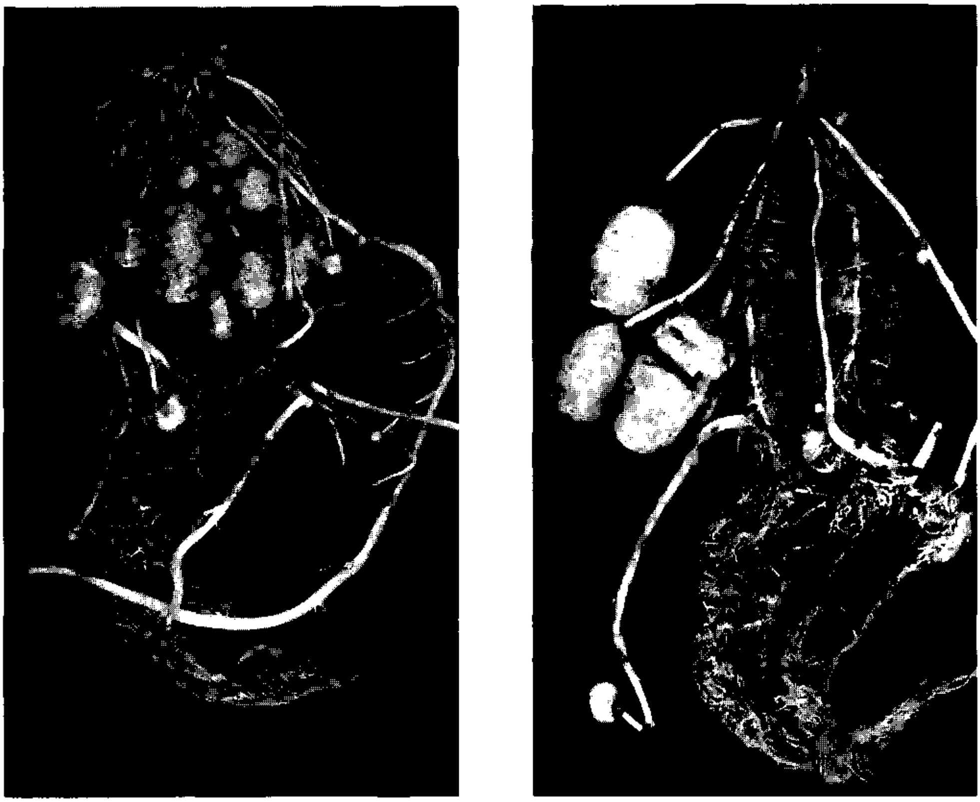

Fig. 5. Plants from Experiment 3. Left: control. Right: russet (netted) scab caused by *Streptomyces* spp.

terim harvest (21 October) the root system was still unaffected. However, at the end of the growing season leaf senescence accelerated (Table 4). At final harvest, *C.coccodes* was present on all underground plant parts, including tubers, showing numerous microsclerotia and there was a greyish discoloration on many roots.

Experiment 4

The addition of *Streptomyces* isolates to the soil caused a yield reduction averaging 7 % in cv. Bintje (Table 5) but not in the resistant cvs Amethyst and Mirka. As in Experiment 3, yield reduction of Bintje was associated with an extensive attack of the underground plant parts, especially of the roots. Again, growth was retarded mainly during the early stages and this was associated with fewer tubers per pot (Table 6). There was no evident interaction

Table 2. Dry matter yield of tubers (g/pot) and number of tubers per pot. Experiment 3.

	Tuber yield				Numbers of tubers			
	So		S1		So		S1	
Fo	117	112	89	103	13.0	17.0	8.7	10.3
F1	114	114	100	102	13.7	14.0	9.3	10.0
Mean	115		99***		14.4		9.6***	

S = *Streptomyces* spp.; F = *F.tabacinum*; C= *C.coccodes*.

o = inoculum sterilized; 1 = inoculum alive.

*** Significantly different from So at P ≤ 0.001.

Table 3. Plant height (cm) at successive dates. Experiment 3.

Date	So	S1	Fo	F1	Co	C1
18/ 9	9.6	8.1**	9.0	8.8	8.5	9.3
25/ 9	14.7	13.2**	14.2	13.7	13.4	14.5
2/10	22.0	19.5**	21.4	20.2	20.3	21.3
9/10	31.3	27.8**	30.3	28.9	29.1	30.1
16/10	35.5	32.2**	34.3	33.4	33.5	34.2
23/10	41.4	38.1**	40.1	39.4	39.5	40.0
30/10	48.1	46.0	47.1	47.0	47.1	47.0
6/11	50.8	50.8	51.0	50.6	51.1	50.6
13/11	51.1	51.8	51.8	51.1	51.8	51.0

Symbols are explained in Table 2.

** 1 significantly different from o at P ≤ 0.01.

Table 4. Number of senescent leaves per plant at successive dates. Experiment 1.

Date	So	S1	Fo	F1	Co	C1
12/11	3.0	1.5***	2.9	1.6***	1.8	2.6*
20/11	4.3	1.9***	3.9	2.3***	2.8	3.4
27/11	10.7	4.2***	8.8	6.0***	6.9	7.9
1/12	16.2	7.4***	14.0	9.6***	10.7	13.0**

Symbols are explained in Table 2.

*, **, *** 1 significantly different from o at P ≤ 0.05, P ≤ 0.01 and P ≤ 0.001, respectively.

Table 5. Dry matter yield of tubers (g/pot). Experiment 4.

Cultivar	0	S	0	V	0	C	0	VC
Bintje	224	209***	225	207***	217	215		
Amethyst	202	200	216	195***	216	219	216	176***
Mirka	242	245	244	243	244	243		

0 = control; S = *Streptomyces* spp.; V = *V.dahliae*; C = *C.coccodes*.

*** Significantly different from control at $P \leq 0.001$.

Table 6. Number of tubers per pot. Experiment 4.

Cultivar	0	S	0	V	0	C
Bintje	13.3	9.8***	11.3	11.8	11.6	11.4
Amethyst	19.5	18.9	20.0	18.4	20.3	18.2
Mirka	15.0	16.4	15.9	15.5	15.3	16.1

0, S, V, C and *** are explained in Table 5.

Table 7. Relation between russet (netted) scab index (0-100) on tubers and frequency of potatoes in the rotation. Field experiment on clay soil.

Crop sequence						Netted scab index 1981	
1976	1977	1978	1979	1980	1981	Bintje	Allerfr. Gelbe
potato[a]	wheat	sugar beet	wheat	barley	potato[b]	23	20
potato[a]	wheat	sugar beet	wheat	potato[a]	potato[b]	64	76

[a] Cultivar Bintje.

[b] Cultivar Bintje and Allerfrüheste Gelbe.

between *Streptomyces* and *V.dahliae* or *C.coccodes* in the three cultivars.

V.dahliae caused a yield decrease of ca. 8 and 10 % in Bintje and Amethyst, respectively (Table 5). The yield of cv. Mirka was not reduced by *V.dahliae*. All three cultivars were unaffected by *C.coccodes* when inoculated singly, but when combined with *V.dahliae*, yield reduction by this fungus in cv. Amethyst was increased from 10 to 19 %.

Discussion

Soil pathogens in relation to short potato rotations

There may be yield losses when potatoes are grown in short rotations even in the absence of potato cyst nematodes (*Globodera* spp.). Experiments 1 and 2 showed that soil disinfection with methylbromide or pasteurization at 60 °C for 30 minutes sufficed to eliminate the adverse effects of short rotations on yield. Preparing the soil by sieving and thorough mixing minimized possible effects of texture between otherwise similar soils from the different rotations. Nevertheless there was a substantial yield loss and decreased uptake of nutrients associated with root systems weakened by soil pathogens in soil that frequently carried potatoes compared to a non-potato soil, indicating the potentially important role of these pathogens.

Which soil organisms are responsible for yield reductions when potatoes are grown in short rotations cannot easily be determined. More organisms than we have investigated may be involved and the complex may differ with other crops and their succession in a rotation, the frequency and cultivar of potato grown, soil texture and moisture, climate and the time of year, and from one soil type to another. Pathogenic organisms may be synergistic, e.g. *Pratylenchus thornei* and *V.dahliae* (Siti et al., 1979) or there may be inhibition by non-pathogens, e.g. *Rhizoctonia solani* by strains of *Verticillium biguttatum* (Jager and Velvis, 1983a).

The complicated interactions between organisms and between organisms and their environment makes it difficult to unravel the whole complex, the more so where the interactions take place in the soil. Direct observation is virtually impossible and understanding such a complicated system can be achieved only step by step.

Fusarium tabacinum

Our research and that of van Emden (1972) shows that when potatoes are grown in short rotations all their roots may be contaminated with *F.tabacinum*. This soil fungus is probably stimulated by potato growing, but in Experiment 3 there were neither lesions on the roots nor yield reductions. It is therefore unlikely that *F.tabacinum* is a pathogen of potato roots.

Streptomyces isolates

In Experiments 3 and 4, the *Streptomyces* isolates reduced tuber yield by 14 and 7 %, respectively. There was no interaction between them and *C.coccodes*, *F.tabacinum* or *V.dahliae*.

Mygind and Begtrup (1970) found a reduction in tuber yield after inoculating plants of cv. Bintje with the russet scab organism, and Bång (1979b) noted 15 % loss in field experiments when seed tubers of cv. Bintje were infected with russet scab; Labruyère (1971) also recorded yield loss in that cultivar.

Root infection by russet (netted) scab organism starts during plant emergence. Later, stem bases, stolons and tubers become infected and develop light brown lesions; root infection is most extensive and fine rootlets are more or less systemically invaded, do not function normally and die off. The superficial tuber lesions develop shallow cracks and ridges in square or pentagonal patterns and large areas of the tuber surface may be affected. Early plant growth is retarded, resulting in an inferior leaf development and plant height. Root development is restricted and fewer tubers are initiated. Plants may later recover when growing conditions are good and this may explain why Bång (1979b) noticed less yield reduction in the south of Sweden compared to the middle and northern parts where the growing season is shorter and chances for recovery are less.

Bång also found low numbers of stems per plant, probably because the seed tubers used were heavily infected resulting in a reduced number of buds developing into sprouts. When infection originates from the soil, sprouting is not always affected.

Yield loss in Experiment 3 was twice that of Experiment 4, perhaps because of differences in the soil moisture content. Labruyère (1971) observed more russet scab under moist conditions during tuberization and the pots of Experiment 3, standing outdoors in a rainy period, initially became wet, whereas those of Experiment 4 had a dry period.

Russet scab can be regarded as a disease associated with short rotations. Scholte (unpublished) observed a substantial increase in russet scab in several field experiments with susceptible cultivars when the rotations were short and the results of one of those field experiments are given (Table 7). Hoekstra (1981) also found more russet scab in cv. Bintje in a 1:3 than in a 1:6 rotation.

The russet scab described in this paper seems to be identical with that described by Mygind (1965, 1970) in Denmark, by Bång (1979b) in Sweden and by Labruyère (1971) in the Netherlands on cv. Bintje. The russet scab described by Harrison (1962) in the US, however, differs in several characteristics from the one described here. Scholte and Labruyère (1985) therefore propose to change the name of russet scab as it occurs in Western Europe to 'netted scab'.

Verticillium dahliae and Colletotrichum coccodes

Our results show that both fungi belong to a complex of organisms which adversely affect the yield of potatoes grown in short rotation. The potato plant is a good host for both fungi and at the end of the growing season they produce large numbers of microsclerotia on all plants parts. Microsclerotia of *V.dahliae* (Coley-Smith and Cooke, 1971) and of *C.coccodes* (Farley, 1976; Blakeman and Hornby, 1966) survive in soil for a long time.

Huisman and Asworth (1976) concluded that once *V.dahliae* has reached a high inoculum density in the soil its reduction under non-host crops is slow. However, Evans and McKeen (1975) recorded a considerable reduction in the number of viable microsclerotia by growing a non-host like oats or by fallow period.

Besides the potato and other *Solanaceae*, *V.dahliae* has many hosts belonging to widely different plant genera (Woolliams, 1966) and growing them may increase or maintain inoculum levels in soil. *Chenopodium album* (Busch et al., 1978; Woolliams, 1966) is an excellent weed host that often occurs extensively in crop rotations with potatoes.

Yield reduction caused by *V.dahliae* depends on cultivar susceptibility (Susnoschi et al., 1975, 1976) and on the population density of certain nematodes, e.g. *Pratylenchus penetrans* (Martin et al., 1982), *P.thornei* (Siti et al., 1979) and *Meloidogyne hapla* (Jacobsen et al., 1979).

C.coccodes is generally considered to be a weak pathogen and according to Schmiedeknecht (1956) lives predominantly on *Solanaceae*. Komm and Stevenson (1978) concluded that infection occurs early in the season and that the seed tuber is usually the source of inoculum; they therefore, doubt the preventive effect of crop rotation. Infection from the seed tuber can be prevented only by early disinfection with organo-mercury compounds (Mooi, 1956), because later the fungus has penetrated too deeply into the tuber tissue to be completely killed.

In our research, *C.coccodes*, when alone, did not adversely affect tuber yield, although at final harvest symptoms of the black dot disease (*C.coccodes*) were present in abundance on roots and the other underground parts and leaf senescence was accelerated. When plants were harvested half-way the growing season no symptoms were observed on the roots. According to Schmiedeknecht (1956) *C.coccodes* has a long incubation period, and Hornby (1968) observed an initial slow colonization of tomato roots that accelerated when flowering started.

No synergism between *C.coccodes* and *Streptomyces* was noticed. *V.dahliae* decreased tuber yield of both Bintje and Amethyst, but not of Mirka in our

Experiment 4. Krikun and Orion (1979) found the last named cultivar to be highly tolerant to *V.dahliae*. On cv. Bintje, no synergism was found between *V.dahliae* and *Streptomyces* or between *V.dahliae* and *C.coccodes*. On Amethyst, however, synergism between the last two fungi did occur and yield loss was nearly doubled compared to the loss caused by *V.dahliae* alone. Amethyst is highly susceptible to *V.dahliae*, showing severe leaf symptoms. Davis and Howard (1976) also noticed synergism of these two fungi on cv. Russet Burbank. Synergism between *C.coccodes* and other pathogens possibly occurs when the other organism tends to express its main effect in the second half of the growing season, as *V.dahliae* does. Any other stress at that time in combination with *C.coccodes* may also cause loss of yield, as shown by Otazu et al. (1978) in the case of heavy rainfall.

Conclusions

1. Yield of potatoes decreases with an increasing frequency of potato crop in the crop rotation even in the absence of *Globodera* spp.
2. The main cause of the yield loss is due to action of other soil organisms.
3. The russet (netted) scab organism (*Streptomyces* spp.) causes a yield reduction in susceptible cultivars by a severe attack on the root system early in the growing season.
4. *C.coccodes* is a weak pathogen that damages potato plants during the growing season only when they are already weakened by other causes, e.g. by an attack of *V.dahliae*.
5. Damage caused by *V.dahliae* is strongly influenced by cultivar susceptibility.
6. *F.tabacinum* is strongly stimulated by potato cropping but causes no damage to the potato plant.

Potato Research 28 (1985) 443-448

CHAPTER 3

NETTED SCAB: A NEW NAME FOR AN OLD DISEASE IN EUROPE

K. Scholte and R.E. Labruyère

Summary

In this first paper it is argued from published descriptions and experimental results, that russet scab in the USA and russet scab in Europe are two different diseases. To resolve this nomenclatural problem in the English language we propose that the name 'netted scab' should henceforth be used for the russet scab in Europe in agreement with the other European common names, viz. the Danish 'netskurv', the Dutch 'netschurft', the Swedish 'Nätskorv' and the German 'Netzschorf'.

Introduction

Both in the USA and in various countries of Europe a type of scab is found that differs in many aspects from common scab caused by *Streptomyces scabies*, although it too is caused by *Streptomyces* species. When European research-workers refer to this deviant scab-type in English they called it russet scab because of certain similarities between it and the American russet scab. From a careful appraisal of the literature and the results of our own research we have concluded that russet scab in Europe and in America are two different diseases. This paper advances reasons for renaming the European russet scab as 'netted scab'. We shall use this new name forthwith.

The occurrence of netted scab in Europe

It is likely that the netted scab found in the Netherlands and described by de Bruyn (1939), Labruyère (1971) and Scholte et al. (1985) is identical with the netted scab (European russet scab) described by Mygind (1965) in Denmark, Bång (1979) in Sweden, Sundheim (1968) in Norway, Salzmann (1960)

Table 1. Differences in characteristics between common scab, netted scab and russet scab.

	Common scab	Netted scab	Russet scab
Tuber attack	superficial to deep	superficial, net structure	superficial
Root attack	mild	severe	not observed
Effect on tuber yield	none	negative	none
Cultivar resistance	quantitative	qualitative	quantitative
Reaction to high soil moisture	attack reduced	attack increased	attack increased
Optimum soil temperature	19-24 °C[a]	13-17 °C[a]	23-27 °C[b]
Respons to frequent cropping of susceptible cultivars	weakly positive	strongly positive	unknown
Tyrosinase reaction	positive	positive/negative	negative

[a] Labruyère (1971).

[b] Harrison (1962).

in Switzerland and Wenzl (1970) in Austria. That all these authors refer to the same disease can be inferred from their descriptions of the symptoms and from the fact that in all these countries mainly cv. Bintje is attacked (except Austria, where cv. Allerfrüheste Gelbe is attacked).

Disease symptoms

The differences between netted scab, russet scab and common scab gives Table 1. Netted scab causes only superficial, brown, netted lesions of the tuber skin that can easily be distinguished from common scab, which generally extends deeper into the tissue but may also produce a more superficial lesion but than without the characteristic net structure. A severe attack of netted scab can be accompanied by growth cracks in the tubers. From Harrison's description (1962) one may conclude that russet scab lesions closely resemble those of netted scab; there is however an important difference in that the netted scab pathogen attacks all underground plant parts, but especially the roots (Labruyère, 1971; Scholte et al., 1985; Mygind, 1965; Bång, 1979). No root lesions have been observed on plants with russet scab lesions on their tubers (Harrisson, pers. comm.) and it is unlikely that this striking symptom has been overlooked by American potato research workers.

The root lesions that accompany netted scab may retard growth of the plant considerably and thus reduce the final tuber yield (Mygind, 1965; Labruyère, 1971; Bång, 1979; Scholte et al. 1985). Such an effect on crop yield is not known for russet scab and does not accompany the attack of common scab either.

Influence of environmental conditions

Lesions of netted scab (Labruyère, 1971) and of russet scab (Harrison, 1962) increase in severity with increasing levels of soil moisture content whereas common scab severity is enhanced by low soil moisture levels. However, there are clear differences in soil temperatures optimum for development of the three forms of scab on tubers (Table 1).

Susceptibility of cultivars

No cultivars are known to be immune to common scab and differences in susceptibility are quantitative. Similarly, Harrison (1962) found that none of the cultivars he tested were immune to russet scab and that differences in susceptibility were also quantitative; he observed no great differences in susceptibility among 15 genotypes. At the Department of Field Crops and Grassland Science, 95 cultivars from the 1982 Dutch Descriptive List of Varieties of Field Crops were investigated for susceptibility to netted scab by planting tubers in naturally infested clay soil in one-litre pots, in 4 replications. Tuber and root lesions always occurred in susceptible cultivars and their amounts were used as a measure of susceptibility; 87 were immune and 8 susceptible to netted scab. The latter group comprised of cvs Bintje, Eba, Climax, Meerlander, Edzina, Désirée, Gracia and Allerfrüheste Gelbe, which was the most susceptible one; cv. Kennebec was immune although it is susceptible to russet scab (Harrison, 1962).

At the same Department, in 1984 the russet scab susceptible cvs Irish Cobbler, Kennebec, Norland and Red Pontiac (Harrison, 1962) were tested for susceptibility to netted scab by planting them in naturally infested sandy

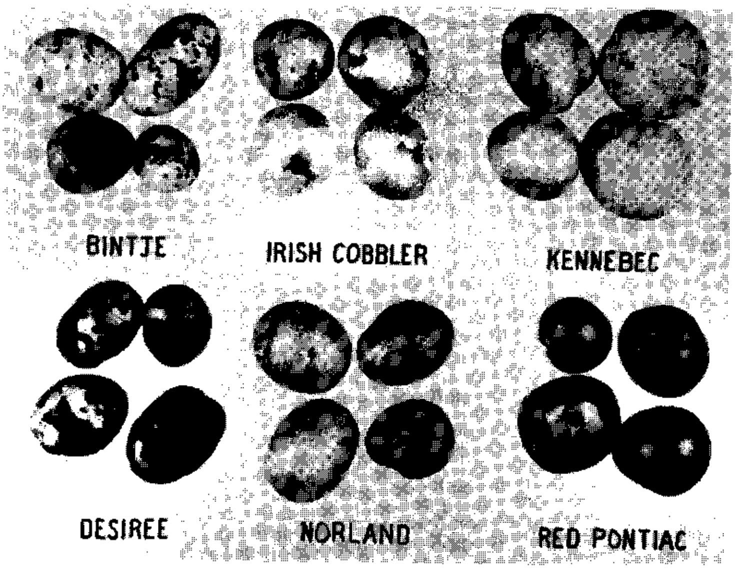

Fig. 1. Tubers of six cultivars grown in soil heavily infested with the netted scab pathogen (*Streptomyces* spp.). Tubers of cvs Bintje and Désirée are affected, but those of cvs Irish Cobler, Kennebec, Norland and Red Pontiac, all susceptible to russet scab, are unaffected.

Fig. 2. Brown infected roots of cvs Bintje and Désirée and white uninfected roots of cv. Irish Cobler, grown in soil heavily infested with the netted scab pathogen (*Streptomyces* spp.)

Table 2. The effect of cropping sequence on the index (0-100) for common scab and netted scab on tubers in three potato cultivars (field trial 1982, split-plot design with four replications).

Scab type	Crop sequence	Scab index[a]		
		Eersteling	Alpha	Bintje
Common scab	wheat - barley - potato	22	26	8
	wheat - potato[b] - potato	22	24	3
Netted scab	wheat - barley - potato	0	0	50
	wheat - potato[b] - potato	0	0	74*

[a] 0 = all tubers free of scab, 100 = all tubers heavily infested with scab.

[b] Cultivar Bintje.

* The netted scab index of wheat-potato-potato (74) differs significantly from that of wheat-barley-potato (50) at $P \leq 0.05$.

soil and clay soil, together with the netted scab susceptible cvs Bintje and Désirée. Tubers and roots of the last two cultivars were attacked by netted scab in both soils but those of the other four cultivars were not attacked in either type of soil (Figs 1 and 2).

In Denmark, Mygind (1965) found that of 13 cultivars tested in 6 trials only cv. Bintje was susceptible to netted scab. Resistance to netted scab is absolute, which means that resistant cultivars are wholly immune. However, Vruggink and Maat (1968) and Labruyère (1972) found that among many isolates of the netted scab pathogen, one was able to cause common scab lesions in cv. Eigenheimer.

The cultivars susceptible to netted scab are also susceptible to common scab and both diseases can occur on the same tuber. However, de Bruyn (1939) found that as a result of repeated cropping of Bintje on the same field, the incidence of netted scab progressively increased whereas that of common scab decreased, ultimately to zero. A similar effect was observed at the Department of Field Crops and Grassland Science in Wageningen: cvs Eersteling and Alpha, which are immune to netted scab, were severely attacked by common scab whereas cv. Bintje, equally susceptible to both common and netted scab, was scarcely affected by common scab while its tubers were severely attacked by netted scab (Table 2).

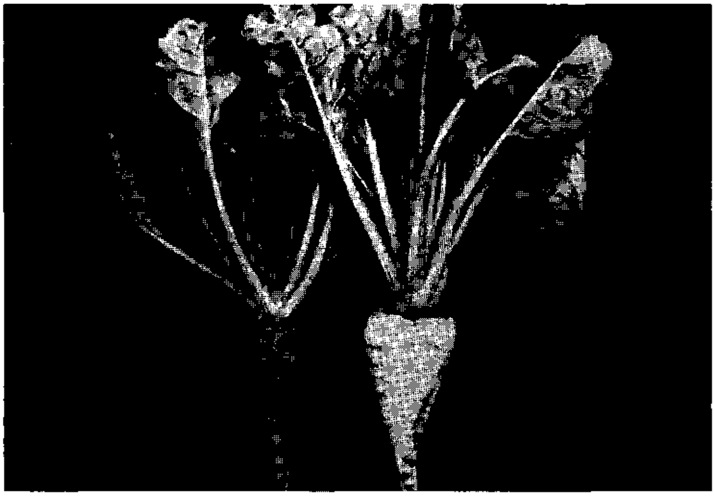

Fig. 3. Sugar beet cv. Monohil grown in soil heavily infested with the netted scab pathogen (left) and grown in the same type of soil with only a light infestation (right).

The pathogen

Labruyère (1979) observed that in the Netherlands most of *Streptomyces* causing netted scab that were isolated from Bintje corresponded with the description of *Streptomyces scabies*. When isolating possible pathogens, he selected only tyrosinase-positive strains and excluded those that were tyrosinase-negative from further research. Wiersema (pers. comm.) also found netted scab isolates in the Netherlands that were tyrosinase-negative. Vruggink and Maat (1968) found considerable differences among isolates from netted scab lesions and concluded that it was improbable that all belonged to the same species. However, a substantial number of them were assignable to *S.scabies*.

Mygind and Begtrup (1970) concluded that the organism causing netted scab on Bintje was closely related to *S.fimicarius* and was tyrosinase-negative, like the ones found by Sundheim (1968) in Norway and by Bång (1979) in Sweden.

There is evidence that the pathogen causing netted scab in potato also attacks other crops. Mygind and Begtrup (1970) demonstrated that isolates causing netted scab on cv. Bintje were able to damage the roots of tomato plants (brown root rot). At the Department of Field Crops and Grassland Science, Bintje and the sugarbeet cultivar Monohil were grown in pots in clay soil that had been heavily infested with the netted scab organism by repeated cultivation of Bintje. The Bintje plants reacted severely and showed typical netted scab symptoms on tubers and lesions on roots. The sugar-beet plants had brown, superficial, mostly continuous, corky lesions, which covered most of the surface of the beet and greatly resembled the symptoms of netted scab on potato tubers in colour and shallowness (Fig. 3). The true roots showed severe brown root rot and growth of the plants was considerably reduced in comparison with those grown in pots with clay soil that was not so heavily infested with the netted scab pathogen. The symptoms resemble those of girth scab, which, according to Heijbroek (1982) may be caused by *Actinomyces albus*, *A.intermedius* and *A.nigricans*.

Conclusions

Russet scab as described by Mygind (1965, 1970) in Denmark, Sundheim (1968) in Norway, Bång (1979) in Sweden, Salzmann (1960) in Switzerland and Wenzl (1970) in Austria appears to be identical to that described by de Bruyn (1939), Labruyère (1971) and Scholte et al. (1985) in the Netherlands. The russet scab occurring in the USA, and comprehensively described by Harrison (1962), differs from the European russet scab in several characteristics, such as cultivar susceptibility, root attack and optimum soil temperature. Russet scab in the USA and russet scab in Europe therefore seem to be two different diseases. To resolve this nomenclatural problem we propose that henceforth the name in the English language for the European form of russet scab should be 'netted scab' in agreement with the other European common names, viz. the Danish 'netskurv', the Dutch 'netschurft', the Swedish 'Nätskorv' and the German 'Netzschorf'.

The pathogen has not yet been identified, but the diversity of certain characteristics such as tyrosinase reaction, growth habit, temperature range and pH reaction makes it probable that more than one species of the genus *Streptomyces* is able to cause netted scab.

Potato Research 32 (1989) 65-73

CHAPTER 4

THE EFFECT OF NETTED SCAB (*STREPTOMYCES* SPP.) AND *VERTICILLIUM DAHLIAE* ON GROWTH AND YIELD OF POTATO

K.Scholte

Summary

The effect of *Streptomyces* spp.(netted scab) on the growth of potato was investigated in three pot experiments, in two of which the effect of *Verticillium dahliae* was also assessed.

The netted scab organisms attacked all underground plant parts of susceptible potato cultivars early in the growing season; the roots were especially seriously attacked, markedly reducing tuber yield and number but prolonging the duration of the growing season. The nematicide oxamyl had little effect on the incidence of netted scab. Repeated growing of the susceptible cv. Bintje greatly increased soil contamination with the netted scab pathogens.

V.dahliae reduced haulm growth before wilt symptoms were evident and it reduced tuber yield but not number. Oxamyl delayed infection by *V.dahliae* by controlling parasitic *Pratylenchus* nematodes (mainly *P.thornei*).

Introduction

Netted scab caused by *Streptomyces* spp., occurs mainly in areas where susceptible cultivars of potato (*Solanum tuberosum*) are grown on a large scale. It differs from common scab in many ways (Scholte and Labruyère, 1985); the most important is that the pathogens attack the roots as well as the tubers, resulting in lower yields.

Because cv. Bintje is one of the few susceptible cultivars (Scholte and Labruyère, 1985), the disease is found most commonly in the Netherlands (Scholte et al.,1985), Sweden (Bång, 1979b), Denmark (Mygind, 1965) and Switzerland (Salzman, 1960). It occurs too in those parts of Austria where the susceptible cultivar Allerfrüheste Gelbe is grown (Wenzl, 1970). There are no reports from countries outside Europe where another susceptible cultivar, Désirée, is grown on a large scale.

Frequent cropping of susceptible cultivars of potato leads not only to an increasing contamination of the soil with the netted scab pathogens, but also to higher inoculum densities of other pathogens such as *Verticillium dahliae*. Therefore, attention was also paid to this fungus in two of the three pot experiments reported here that were designed to study the effects of netted scab on growth and tuber yield.

Materials and methods

Experiment 1, 1979

The soil used was a heavy river clay containing 2.8 % organic matter and having a clay fraction (< 2 mu) of 35 % and a pH-KCl of 6.9. It was taken from two adjacent and comparable fields, A and B, differing only in cropping history, where frequent cropping of cv. Bintje was known to have increased the inoculum density of the netted scab pathogens.

In early October 1978, after a wheat crop (field A) and a potato crop (field B), soil sampled from each field was separately sieved and thoroughly mixed. Twice as much soil was taken from field B as from field A and the soil from field B was divided into two parts; one part was put in pots in which cv. Bintje was grown in a glasshouse, kept at 15 °C, until the following April. During this period the soil from field A and the remaining soil from field B was stored in plastic bags outdoors.

On 18 April 1979 a pot experiment was started with the three soil lots that now differed in cropping history of potato. The soil lots were then coded as W soil (field A), P soil (field B) and PP soil (field B, additionally cropped with potato in pots) and had the following histories from 1972 to 1978:

W: potato - wheat - sugar beet - barley - maize - wheat - wheat
P: sugar beet - wheat - potato - wheat - sugar beet - maize - potato
PP: sugar beet - wheat - potato - wheat - sugar beet - maize - potato,potato
All potato crops were of cv. Bintje.

On 18 April, black plastic pots (5.8 l) were filled with soil and put in white enamel pots, which were then placed in the field in a randomized block design of 12 replicates after planting in each pot a singly sprouted 15-g tuber of cv. Bintje, previously disinfected with ethylmercurybromide (AArdisan, AAgrunol, Haren, 4 % a.i., tubers were immersed for 5 minutes in a 0.3

% solution of the trade product).

Three pots per treatment (soil type) were harvested 73 days later to record the extend of attacks on the roots. The other 9 pots were harvested 120 days after planting to determine the yield.

The following quantities of nutrients were applied per pot, apportioned over four applications from planting date to 10 weeks after planting: 3780 mg N, 930 mg P, 5256 mg K, 360 mg Mg and 10 ml of a trace element solution containing 20 g $MnSO_4 . 1H_2O$, 30 g H_3BO_3, 5 g $ZnSO_4 . 7H_2O$, 1 g $CuSO_4 . 5H_2O$ and 1 g $Na_2MoO_4 . 2H_2O$ per litre of water. The amounts of the main elements were based on expected dry matter yield of haulm and tubers and their mineral content.

Experiment 2, 1980

Early in October 1979 soil was collected from two adjacent and comparable fields with the same cropping history, but in a different phase of the rotation. Soil was taken from field A after a wheat crop (soil W) and from field B after a potato crop (soil P). Each soil lot was sieved, mixed and stored in plastic bags until April of the following year, 1980. From 1975 to 1979 the cropping sequences of the fields were as follows:

W soil: wheat - potato - wheat - sugar beet - wheat

P soil: potato - wheat - sugar beet - wheat - potato

All potato crops were of cv. Bintje

On 16 April, 8 pots per treatment were each planted with a singly sprouted 15-g tuber of one of three cultivars susceptible to netted scab, Allerfrüheste Gelbe, Bintje and Eba, or one of three immune cultivars, Amethyst, Corine and Sinaeda. Six pots per treatment (soil) were used to determine yield and two pots for observations on the root system during growth.

Pot types and sizes, seed treatment, soil characteristics, total amount of nutrients applied and layout of the experiment were the same as in Experiment 1.

Experiment 3, 1980

The same soils, W and P, were used as in Experiment 2 but in this experiment there were two nematicide treatments:

N_0 = untreated (control)

N_1 = 0.05 ml oxamyl per pot two weeks before planting, 0.05 ml oxamyl per pot at planting and 0.025 ml oxamyl per pot 5 weeks after planting.

Oxamyl was applied as Vydate L (Shell Chemie, Den Haag, 24 % a.i.).

Singly sprouted 15-g tubers, cvs Bintje, susceptible, and Eersteling, immune, to netted scab were planted singly in pots on 16 April.

Pot types and all other details were as in Experiment 1.

Analyses

During the growing season the height of the plants was recorded periodically and two or three pots were sampled for observations on roots and tubers. At harvest the dry matter yield of tubers and their number was determined.

In Experiments 2 and 3 the time of onset of wilt symptoms was recorded. The first symptom was unilateral wilting of the leaves; later, numerous microslerotia formed on the dead stems of affected plants, resulting in a greyish-blue discoloration. Those symptoms are typical of those caused by *V.dahliae* (Isaac and Harrison, 1968) which was assumed to be the causal fungus.

Netted scab on each tuber was scored using four classes; 0 = no attack, 1 = slight attack, 2 = moderate attack and 3 = severe attack and a netted scab index (NSI) was then calculated using the formula:

$$NSI = 100 \times (0 \times n_0 + 0.33 \times n_1 + 0.67 \times n_2 + n_3) \; / \; n_{total}.$$

In Experiment 3, endoparasitic nematodes were extracted from the roots by the funnel-spray method (extraction time six days; Oostenbrink, 1960) and nematode densities in the soil ascertained by extracting them with an Oostenbrink elutriator (Oostenbrink, 1960).

Results

Experiment 1

From the outset plants grew better in W soil than in P soil and plants in PP soil grew very poorly (Fig.1). Later, plants in P soil and PP soil made up some of their arrears in height but, especially in the PP soil, they remained spindly with thin stems and small leaves.

The roots of plants harvested periodically from the P and PP soils were so severely attacked by the netted scab pathogen (symptoms described by Scholte et al., 1985) that the yields and number of tubers were much lower than in plants from the W soil (Table 1).

Experiment 2

Initially cv. Sinaeda (immune to netted scab) grew at the same rate in both

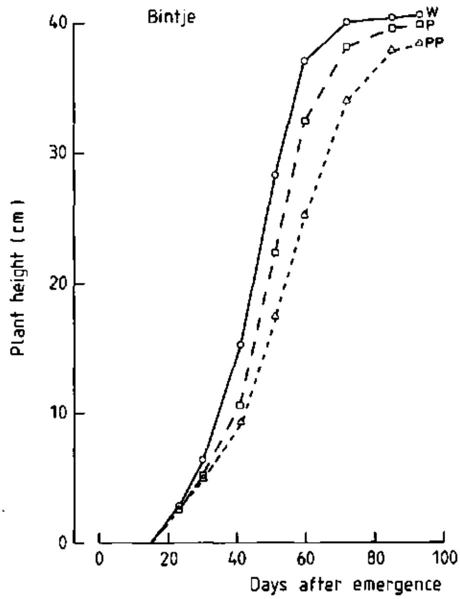

Fig. 1. Plant height development of cv. Bintje in W , P and PP soils (preceding crops: wheat, potato, and potato twice, respectively). Experiment 1.

Table 1. Dry matter yield of tubers and haulm (g/pot) and number of tubers per pot at harvest. Experiment 1.

	Dry weight		Number of tubers[a]
	Tubers[a]	Haulm[a]	
W soil	186 a	20.2 a	16.6 a
P soil	128 b	19.0 a	7.4 b
PP soil	57 c	9.3 b	4.9 c

[a] Dissimilar letters indicate significant differences between soils at $P \leq 0.001$ (according to the Studentized range test of Tukey).

the P soil and in the W soil (Fig.2) but later its growth slowed earlier in P soil than in W soil. In P soil reduced haulm growth preceded the appearance of wilt symptoms typical of *V.dahliae* and the plants died earlier. Cvs Amethyst and Corine, also both immune to netted scab, reacted in the same way as Sinaeda but the symptoms of Verticillium wilt were more severe in Amethyst than in the other two cultivars.

The growth of cv. Allerfrüheste Gelbe, susceptible to netted scab, ini-

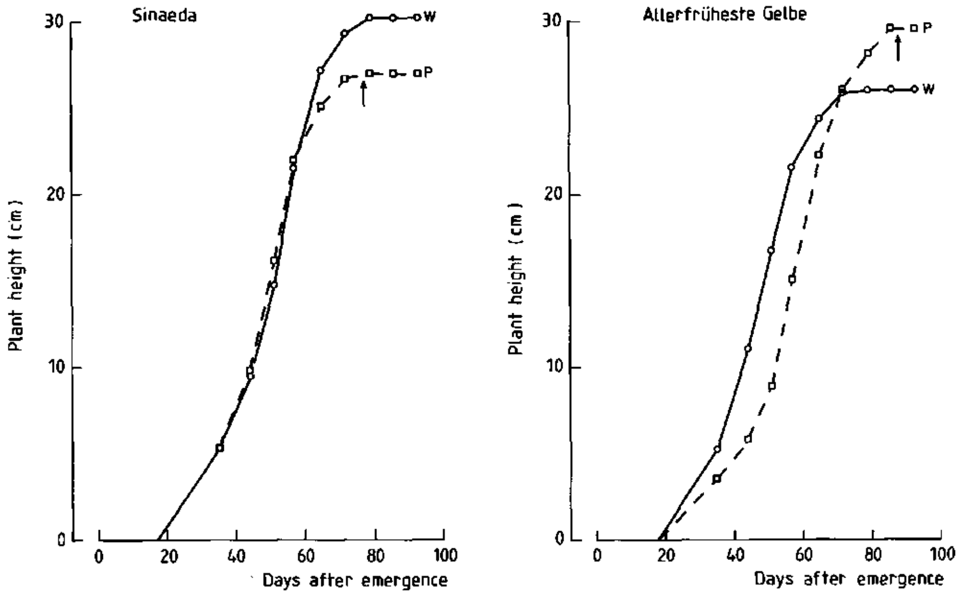

Fig. 2. Plant height development and the appearance of the first symptoms of Verticillium wilt (arrowed) in cultivars Sinaeda and Allerfrüheste Gelbe in W and P soil (for codes, see Fig.1). Experiment 2.

tially lagged markedly in the P compared with the W soil, resulting in shorter and thinner plants although the duration of haulm growth was longer so that the plants in P soil were taller but thinner than those in W soil. Cvs Bintje and Eba, both susceptible to netted scab, reacted in a like manner to Allerfrüheste Gelbe.

Two pots per treatment per cultivar were harvested on 6 July, 51 days after planting. The roots and tubers of the cvs Allerfrüheste Gelbe, Bintje and Eba were severely attacked in the P soil but only slightly so in the W soil, whereas cvs Amethyst, Corine and Sinaeda had unblemished roots and tubers in both soils.

At the final harvest, although all cultivars had a lower yield in the P than in the W soil, they did not all react alike (Table 2). The yields of Corine, Sinaeda and Amethyst (all immune to netted scab, with Amethyst very susceptible to *V.dahliae*) were reduced by 10, 10 and 31 %, respectively, and those of Bintje, Eba and Allerfrüheste Gelbe (in the order of increasing susceptibility to netted scab) reduced by 37, 46 and 50 %, respectively. There were only a few tubers per pot of Bintje, Eba and Allerfrüheste Gelbe

Table 2. Dry matter yield of tubers (g/pot), number of tubers per pot and netted scab index (0-100) on tubers at final harvest. Experiment 2.

Cultivar	Tuber yield		Number of tubers		Netted scab index	
	W soil	P soil	W soil	P soil	W soil	P soil
Amethyst	185	127***	23.8	21.7	0	0
Corine	157	141*	12.3	11.5	0	0
Sinaeda	223	201**	19.3	22.7	0	0
Allerfr. Gelbe	167	84***	17.8	8.0***	25	60***
Eba	201	109***	10.0	5.0**	21	56***
Bintje	190	120***	20.8	9.8***	11	40***

*, ** and *** The P and W soils differ significantly at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

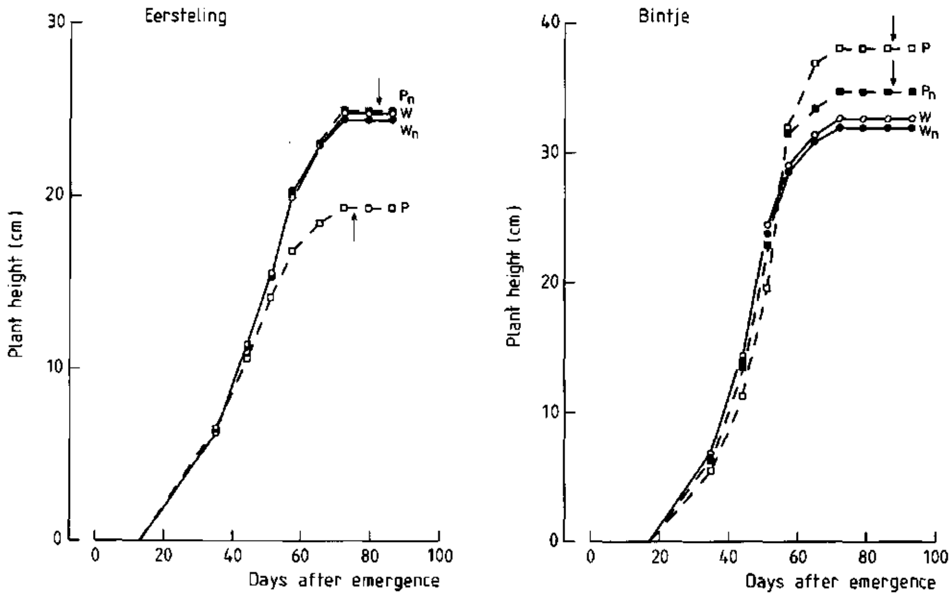

Fig. 3. Plant height development and the appearance of the first symptoms of Verticillium wilt (arrowed) in cultivars Eersteling and Bintje in untreated W and P soil (for codes, see Fig.1) and in W and P soil treated with a nematicide (W_n and P_n). Experiment 3.

Table 3. Dry matter tuber yield (g/pot), number of tubers per pot and netted scab index (0-100) on tubers at final harvest. Experiment 3.

Cultivar	Eersteling				Bintje			
Soil origin	W soil		P soil		W soil		P soil	
Nematicide	N0	N1	N0	N1	N0	N1	N0	N1
Tuber yield[a]	151 a	153 a	117 c	131 b	213 a	214 a	144 b	151 b
Rel. tuber yield	100	101	77	87	100	100	68	71
Number of tubers[a]	16.4 a	16.4 a	14.8 a	15.9 a	23.0 a	22.5 a	14.5 b	17.4 b
Netted scab index[a]	0	0	0	0	17 a	10 a	46 b	52 b

[a] Dissimilar letters indicate significant differences between the four treatments within a cultivar at $P \leq 0.05$ (Studentized range test of Tukey).

growing in the P soil and these were severely attacked by netted scab. The tuber numbers of the other cultivars were not affected.

Experiment 3

The application of the nematicide oxamyl in W soil did not affect the growth of either Eersteling or Bintje (Fig.3). Early plant growth of Eersteling in both soil types was similar, but later its growth was reduced in the P soil where no oxamyl had been applied. Wilt symptoms, characteristic of *V.dahliae*, appeared five days earlier in the untreated P soil than in the treated P soil but none were seen on plants growing in the W soil.

At first, cv. Bintje developed very poorly in the P soil. Later the plants became taller in P soil than in W soil but they remained thin. Wilt symptoms did not occur in W soil and oxamyl delayed the appearance of wilt symptoms by two days in the treated P soil. Wilt symptoms were more severe in cv. Eersteling than in cv. Bintje.

At the final harvest there were no differences in dry matter tuber yield and tuber number, either for Eersteling or for Bintje that had been growing in the untreated or oxamyl-treated W soil (Table 3). Oxamyl increased the tuber yield of Eersteling in the treated P soil but in the untreated P soil it was 23 % lower than in untreated W soil. Tuber number of cv. Eersteling was not affected by soil or treatment.

Tuber yields of cv. Bintje were 32 % lower in the untreated P soil than in untreated W soil. Oxamyl application to the P soil did not statistically increase tuber yield. Tuber number was much lower and netted scab index was higher in P soil than in W soil.

At the final harvest, there were 780 nematodes per 10 g roots in the W soil and only 100 per 10 g roots in the P soil; two-thirds of the population was *Pratylenchus thornei* and one-third *P.neglectus*. Oxamyl reduced the population in both soils to only 10 nematodes per 10 g of roots. Other nematode species were very rare.

Discussion

All the experiments showed that the levels of contamination of soil with the *Streptomyces* spp. causing netted scab are greatly increased by planting a susceptible cultivar. The subsequent decline in yield of a susceptible potato crop is much more serious than the effects of netted scab on tuber quality. The pathogens attack on the root system of young plants and their decreased growth rate at emergence led to fewer tubers per plant, and severe root attack (as in Experiments 1 and 2) reduced tuber number by half. The attacked plants not only grew more slowly, but they also remained thinner and had a smaller leaf area. Although the duration of their growth was slightly prolonged, final yield reductions were high. Serious yield losses were also recorded in the Netherlands elsewhere in farmers' fields on which cv. Bintje had been grown every three or four years. Netted scab was also associated with lower yields in field experiments by Labruyère (1971) and Bång (1979b), and Scholte et al.(1985) showed that artificial inoculation with *Streptomyces* spp. could reduce plant growth, yield and tuber number.

In the three experiments reported here the natural inoculum level was increased by repeatedly growing the susceptible cv. Bintje. This also increased the levels of other potato pathogens, noteably that of *V.dahliae* and its effects were assessed in Experiments 2 and 3 by growing cultivars, Amethyst, Corine, Sinaeda and Eersteling, that are wholly immune to netted scab. In the P soil their growth pattern differed markedly from that of the three susceptible cultivars Allerfrüheste Gelbe, Bintje and Eba. Initially the immune cultivars grew as well in the P as in the W soil so that their tuber numbers were not affected. However, later, their growth rate decreased on the P soil and the first symptom of reduced haulm growth was followed by wilt symptoms characteristic of *V.dahliae*, cvs Amethyst and Eersteling being more sensitive than Corine and Sinaeda.

In P soil the cultivars susceptible to netted scab showed symptoms of Verticillium wilt on average 10 days later than those immune. Although this difference may reflect different sensitivities to *V.dahliae*, it is more likely that it can be partly attributed to the severity of attack by the netted scab pathogens. A severe root attack resulted in a less extensive root system and a lower likelihood of attack by *V.dahliae*.

Applying a nematicide had no effect on the incidence of netted scab but it clearly delayed the onset of Verticillium wilt. Only *V.dahliae* caused a decline in tuber yield of cv. Eersteling in the P soil and this was offset by the application of oxamyl which, however, did not affect cv. Bintje because the predominating yield-limiting factor for this cultivar was netted scab, *V.dahliae* being of only minor importance.

Oxamyl delayed attack by *V.dahliae* by eliminating most of the parasitic nematodes: fewer nematodes means fewer wounds in roots and, consequently, less infection by *V.dahliae*. Siti et al. (1979) for example, showed that *P.thornei*, the dominant nematode found in Experiments 2 and 3, may stimulate infection by *V.dahliae*. In these experiments the yield increase in the P soil after application of oxamyl could not have been a direct effect from controlling *P.thornei*, because oxamyl did not increase growth or yield in the W soil with the highest nematode density.

Conclusions

1. Frequent cultivation of a susceptible potato cultivar markedly increases the soil contamination levels of the netted scab pathogens (*Streptomyces* spp.).
2. These pathogens attack all the underground parts of a susceptible potato cultivar, especially the roots, resulting in severe yield depressions and fewer tubers per plant.
3. Netted scab does not shorten the growing season.
4. Nematicides do not affect the incidence of netted scab.
5. *V.dahliae* may reduce haulm growth before wilt symptoms appear.
6. Nematicides indirectly decrease the incidence of *V.dahliae*.

Potato Research 30 (1987) 187-199

CHAPTER 5

THE EFFECT OF CROP ROTATION AND GRANULAR NEMATICIDES ON THE INCIDENCE OF *RHIZOCTONIA SOLANI* IN POTATO

K. Scholte

Summary

The incidence of *Rhizoctonia solani* in potato was studied in two crop rotation experiments from 1981 to 1985. The greater the frequency of potato cropping, the more severe the attack on stems and stolons by *R.solani*. Severity of black scurf on progeny tubers and cropping frequency were also correlated, but less significantly. In fields with antagonists to *R.solani*, continuous potato cropping caused less black scurf on tubers than did 1:2 rotations.

Application of the nematicides oxamyl, ethoprophos and aldicarb resulted in a marked increase in *R.solani* infection of stems and stolons.

Introduction

In many parts of the Netherlands potatoes are grown on the same field once every two or three years. In such close rotations, nematicides are often applied to prevent damage caused by certain nematodes and to stop them from multiplying.

At the Department of Field Crops and Grassland Science in 1979, two experiments were laid out to study the effects of short rotations on yield and on the development of diseases in potato. One of the pathogens being investigated in detail in these experiments is *Rhizoctonia solani*. It forms disfiguring sicerotia (black scurf) on tubers and it attacks both stems (stem canker) and stolons (stolon lesions/pruning) thereby reducing both total yield and its quality. This paper reports the effects of different rotations and the application of granular nematicides on the incidence of *R.solani*.

Material and methods

Experiment 1

This experiment was laid out in 1979 near Wageningen on light sandy soil containing 2.6 % organic matter and having a pH-KCl of 5.2. Prior to the experiment, potatoes (1977) and winter rye (1978) had been grown on the trial field. The experiment was terminated in 1986 and comprised four rotations:

P = continuous cropping of potato
MP = maize - potato
SP = sugar beet - potato
MSBBP = maize - sugar beet - barley - barley - potato.

They were compared on untreated plots and on plots that were treated annually with a granular nematicide even when a crop other than potato is grown. The nematicide was always broadcast one day before planting and then incorporated into the soil using a spring-tine cultivator. Oxamyl (Vydate 10G, Chell Nederland Chemie, 10 % a.i., 50 kg ha^{-1}) was applied from 1979 to 1984, and aldicarb (Temik 10G, Union Carbide Benelux, 10 % a.i., 30 kg ha^{-1}) in 1985 and 1986.

The experiment was laid out in a randomized complete block design with four replications; every crop in a rotation was grown in each year. Within each block, continuous cropping of potatoes (P) occurred in duplicate. The trial therefore involved 11 x 2 x 4 = 88 plots. The plots were 12 x 6 = 72 m^2, of which 10 x 4.5 = 45 m^2 was harvested. The blocks were separated by strips 12 m wide, on which barley was grown each year. The strips served as headland for mechanized cultivation.

Every year the fields were worked with a cultivator in autumn, after the crops have been harvested. They were ploughed early in March the following year. Averaged over 1981 to 1985, yearly rates of fertilizers were 232 kg N, 121 kg P_2O_5, 242 kg K_2O, 94 kg MgO, 0.8 kg Cu and 0.7 kg B per hectare. The high rates were necessary because of the very poor natural fertility of the soil.

The cultivar used was Element, which is resistant to biotype A of potato cyst eelworm. Seed tubers (32-35 mm), not pre-sprouted, were planted by hand 25 cm apart in rows 75 cm apart on 3/4/1981, 5/4/1982, 15/4/1983, 30/3/1984, 9/4/1985 and 8/4/1986. The final harvest of the mature crop took place on 22/9/1981, 22/9/1982, 22/9/1983, 20/9/1984, 25/9/1985 and 15/9/1986.

Experiment 2

This experiment was laid out in 1979 in the East Flevoland Polder on a calcareous marine clay containing 3.1 % organic matter and having a clay fraction (< 2 μm) of 27 % and a pH-KCl of 7.3. On the trial field potatoes had been grown only once (1974) since the polder had been reclaimed from the sea in 1957. The crop in the year before the experiment began (1978) was oats. The experiment was terminated in 1985. Four rotations were compared:

P = continuous cropping of potato

WP = wheat - potato

SP = sugar beet - potato

WSOP = wheat - sugar beet - oats - potato.

The comparisons were made between untreated fields and fields that were treated annually with a granular nematicide even if a crop other than potato was grown. The nematicide was always broadcast over the field one day before planting and incorporated into the soil using an oscillating harrow. In 1979, oxamyl (Vydate 10G, 50 kg ha^{-1}) was applied, from 1980 to 1984 ethoprophos (Mocap 20G, Duphar, 20 % a.i., 50 kg ha^{-1}) and in 1985 aldicarb (Temik 10G, 30 kg ha^{-1}).

The experiment was laid out in a randomized complete block design, every crop in a rotation was grown in each year. Within each block continuous cropping of potato (P) occurred in duplicate. The experiment involved a total of 10 x 2 x 2 = 40 plots. The plots were 40 x 6 = 240 m^2, of which 40 x 3 = 120 m^2 was harvested. The blocks were separated by grass strips 12 m wide, which served as headland for mechanized cultivation.

Every year the experimental field was ploughed in November before the onset of winter. Immediately before planting the soil was worked with an oscillating harrow. Averaged over the period 1981 to 1985, the yearly fertilizer applications amounted to 167 kg N, 134 kg P_2O_5 and 160 kg K_2O per hectare. In 1985 an additional dressing of 40 kg MgO per hectare was given.

The cultivar used was Hertha, resistant to biotype A of potato cyst eelworm. Every year the tubers were pre-sprouted before planting. Seed tuber size and plant spacing were the same as in Experiment 1. The planting dates were 15/4/1981, 16/4/1982, 8/6/1983, 17/4/1984 and 23/4/1985. The final harvest took place on 7/9/1981, 20/9/1982, 20/10/1983, 18/9/1984 and 24/9/1985. In 1983, wet fields caused planting to be delayed until 8/6; as a result, the plants did not die off naturally, and the haulms were killed by spraying with dinoseb (Brabant dnbp olie g.c., 250 g/l a.i., 20 l ha^{-1}).

Crop protection

Before planting, seed tubers, visibly free from black scurf, were immersed for 5 minutes in a fungicide solution to kill any superficial mycelium of *R.solani*. In Experiment 1 validamycine (Solacol, AAgrunol, 30 g/l a.i., 3 % solution) was used and in Experiment 2 ethylmercurybromide (AArdisan, AAgrunol, 4 % a.i., 0.3 % solution).

In both experiments chemical weed killers, such as metribuzin (Sencor, 70 % a.i.), metobromuron (Patoran, 50 % a.i.), metobromuron/terbutryn (Igrater, 25/25 % a.i.) and dinoseb-acetate/monolinuron (Ivorin super, 25/11.5 % a.i.) were applied before emergence. If necessary after emergence the spaces between plants and rows were sprayed with a mixture of paraquat (Gramoxone, 200 g/l a.i.) and diquat (Reglone, 200 g/l a.i.), using a protective cover over the nozzle.

Aphids were controlled annually by 1-3 sprayings of pirimicarb (Pirimor, 50% a.i.) and/or fosfamidon (Dimecron, 250 g/l a.i.). *Phytophthora infestans* was controlled by 5-12 sprayings annually of agents containing maneb/fentin-acetate. Herbicides, insecticides and fungicides were applied at the recommended rates.

Determination of R.solani attack

In Experiment 1, 18 plants were harvested from each field ca. 74 (1981 to 1985) and ca. 117 (1981, 1983 to 1985) days after planting. They were dug from each plot according to a predetermined pattern. In Experiment 2, 30 plants were harvested from each plot ca. 61 and ca. 108 days after planting, in the same pattern as for Experiment 1. For each plant, infection by *R.solani* was classified as follows:

0 = no attack on stolons or stems;

1 = slight attack: some scattered lesions on the stems;

2 = moderate attack: not more than half the number of stems with a lesion girdling the stem, usually with additional attacks on the stolons;

3 = severe attack: more than half of the stems with a lesion girdling the stem and with the stolons severely attacked;

4 = very severe attack: the attack on stems and stolons so severe as to cause 'little potato': many small tubers form near and many break through the soil surface, sometimes aerial tubers form immediately above the ground.

The fresh and dry matter yields of tops and tubers per plant and the number of stems and tubers per plant were also determined. The relation between these parameters and the degree of *R.solani* attack will be reported in a separate paper.

Because yields in the group with class 1 attack were found not to have suffered, and infections in this group could not irrefutably be attributed to *R.solani*, classes 0 and 1 were combined. As the number of plants of class 4 in both experiments was low, class 4 was combined with class 3. Thus together, the modified classes 2 and 3 represent the total percentage of attacked plants, with class 3 encompassing the severely attacked plants.

At final harvest the percentage of tubers with clearly visible sclerotia (black scurf) was determined per plot from samples of 100-150 tubers.

Determination of the occurrence of Verticillium biguttatum

In Experiment 1, the occurrence of *V.biguttatum*, a hyperparasite of *R.solani*, was determined in 1984 and 1985. At 74 and 117 days after planting, 72 stolon pieces per plot (4 per plant) 1 cm long were put in petri dishes (8 pieces per dish) containing a 5-day-old culture of *R.solani* growing on malt extract agar. About 2 weeks later the percentage of stolon pieces with *V.biguttatum* was recorded.

Results

In Experiment 1, the largest percentage of plants with *R.solani* infection on stems and stolons (Table 1) was found in plots continuously cropped with potato (P). Significantly lower levels were found in the 1:2 rotations (MP and SP), which did not differ significantly from each other, and the 1:5 rotation (MSBBP) had significantly the lowest level. The yearly application of nematicides resulted in a marked increase in infection levels especially of the severely infected plants, and produced a significant interaction between rotation and nematicide application.

The results of Experiment 2 (Table 2) largely agree with those of Experiment 1. The difference between continuous cropping of potato (P) and 1:2 rotation (WP and SP) was less marked than in Experiment 1. Again, the 1:2 rotations do not differ. The application of nematicides also caused an increase in infection, the percentage of severely infested plants being doubled. The interaction between rotation and nematicides in this trial must be ascribed to the fact that there was no increase in infection after applying nematicides in the 1:4 rotation (WSOP).

At the end of the growing season the percentage of tubers with black scurf in Experiment 1 was significantly higher in MP and SP than in P (Table

Table 1. Percentage of plants attacked by R.solani in 4 rotations in control plots and plots treated with a nematicide, 74 days after planting (averaged over 1981-1986) and 117 days after planting (averaged over 1981, 1983-1985). Experiment 1.

Day	Rotation	Total % of attacked plants			Severely attacked plants (%)		
		Control	Nematicide	Mean[a]	Control	Nematicide	Mean[a]
74	P	48	62	55 a	14	34	24 a
	MP	22	41	31 b	7	18	13 b
	SP	23	32	28 b	9	14	11 b
	MSBBP	9	14	12 c	1	4	3 c
	Mean	26	37***		8	18***	rn
117	P	62	70	66 a	29	31	30 a
	MP	29	55	42 b	9	24	16 b
	SP	43	38	41 b	13	13	13 b
	MSBBP	7	18	13 c	2	7	4 c
	Mean	35	45**	rn	13	19**	rn

[a] Dissimilar letters indicate significant differences between rotations at $P \leq 0.05$ (according to the Studentized range test of Tukey).

*, ** and *** Nematicide treatment differs significantly from control at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

rn: interaction between rotation and nematicide treatment is significant at $P \leq 0.05$.

3) and least in MSBBP. In P, MP and SP, nematicides did not result in an increase in this percentage, whereas in MSBBP the applications apparently caused the percentage to double. The interaction between rotation and nematicides was statistically significant.

In Experiment 2, the percentage of tubers with black scurf was significantly the lowest in WSOP but did not differ among P, WP and SP (Table 4). In all rotations, application of nematicides resulted in a significant, albeit limited, increase in this percentage.

In a preliminary investigation in 1983 into the occurrence of *R.solani* parasites, tubers with sclerotia from both experiments were rinsed with water and incubated for 14 days at 20 °C at a high relative humidity. Mycelium of *Verticillium biguttatum*, an important antagonist of *R.solani* (Velvis & Jager, 1983; Jager & Velvis, 1985), developed extensively on the sclerotia of tubers from Experiment 1 (Fig. 1), but none grew on those from Experiment

Table 2. Percentage of plants attacked by *R.solani* in 4 rotations in control plots and plots treated with a nematicide, 61 days after planting (averaged over 1981-1985) and 108 days after planting (averaged over 1981, 1983-1985). Experiment 2.

Day	Rotation	Total % of attacked plants			Severely attacked plants (%)		
		Control	Nematicide	Mean	Control	Nematicide	Mean
61	P	30	53	42 a	11	24	18 a
	WP	23	33	28 b	12	15	14 a
	SP	22	41	32 ab	12	27	19 a
	WSOP	3	8	6 c	1	2	2 b
	Mean	20	34***	rn	9	17***	rn
108	P	50	72	61 a	18	32	25 a
	WP	46	57	52 a	25	34	29 a
	SP	42	72	57 a	21	40	30 a
	WSOP	27	25	26 b	7	6	7 b
	Mean	41	56***	rn	18	28**	rn

Symbols as in Table 1.

Table 3. Percentage of tubers with sclerotia (black scurf) at final harvest in 4 rotations in control plots and plots treated with a nematicide (averaged over 1981-1985). Experiment 1.

Rotation	Total % of tubers with sclerotia		
	Control	Nematicide	Mean
P	56	54	55 b
MP	66	64	65 a
SP	62	68	65 a
MSBBP	11	22	16 c
Mean	49	52	rn

Symbols as in Table 1.

2. A soil analysis by G.Jager (Institute for Soil Fertility, Haren, the Netherlands) also showed the presence of *V.biguttatum* in the field used for Experiment 1 but there was no sign of mycoparasitism in Experiment 2.

During the growing season in 1984 and 1985 the percentage stolon pieces infested with *V.biguttatum* was determined in Experiment 1. The largest per-

Table 4. Percentage of tubers with sclerotia (black scurf) at final harvest in 4 rotations in control plots and plots treated with a nematicide (averaged over 1981-1985). Experiment 2.

Rotation	Total % of tubers with sclerotia		
	Control	Nematicide	Mean
P	64	70	67 a
WP	57	70	64 a
SP	57	63	60 a
WSOP	15	20	17 b
Mean	48	56*	

Symbols as in Table 1.

Table 5. Percentage of stolon pieces with *V.biguttatum* in 4 rotations in control plots and plots treated with a nematicide, 74 and 117 days after planting. Experiment 1.

Day	Year		Rotation				
			P	MP	SP	MSBBP	Mean
74	1984	Control	20	15	9	1	11 a
		Nematicide	21	9	8	4	11 a
	1985	Control	26	23	23	14	21 a
		Nematicide	56	42	37	16	37 b
	Mean		31 a	22 b	19 b	9 c	
117	1984	Control	46	43	30	10	32 a
		Nematicide	46	41	13	15	29 a
	1985	Control	65	42	67	38	53 a
		Nematicide	70	59	63	49	60 a
	Mean		57 a	46 ab	43 b	28 c	

Symbols as in Table 1.

centage was found in the continuously cropped plots (P) (Table 5), followed by the 1:2 rotations (MP and SP) and, significantly the lowest, the 1:5 rotation (MSBBP). Between 74 and 117 days after planting, the percentage increased considerably and in 1985, but not in 1984, it increased following the application of nematicides.

Fig. 1. A tuber bearing sclerotia infected with *Verticillium biguttatum*. Experiment 1.

Discussion

Rotational effects

One aim of the experiments was to investigate the extent to which crop rotation affects *R.solani* infection of potato plants. To do this, infection via planting material was excluded by using seed potatoes that were free from black scurf and that had been chemically disinfected.

The experiments showed that although the levels of infection of stems and stolons by *R.solani* increased with increasing frequency of potatoes in a rotation, there was not inevitably a concomitant increase in the density of black scurf on the harvested progeny tubers. Stem and stolon infection and black scurf development are different processes, the former being greatly influenced by the density of the inoculum in the soil at the beginning of the growing season. During crop growth the fungus multiplies because the potato plant is an excellent host and any initial differences in density of the fungus tend to level out as the growing season proceeds; even when the initial density of the inoculum is low there is ample time for the fungus to multiply. Sclerotia usually form at the end of the growing season when the haulms are dying. As a result, the effects of cropping frequency on incidence of *R.solani* are more clearly expressed by the extent of stem infection than by the extent of black scurf on the progeny tubers, a conclusion also reached by Lamers (1981).

If there are very great differences in *R.solani* soil infestation at the beginning of the growing season, these differences will be clearly reflected by differences in extent of black scurf. This is why less black scurf was observed in the 1:4 and 1:5 than in the 1:2 rotations and continuous cropping. In both experiments continuous cropping resulted in a higher stem infection with *R.solani* than the 1:2 rotations. In Experiment 2 there was no difference in the incidence of black scurf between the 1:2 rotations and continuous cropping. In contrast, continuous cropping in Experiment 1 resulted in less black scurf - a finding closely related to the presence of an antagonist to *R.solani* in the soil. In the Netherlands, Jager & Velvis (1983a, 1983b, 1985), who have conducted pioneering research on the suppression of *R.solani* by hyperparasites, discovered that *V.biguttatum* was by far the most effective hyperparasite of *R.solani* and that it occurs more frequently in sandy than in clay soils (Velvis & Jager, 1983). In Experiment 1 (sandy soil) *V.biguttatum* was abundantly present and a great many of the sclerotia were parasitized at the end of the growing season (Fig. 1). The inoculum density of *V.biguttatum* seems to be largely determined by the extent of *R.solani* and it was apparently greatest in the continuously cropped plots, intermediate in the 1:2 rotations (MP and SP) and least in the 1:5 rotation (MSBBP) (Table 5).

Notwithstanding the presence of *V.biguttatum*, sufficient viable *R.solani* inoculum remains in the soil of the continuously cropped plots to enable a severe stem infestation of the potato plants to develop. In spring, *V.biguttatum* cannot adequately hinder infection. Temperature seems to be an important factor because whereas *R.solani* can grow vigorously at low temperatures, *V.biguttatum* is inactive when the temperature falls below 12 °C (Jager & Velvis, 1985). With higher soil temperature later in the growing season, the activity of the antagonist increases and it parasitizes the mycelium of *R.solani*. This occurs more in continuous cropping than in a 1:2 rotation, because with continuous cropping the density of the antagonist is greater than with a 1:2 rotation (Table 5) and as a result fewer sclerotia were formed at the end of the growing season (Table 3). Stem infestation in continuous cropping is more severe than that in the 1:2 rotations because the reduction of inoculum in the year when potato is not grown in the 1:2 rotations exceeds the reduction of inoculum by antagonists with continuous cropping. With continuous cropping, the inoculum density of *R.solani* remains high despite hyperparasitism.

Between days 74 and 117 in Experiment 1 and between days 61 and 108 in Experiment 2 infection of stems and stolons increased (Tables 1 and 2). Although infection of the stems and that of the stolons were not scored separately, the impression is that in the periods mentioned, stolon infection expanded further than that of the stems.

In these experiments two 1:2 rotations can be compared, namely in Experiment 1 sugar beet-potato and maize-potato and in Experiment 2 sugar beet-potato and wheat-potato. In neither experiment was there a clear difference between these rotations in the levels of stem and stolon infection or the amount of black scurf on tubers. The frequency of potato cropping therefore has much more effect on the occurrence of *R.solani* than does the type of the preceding crop.

Effect of nematicides

In both Experiment 1 and Experiment 2 the application of nematicides was accompanied by increases of up to double the levels of infection by *R.solani*. In Experiment 2 the application of nematicides in the WSOP rotation produced a less strong stimulation of *R.solani* than the application of nematicides in the SP, WP and P rotations. A possible explanation could be that in the WSOP plots *R.solani* occurred only at a very low level.

The incidence of *R.solani* was increased in Experiment 1 by applying oxamyl and in Experiment 2 by applying ethoprophos. In Experiment 1, aldicarb was used only in 1985 and 1986 and in Experiment 2 only in 1985. What was designated as the effect of aldicarb in the two experiments could have been the after-effect of applying oxamyl and ethoprophos in preceding years. However, in other trials, not reported in this paper, there were indications that aldicarb caused the same increase of *R.solani* infection as oxamyl and ethoprophos. Leach and Frank (1982) also found an increase of *R.solani* incidence in potato after the application of aldicarb. In field experiments, Ruppel and Hecker (1982) found that in addition to aldicarb, phorate and, less markedly, carbofuran also caused an increase of root rot in sugar beet from *R.solani*. In laboratory tests, Tisserat et al. (1977) observed an increased damping-off of sugar beet seedlings caused by *R.solani* after aldicarb had been applied to sterilized soil that had been artificially infested with *R.solani*.

It is not impossible that in the experiments reported in the present paper the pronounced effect from nematicides may have resulted from their use year after year on the same field.

In 1985, oxamyl in Experiment 1 and ethoprophos in Experiment 2 were both replaced by aldicarb, because research done by J.H.Smelt (Institute for Pesticide Research, Wageningen) indicated that under laboratory conditions the breakdown of oxamyl in Experiment 1 and ethoprophos in Experiment 2 was considerably faster in the plots treated yearly than in those that were not treated. When repeatedly applied to the same plot, the rate of breakdown of a nematicide can increase, because the soil organisms adapt to the chemical and this decreases its effectiveness (Smelt et al., 1987).

In 1984, the infection with *R.solani* in all rotations of Experiment 1 was low, probably because of high temperatures in the autumn of 1983 in combination with a high moisture content of the soil caused by irrigation. These combined factors created ideal conditions for mycoparasitism of *R.solani* by *V.biguttatum*. For this reason the positive effects of nematicides on *R.solani* were less pronounced in 1984 than in the other years. In 1984, in contrast to 1985, the nematicide therefore probably had no positive effect on the stolon pieces infected with *V.biguttatum* (Table 5). When nematicides are applied, *R.solani* has more chance to develop, and this stimulates *V.biguttatum* to multiply. Therefore, the higher infestation of stems and stolons by *R.solani* in the first part of the growing season following the application of nematicides does not result in a higher incidence of black scurf at the end of the growing season (Expt. 1). In fields where there is no clear antagonism for *R.solani*, multiplication of this fungus caused by nematicide application can lead to an increase in the amount of black scurf on the tubers (Expt. 2).

It is not clear why the use of nematicides in a potato field increases the incidence of *R.solani*. There are several possible causes: a) mycophagous species of the soil fauna (nematodes, micro-arthropods) are mostly eliminated by the nematicides, as a result of which *R.solani* can develop unchecked; b) the development of *R.solani* is directly stimulated by the nematicides; c) nematicides decrease the plant resistance; d) nematicides weaken the microbial antagonism and e) nematodes and/or micro-arthropods wound the plant roots and thus the antagonists are favoured by the increased formation of exudates. More detailed research is needed to elucidate the active process. Since nematicides of a greatly varying nature cause the same effect, a common mechanism seems a more likely proposition than a specific mechanism for each nematicide.

Conclusions

1. Increasing the frequency of cropping potato on the same field results in an increase in infection of stems and stolons by *R.solani*.
2. The frequency of cropping potato has a greater effect on the incidence of

R.solani than the type of preceding crop.

3. The effects of cropping frequency are more clearly expressed by the levels of infection of the stems and the stolons of the potato plant than in the occurrence of black scurf on progeny tubers.

4. With a high cropping frequency of potato the antagonist *V.biguttatum* is unable sufficiently to inhibit stem and stolon infection by *R.solani*, notwithstanding its being present in very great density.

5. Application of granular nematicides such as aldicarb, oxamyl and ethoprophos results in a marked increase of infection of potato stems and stolons by *R.solani*.

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CHAPTER 6

EFFECTS OF SOIL-BORNE *RHIZOCTONIA SOLANI* ON YIELD AND QUALITY OF TEN POTATO CULTIVARS

K.Scholte

Summary

The effects of soil-borne *Rhizoctonia solani* on yield and quality of potato were studied by an extensive individual plant sampling procedure. From 1983 to 1986, stem canker and stolon pruning were examined in 10768 plants growing on a sandy soil. Tuber yield and quality and haulm yield per plant were also recorded.

The degree of attack by *R.solani* depended on the cropping frequency of potato. Severe and very severe stem and stolon attacks decreased fresh yield, dry matter yield and dry matter content of tubers and increased the number of deformed and small tubers, whereas the effect on haulm yield and stem number was small.

Potato cultivars differed in susceptibility to *R.solani*, but yield response did not differ significantly between cultivars at the same levels of stem and stolon infection.

Introduction

Rhizoctonia solani is a serious pathogen of potato, causing stem canker and stolon pruning. Infections can occur from both tuber- and soil-borne inoculum. Scholte (1987) showed that the infection through soil-borne inoculum depended on the frequency with which potatoes had been grown; preceding crops other than potato had little effect, a finding confirmed by Specht and Leach (1987).

The effects of stem canker and stolon pruning caused by *R.solani*, on growth, yield or quality have been investigated by Cother and Cullis (1985), Roth (1985), and Hide et al. (1985). There was stem canker and stolon pruning in their experiments, but whereas Hide et al. artificially infected their seed tubers, in the other two studies infection could have been caused by soil- and/or tuber-borne inoculum.

This paper describes experiments designed to elucidate the contribution of *R.solani* to the yield depression of potato in short rotations. The effects of soil-borne inoculum on stem and stolon attack in relation to yield and quality of the potato were investigated. An experiment with long and short rotations supplied excellent inoculum, but had only one cultivar. The effects of cultivar were studied in two experiments with severe levels of soil infestation.

Materials and methods

Experiment 1

In 1983, 1984 and 1985, 18 plants of the cv. Element were harvested individually from each of 32 potato plots 74 and 117 days after planting in a rotation experiment described by Scholte (1987: Experiment 1). The levels of *Rhizoctonia solani* infection, numbers of stems and tubers, and fresh yield, dry matter yield and dry matter content of tops and tubers were measured for each of 3456 plants.

In 1986, cv. Mirka was included in the experiment by dividing each plot into two: 83 days after planting, 18 plants of each cultivar were harvested per plot and infection by *R.solani* assessed.

Experiment 2

This experiment was laid out in 1984 on a field of light sandy soil, containing 2.2 % organic matter and with a pH-KCl of 5.2, where potatoes (1982) and maize (1983) had previously been grown.

In November 1983, 30 000 l ha^{-1} cattle slurry was applied to the field and then ploughed early in March 1984. Before planting, N, P and K fertilizers at 201, 22 and 83 kg ha^{-1}, respectively, were incorporated with a cultivator.

Two very early maturing cultivars, Eersteling and Ostara, and two very late maturing cultivars, Multa and Alpha, were compared at two stem densities, 12 and 24 stems per m^2, achieved by planting one or two seed tubers per hill.

The experiment was a randomized complete block design with four replicates. The plots were 9.0 x 4.5 = 40.5 m^2, of which 7.5 x 3.3 = 24.75 m^2 was harvested. Seed tubers were planted on 8 April at 75 x 30 cm. Weeds, aphids and late blight were controlled.

Two weeks before the expected maturing date, 110 plants per plot were individually harvested. Rhizoctonia infection, stem number, and fresh and dry matter yield of tubers were recorded for each of 3520 plants.

Experiment 3

This experiment was laid out in 1985 on light sandy soil (2.2 % organic matter, pH-KCl 5.2) in a field where maize (1983) and potatoes (1984) had been grown.

To encourage *R.solani*, the field was treated with aldicarb (Temik 10G, Union Carbide Benelux, Maarsen, 10 % a.i., 30 kg ha^{-1} broadcast) one day before planting.

The early maturing cultivars Eersteling, Saskia and Vindika and the late maturing cultivars Alpha, Amigo and Baraka were compared for their sensitivity to *R.solani*.

Experimental design, plot size, plant spacing and other cultural practices were as for Experiment 2. The planting date was 10 April. Harvesting and recording of 2640 plants was also done as in Experiment 2 but tuber quality was additionally assessed.

Determination of R.solani attack

In all experiments *R.solani* attack was classified as:

0 = no attack on stems or stolons;

1 = slight attack: some scattered lesions on the stems;

2 = moderate attack: not more than half the number of stems with a lesion girdling the stem, usually with additional attacks on the stolons;

3 = severe attack: more than half the stems with a lesion girdling the stem and with the stolons severely attacked;

4 = very severe attack: the attack on stems and stolons so severe as to cause 'little potato': many small tubers form near and many break through the soil surface, sometimes aerial tubers form immediately above the ground.

Yields in the group with class 1 attack were found not to have suffered (Experiment 1) and infections in this group could not irrefutably be attributed to *R.solani*, therefore classes 0 and 1 were combined in Experiments 2 and 3. As there were few plants of class 4 in Experiments 1 and 2, class 4 was combined with class 3.

Table 1. Effect of *R.solani* on yield and dry matter (DM) content of haulm, tubers and stems, and tuber number per plant on two different dates (days after planting). Experiment 1.

Time	*R.solani* attack	Rel.DM yield(%)		% DM		Numbers/plant	
		Haulm	Tubers	Haulm	Tubers	Stems	Tubers
74	none	100[a]	100[b]	9.8	14.8	3.9	15.0
	slight	101	99	9.9	14.7	3.8	15.0
	moderate	96*	78*	10.0*	14.5*	3.8	14.0*
	severe	95*	64*	10.2*	13.9*	3.7*	11.8*
117	none	100[c]	100[d]	14.4	22.9	3.5	14.9
	slight	101	102	14.6	23.1	3.6	14.8
	moderate	109*	100	14.6	22.6*	3.5	15.5*
	severe	100	80*	14.7	22.1*	3.3*	15.8*

[a], [b], [c], [d]: 100 = 23.2, 17.0, 31.4 and 144.0 g m^2, respectively.

* Attacked plants differ significantly from healthy plants at $P \leq 0.05$ (according to the test of Dunnett (Steel and Torrie, 1980)).

Seed tuber treatment

Before planting, seed tubers (32-35 mm) visibly free from black scurf were immersed in a solution of validamycine (Solacol, AAgrunol, Haren, 30 g l^{-1} a.i., 3 % solution) to control superficial *R.solani* mycelium.

For Experiments 1 and 2, seed tubers were not pre-sprouted. For Experiment 3, tubers were pre-sprouted for two weeks in light and short, dark sprouts developed on the tubers. Planting was done by hand.

Results

Experiment 1

Dry matter haulm yield was reduced slightly (day 74) or not at all (day 117) by stem and stolon infection by *R.solani* (Table 1), but tuber yield decreased markedly. The relative effect on tuber yield was larger on day 74 than on day 117.

In severely attacked plants the dry matter content of the haulm increased slightly, whereas that of the tubers decreased.

The number of stems was significantly reduced by *R.solani*, but only slightly. Initially, tuber number decreased with increasing severity of Rhizoctonia attack, but on day 117 tuber number was higher for moderately

Table 2. Percentage of plants of cvs Element and Mirka severely or very severely attacked by *R.solani* when grown in different crop rotations. Experiment 1.

Crop rotation[a]	% potato	Element	Mirka	Mean[b]
MSBBP	20	0	1	0 a
MP	50	10	27	18 b
SP	50	10	25	17 b
P	100	40	78	59 c
Mean		15	33***	

[a] MSBBP = maize-sugar beet-barley-barley-potato; MP = maize-potato; SP = sugar beet-potato; P = continuous cropping of potato.

[b] Different letters indicate that means of rotations differ significantly at $P \leq 0.01$ (according to the Studentized range test of Tukey).

*** Means for Mirka and Element differ significantly at $P \leq 0.001$.

and severely attacked plants than for plants free from attack. On average, the incidence of *R.solani* in cv. Mirka was twice as high as in cv. Element (Table 2). This was true for all crop rotations. The incidence and severity of attack by *R.solani* depended on the cropping frequency of potato, but not on the cropping sequence.

Experiment 2

The stem density had no effect on Rhizoctonia attack so in Tables 3 and 4 the effects of densities have been averaged.

Severe but not moderate levels of attack significantly depressed yield and dry matter content of tubers and number of stems per plant (Table 3). Dry matter tuber yield decreased on average by 20 % and the dry matter content of tubers and the number of stems per plant were markedly reduced.

The early maturing cultivars Eersteling and Ostara were less severely attacked than Multa and Alpha (Table 4) and Multa was much more severely attacked than Alpha.

The yield depression of severely attacked plants did not differ significantly between cultivars. Apparently, cv. Ostara reacted more strongly than the other cultivars. However, there was much variation in the yields of severely attacked plants of cv. Ostara because of the small number of infected plants so that the results for this cultivar cannot be considered as reliable.

Table 3. Effect of an *R.solani* attack on relative yield and dry matter (DM) content of tubers, and the number of stems per plant, averaged over four cultivars. Experiment 2.

R.solani attack	Fresh yield tubers	DM yield tubers	% DM tubers	Number of stems per plant
none-slight	100	100	20.9	3.9
moderate	99	97	20.5	3.8
severe	85*	80*	19.6*	3.2*

* Attacked plants differ significantly from healthy plants at $P \leq 0.05$ (according to the test of Dunnet).

Table 4. Percentage of plants moderately or severely attacked by *R.solani* and relative dry matter tuber yield of severely (S) attacked plants, compared with healthy plants, for cultivars of different maturity classes. Experiment 2.

Cultivar	Maturity class	*R.solani* attack			Rel. DM tuber yield (%) for S[a]
		moderate	severe	total[a]	
Eersteling	early	15	8	23 a	82 a
Ostara	early	10	7	17 a	69 a
Multa	late	34	20	54 c	83 a
Alpha	late	26	12	38 b	84 a

[a] Different letters indicate that differences between cultivars are significant at $P \leq 0.05$ (according to the Studentized range test of Tukey).

Experiment 3

The dry matter yield of tubers was reduced more than the fresh yield and both decreased with increasing severity of *R.solani* attack on stems and stolons (Table 5). The weight percentage of small tubers (<35 mm) was greatly increased in very severely attacked ('little potato') plants. The weight percentage of misshapen tubers increased greatly with increasing levels of Rhizoctonia attack. Moderate attack had little effect on tuber yield and quality.

There were differences in the incidence of severely plus very severely attacked plants between cultivars (Table 6). Cv. Amigo was less infected than most of the other cultivars whereas cv. Eersteling seemed to be very susceptible. The number of very severely attacked ('little potato') plants

Table 5. Effect of an *R.solani* attack on relative dry matter tuber yield and dry matter content of tubers, and proportion of small and deformed tubers, averaged over six cultivars of different maturity classes. Experiment 3.

R.solani attack	Fresh yield tubers	DM yield tubers	% DM tubers	Weight % of tubers	
				<35 mm	deformed >35 mm
none-slight	100	100	20.9	8	23
moderate	97	95	20.7	8	28
severe	87*	82*	19.7*	10	40*
very severe	79*	71*	18.9*	23*	59*

* Attacked plants differ significantly from healthy plants at $P \leq 0.05$ (according to the test of Dunnet).

Table 6. % plants severely or very severely attacked by *R.solani* and relative mean dry matter (DM) tuber yield of severely (S) and very severely (VS) attacked plants compared with healthy plants. Experiment 3.

Cultivar	Maturity class	*R.solani* attack (% plants)			Rel.DM tuber yield of S+VS plants (%)[a]
		severe	very severe	total[a]	
Amigo	late	40	7	47 a	75 a
Vindika	early	47	11	58 ab	75 a
Alpha	late	44	17	61 bc	74 a
Baraka	late	59	3	62 bc	78 a
Saskia	early	52	14	66 bc	72 a
Eersteling	early	49	22	71 c	85 a

[a] Different letters indicate that differences between cultivars are significant at $P \leq 0.05$ (according to the Studentized range test of Tukey).

was high for cv. Eersteling and Alpha but very low for cv. Baraka.

The mean yield depression of severely and very severely attacked plants did not differ significantly between cultivars.

Discussion

Because the seed tubers planted in the experiments were free from black scurf and had been disinfected, only soil-borne inoculum of *R.solani* could be held responsible for infections.

Severe attacks reduced the yield and quality of tubers but a slight or moderate attack had little or no effect. The fresh tuber yields of severely and very severely attacked plants were reduced by ca. 16 and 21 %, respectively, and dry matter tuber yields were reduced by ca. 20 and 29 %, respectively. Marketable yield was reduced even more because the proportion of tubers >35 mm decreased and the proportion of misshapen tubers greatly increased.

Roth (1985) and Cother and Cullis (1985) also used an individual plant sampling procedure to study the effects of *R.solani* infections on yield. However, because they did not disinfect their seed tubers, their *R.solani* stem and stolon infections could have been caused by soil-borne and/or tuber-borne inoculum. In severely attacked plants, Roth found fresh tuber yields reduced by 13-24 %, depending on cultivar. Cother and Cullis found that when all stolons of a plant were pruned, fresh tuber yield was reduced by 24 %.

Hide et al. (1985b) inoculated seed tubers in the ridge at planting and found yields reduced by 4 % compared to their controls. Chand and Logan (1982) found, averaged over ten cultivars, a fresh yield reduction of 18 % in plots artificially inoculated with *R.solani* compared with uninoculated plots.

Other workers have applied specific fungicides to the soil to study the effects of soil-borne *R.solani* on yield. Cother (1983) and Davis (1978) used pesticides based on quintozene (PCNB), but this is not a good standard because, at the recommended dosages, it is phytotoxic to potato, lowering yields (Van Emden, 1958). In two experiments on sandy soils, Mulder and Roosjen (1982) planted disinfected seed tubers in plots untreated and treated with tolclofos-methyl, furmecyclox and pencycuron. At the recommended dosages, dry matter yields of tubers were 4-13 % higher on treated than on untreated plots.

The success of soil-applied fungicides depends on the inoculum level of *R.solani*. In plots on sandy soil continuously cropped with potato Scholte (1987) found 30 % severely attacked plants, averaged over four years. The yield reduction of such a crop can be calculated with formulae derived from the results of the experiments discussed in this report. The relationships between the percentage of severe (S) and very severe (V) attacks of stems and stolons caused by *R.solani* and the related total fresh (F) and dry matter (D) tuber yield can be expressed as:

$$F = (100 - S - V) + 0.84S + 0.79V \quad \text{and}$$

$$D = (100 - S - V) + 0.80S + 0.71V.$$

For crops with 30 % severely attacked plants, the fresh and dry matter tuber yields are decreased by about 5 % and 6 %, respectively. As these values are close to the limit for significance at $P \leq 0.05$, it is difficult to prove that the beneficial effects of soil applied fungicides are statistically significant.

The negative effect of an *R.solani* infection on tuber yield tends to decrease towards the end of the growing season: for example 36 % lower yield on day 74 and 20 % on day 117 for severely attacked plants (Table 1). A similar effect was found by Griffith (1984) and Hide et al. (1985b)

Young sprouts are very susceptible to *R.solani* infection and early infection can prune off a stem as occurs especially with tuber-borne rather than soil-borne inoculum (Frank, 1978: Van Emden et al., 1966). This phenomenon may explain why the effects of attack on the number of main stems were small in Experiments 1 and 2.

Van Emden (1965) concluded that when sprouts were exposed to light after emergence they became resistant to *R.solani* but this does not always seem to be true. Scholte (1987), Roth (1985) and Hide et al. (1985a) found a marked increase in stem infection after emergence. Susceptibility seems to decrease gradually with increasing age of stems, probably due to a change in the structure and composition of the outermost cell layers. Similarly, sprouts formed in the light are not attacked by *R.solani* but when seed tubers that have been pre-sprouted under light are planted deeply, the part of the sprout which forms between the original sprout tip and the soil surface is again susceptible to *R.solani* (Roosjen and Mulder, 1982).

Cother and Cullis (1985) found no significant relationship between stem canker and tuber yield and concluded that only stolon pruning results in lower yields. This seems debatable; the effect of stolon attack may be more important for yield than stem attack, but stem attack also affects growth of the plant. A severe stem attack on a young plant results in diminished growth (Table 1, day 74). Clearly, the mean weight of the stems is lower for severely attacked than for healthy plants; this is true in young plants even for those moderately attacked. However, a severe stem attack is often associated with severe stolon attack, a relationship also found by Weinhold et al. (1982). However, late stolon attack may occur without a stem infection.

Initially, stem canker and stolon pruning have a large depressive effect on total plant weight. However, tuber yield is reduced more than haulm yield, and tuber number is also reduced. Stolon infection delays tuber initiation and, as a result, tuber yield is slower to develop. Stem canker and stolon pruning change the distribution pattern of dry matter within the plant. Translocation of carbohydrates from the haulm to underground plant parts is hampered, dry matter accumulates in the haulm so that in attacked plants the haulm dry matter content is higher and that in the tubers is lower compared with healthy plants. These trends are maintained later in the growing season but the initial differences in haulm weight disappear. Hide et al. (1985b) found a lower weight for main stems, but this was compensated by a higher weight for lateral stems. In severely attacked plants tuber number per plant was initially lower, but later in the growing season it was higher than in plants that had not been attacked. In very severely attacked plants, the 'little potato' plants, only a few tubers remained on the underground stem bases; they usually grew into large tubers, whereas near the soil surface many small tubers developed.

Plants severely and very severely attacked by *R.solani* appear to be continuously in a state of secondary growth, resulting in deformed tubers (elongated and knobby tubers with protruding eyes). The second-growth phenomena are probably the result of fluctuating hormone levels in the plant. Tubers situated near the soil surface, sometimes partly exposed, are also exposed to higher temperatures and this also promotes second growth. The dormancy of these tubers is low (Gadewar et al., 1980).

The effects of an *R.solani* attack on tuber yield and quality depend on the cultivar and perhaps, on circumstances. For example in Experiment 2, the two late maturing cultivars were attacked more severely than the two early maturing cultivars. The seed tubers had been planted directly from cold store and were not pre-sprouted so that the late maturing cultivars emerged much later than the early maturing ones. The latter therefore 'escaped' *R.solani* attack.

Of the two early maturing cultivars, Eersteling was more seriously (though not significantly so) attacked than Ostara, whereas of the late maturing cultivars, Multa was much more severely attacked than Alpha. In Experiment 3, seed tubers were pre-sprouted, differences in date of emergence were small, *R.solani* attack was serious, and the differences in attack between cultivars were statistically significant, but were not related to the earliness of the cultivar. Differences were also found in the number of very severely attacked ('little potato') plants. Alpha and Baraka had the same number of plants that were at least severely attacked, but the proportion of 'little potato' plants was much higher for Alpha than for Baraka. Eersteling had very many 'little potato' plants.

Experiment 1 also revealed that cultivars differ in susceptibility. The level of attack was twice as high in Mirka as in Element. Differences between cultivars in susceptibility to *R.solani* were also found by Assenov (1986), Bogucka (1983), Plamadeala (1978), Frank et al. (1976), Dowley (1972) and Hofferbert and Orth (1951).

One conclusion from Experiments 2 and 3 is that if cultivars are to be compared for their resistance to *R.solani*, precautions should be taken, such as pre-sprouting the seed tubers, to ensure that the time between planting and emergence is about the same for all cultivars.

In Experiments 2 and 3 there was no evidence that cultivars differ in sensitivity to *R.solani*; at the same level of attack there were no significant differences in yield reductions.

Conclusions

1. Severe and very severe attacks of stems and stolons by soil-borne *R.solani* decreases fresh yield, dry matter yield and dry matter content of tubers, increases the proportion of deformed and small tubers, but have a negligible effect on haulm yield and stem number.
2. Slight and moderate attacks have very small or no effects on yield and quality.
3. The relative fresh (F) or dry matter (D) yield of tubers can be estimated from the percentage of severely (S) and very severely (V) attacked plants by the formulae:

$$F = (100 - S - V) + 0.84S + 0.79V \quad \text{and}$$

$$D = (100 - S - V) + 0.80S + 0.71V.$$

4. Potato cultivars differ in susceptibility to stem and stolon infection by *R.solani*, but there is no evidence that they differ in sensitivity.

Potato Research 32 (1989) in press

CHAPTER 7

EFFECTS OF CROP ROTATION AND GRANULAR NEMATICIDES ON THE INCIDENCE OF *VERTICILLIUM DAHLIAE* AND *COLLETOTRICHUM COCCODES* IN POTATO

K.Scholte

Summary

The incidence of *Verticillium dahliae* and *Colletotrichum coccodes* was studied in a crop rotation experiment on sandy soil from 1983 to 1986. Early in the growing season the percentage of stems infected by *V.dahliae* increased with increasing cropping frequency of potato, depending on the cropping sequence, and decreased with the application of granular nematicides. However, later in the growing season the initial differences decreased. *C.coccodes* infections of stems were not affected by these factors. The percentage of plants infected by *V.dahliae* closely correlated with the percentage of plants with wilt symptoms but this relationship was absent for *C.coccodes*.

Early in the growing season, the more vigorous the plants, the greater the level of *V.dahliae* infection.

Soil infestation with *V.dahliae* increased with increasing cropping frequency of potato but was not affected by annual applications of granular nematicides.

Introduction

From 1979 experiments were carried out to study the effects of short rotations on the yield of potato and on the development of soil-borne diseases in that crop. The pathogens investigated in detail were *Streptomyces* spp. (causing netted scab), *Rhizoctonia solani*, *Verticillium dahliae* and *Colletotrichum coccodes*. In rotations with a high frequency of potato, nematicides are used to prevent or to control potato cyst nematodes (*Globodera* spp.), but these pesticides may also affect other pathogens of potato.

Earlier reports described the effects of crop rotations and granular nematicides on the incidence of *R.solani* (Scholte, 1987) and the effects of stem and stolon attacks by this fungus on yield and quality (Scholte, 1989b). The effects of crop rotations and granular nematicides on the incidence of *V.dahliae* and *C.coccodes* are presented in this report.

V.dahliae causes wilt symptoms in potato resulting in early senescence. The fungus survives in the soil by microsclerotia which can form in large numbers on infested maturing hosts. *V.dahliae* has a wide host range among dicotyledonous plants (Woolliams, 1966). *C.coccodes* is usually thought to be a weak pathogen (Otazu et al., 1978) and it too survives in soil by microsclerotia (Farley, 1976) formed on all parts of dying potato plants (Schmiedeknecht, 1956).

Material and methods

Crop rotation experiment

This experiment, described by Scholte (1987: Experiment 1), was laid out near Wageningen in 1979 on light sandy soil containing 2.6 % organic matter and with a pH-KCl of 5.2. The experiment comprised four rotations:

P = continuous cropping of potato
MP = maize - potato
SP = sugar beet - potato
MSBBP = maize - sugar beet - barley - barley - potato

These were compared on untreated plots and on plots treated annually with a granular nematicide even when crops other than potato were grown. Nematicide was always broadcast one day before planting and then incorporated into the soil with a spring-tine cultivator. Oxamyl (Vydate 10G, Shell Nederland Chemie, Den Haag, 10 % a.i., 50 kg ha^{-1}) was applied from 1979 to 1984 and aldicarb (Temik 10G, Union Carbide Benelux, Maarssen, 10 % a.i., 30 kg ha^{-1}) in 1985 and 1986.

The experiment was laid out in a randomized complete block design with four replications; every crop in a rotation was grown in each year. For example, for the MSBBP rotation there were five untreated and five treated plots in each replication. Each plot was 12 x 6 = 72 m^2. In 1986 potato was also grown for the first time since 1977, on plots that had grown rye for one year followed by seven years of barley.

The cultivar used was Element but in 1986, cv. Mirka was included on split plots because of its high tolerance to *Verticillium dahliae* (Scholte et al., 1985).

Assessment of V.dahliae and C.coccodes infection

Eighteen plants were harvested from each plot ca. 74 (1983 to 1986) and 133 (1984) days after planting, according to a predetermined scheme. Four stems of each plant were checked for infections by *V.dahliae* and *C.coccodes*. Pieces 2 cm long from the underground stem were disinfected in 1 % NaOCl for one minute and rinsed three times in sterile distilled water for one minute. A cross-section 1-2 mm thickness was cut from the middle of each piece and 8 sections per dish placed on selective pectate-NPX medium (Huisman and Ashworth, 1974) in Petri dishes and incubated at 22 °C. After 4-6 weeks the numbers of stem pieces with colonies (microsclerotia) of *V.dahliae* and/or *C.coccodes* were counted.

The fresh and dry matter yields of haulm and tubers per plant and the numbers of stems and tubers per plant were also determined.

In 1983 and 1984 the percentage of plants with wilt symptoms in the field was observed two weeks after the periodic harvest on day 74.

Assessment of V.dahliae infestation of soil

Before nematicides were applied and potatoes planted in the field, 18 (1983) or 24 (1984) soil samples (0.4 kg) were taken per plot. Each sample was sieved through a 0.5 cm screen to remove stones and coarse plant fragments, and put into a 100 ml pot. The pots from one plot were placed in a tray and the spaces between the pots filled with quartz sand. In each pot three eggplant seeds (*Solanum melongena*, cv. Vedette) were sown at 0.5 cm depth. The trays of pots were placed in a glasshouse at 24 °C. After emergence the seedlings were thinned to one per pot. The number of plants with wilt symptoms was recorded regularly until their number increased slowly (about 8 weeks after sowing). Isolations were made from the base of stems from plants with wilt symptoms.

Results

Early in the growing season the percentage of stems infected with *V.dahliae* depended on the rotation (Table 1). The highest levels of infection were found in plots continuously cropped with potato (P) and in plots from the SP rotation but there were no significant differences between these two cropping systems. Stem infection differed between the rotations with potatoes in alternate years, MP and SP, and was significantly lower in MP than in SP. The lowest infection level was found in the MSBBP rotation. Application of

Table 1. Percentage of potato stems infected with *V.dahliae* and *C.coccodes* ca. 74 days after planting in four rotations in control plots and plots treated with nematicides, averaged over 1983-1986.

Rotation[a]	*V.dahliae*			*C.coccodes*		
	control	nematicide	mean[b]	control	nematicide	mean[b]
P	49	34	41 a	35	32	33 a
MP	39	20	29 b	29	30	30 a
SP	50	38	44 a	33	36	35 a
MSBBP	21	13	17 c	28	27	28 a
Mean	40	26***		31	31	

[a] P = continuous cropping of potato; MP = maize-potato; SP = sugar beet-potato and MSBBP = maize-sugar beet-barley-barley-potato.

[b] Dissimilar letters indicate significant differences between rotations at $P \leq 0.01$ (according to the Studentized range test of Tukey).

*** Nematicide treatment differs significantly from control at $P \leq 0.001$.

Table 2. Percentage of potato stems infected with *V.dahliae* and *C.coccodes* in 1984 133 days after planting in four rotations in control plots and plots treated with a nematicide.

Rotation[a]	*V.dahliae*			*C.coccodes*		
	control	nematicide	mean[b]	control	nematicide	mean[b]
P	82	87	85 a	97	100	99 a
MP	90	76	83 a	97	100	99 a
SP	91	86	89 a	99	99	99 a
MSBBP	56	33	44 b	94	97	96 a
Mean	80	71		97	99	

[a] For explanation: see Table 1.

[b] Dissimilar letters indicate significant differences between rotations at $P \leq 0.05$ (according to the Studentized range test of Tukey).

nematicides greatly reduced the number of infected stems in all rotations.

Later in the growing season, the differences in *V.dahliae* stem infection were smaller (Table 2) and none were significant between the three short rotations; the level was least in the five-course rotation MSBBP. The decreasing effects of the nematicide disappeared in rotations P and SP. The

Table 3. Relationship between (A) the percentage of plants infested with *V.dahliae* detected from stem pieces on Petri dishes containing a selective medium on 16/6/1983, and (B) the percentage of plants with wilt symptoms in the field on 29/6/1983, in four rotations in control plots and plots treated with a nematicide.

	Control					Nematicide				
	Rotation				Mean	Rotation				Mean
	P	MP	SP	MSBBP[a]		P	MP	SP	MSBBP	
A	81	73	73	12	60	62	40	63	9	43*
B[b]	85	81	72	17	64	54	39	54	13	40**

[a] For explanation: see Table 1.

[b] Figures for B are closely correlated with those for A: $r = 0.975$ ($P \leq 0.001$).

* and ** Nematicide treatment differs significantly from control at $P \leq 0.05$ and $P \leq 0.01$, respectively.

percentage of infected plants as detected from the stem pieces on the selective medium (by mid June), was closely correlated with the number of plants with wilt symptoms (two weeks later) (Table 3).

Crop rotation and the application of nematicides did not affect the percentage of plants infected by *C.coccodes* (Tables 1 and 2).

The bioassay with eggplant gave a measure of the level of *V.dahliae* infestation in the soil and this infestation was clearly influenced by the cropping frequency of potato (Table 4). The highest infestation was found in plots continuously cropped with potato (P). Rotations with 50 % potato (MP and SP) showed similar, intermediate levels and the lowest infestation was found in rotation MSBBP with one potato crop in five years. Application of nematicides in the previous years did not affect the level of soil infestation. Isolations from the base of stems from eggplants with wilt symptoms consistently yielded *V.dahliae*.

In 1984, there were indications that early in the growing season plants infected by *V.dahliae* weighed more than healthy plants. Therefore, in 1985 segments of all stems were plated onto the selective medium and Table 5 shows that there were significant positive linear relationships between the percentage infected stems and the weight of haulm and tubers. The heavier the plant, the higher the level of infection with *V.dahliae*. No significant relationships were found between stem infection and stem and tuber number

Table 4. Percentage of eggplants with wilt symptoms in batches of test soils from four rotations in control soil and soil treated with nematicides in previous years, averaged over 1983 and 1984.

Soil treatment	Rotation				Mean
	P	MP	SP	MSBBP[a]	
Control	61	25	32	6	31
Nematicide	69	28	29	4	33
Mean[b]	65 a	26 b	30 b	5 c	

[a] For explanation: see Table 1

[b] Dissimilar letters indicate significant differences between rotations at $P \leq 0.01$ (according to the Studentized range test of Tukey).

Table 5. Relationship between *V.dahliae* infection and plant parameters 76 days after planting in 1985.

Growth parameter	% stems/plant infected with *V.dahliae*					r
	0	25	50	75	100	
Haulm dry matter (g/plant)	29.2	30.4	31.0	31.2	32.7	0.97**
Tuber dry matter (g/plant)	20.3	21.2	22.1	24.3	25.2	0.98**
Total dry matter (g/plant)	49.5	51.6	53.1	55.5	57.9	0.99**
Relative total dry matter	100	104	107	111	117	
Dry matter content haulm (%)	9.3	9.4	9.3	9.4	9.3	0
Dry matter content tubers (%)	14.0	14.2	14.3	14.5	14.5	0.97**
Stem number/plant	4.2	4.4	4.3	4.3	4.0	-0.52
Tuber number/plant	15.0	15.7	15.5	14.9	14.5	-0.59
Number of plants analysed	104	110	118	121	123	

** Correlation coefficient r differs significantly from 0 at $P \leq 0.01$.

per plant. Most plants had four stems and each infection class was represented by more than 100 plants.

No relationship was found between stem infection by *C.coccodes* and plant weight.

In 1986, plants of cv. Mirka had less *V.dahliae* infection and slightly less *C.coccodes* infection than plants of cv. Element (Table 6).

Table 6. Percentage infection of stems by *V.dahliae* and *C.coccodes* 83 days after planting in 1986 for cvs Element and Mirka in control plots and plots treated with a nematicide, averaged over four rotations.

Cultivar	*V.dahliae*			*C.coccodes*		
	control	nematicide	mean	control	nematicide	mean
Element	31	19	25	66	66	66
Mirka	8	5	7***	48	55	52***
Mean	25	12*		57	61	

* Nematicide treatment differs significantly from control at $P \leq 0.05$.
*** Mirka differs significantly from Element at $P \leq 0.001$.

Discussion

This experiment showed that rotations markedly affected the percentage of stems infected by *V.dahliae* and confirms the results obtained by Bollen et al. (1989) and Lamers (1989). The number of infected stems not only depended on the cropping frequency of potato but also on the type of crops in the rotation. The rotation of potato and sugar beet showed a markedly greater number of infected stems than that of potatoes and maize.

The number of infected stems and the rate of infection by *V.dahliae* with time depends on how heavily the soil is infested with its microsclerotia. The inoculum level in soil depends, in turn, on the type of host crops and the proportion of non-host crops in the rotation. Many dicotyledonous crops and weeds are hosts for *V.dahliae* (Evans, 1971; Woolliams, 1966), but the ability of the fungus to produce microsclerotia differs among host plants. Numerous microsclerotia are produced in stems of potato, field beans (Hoekstra, 1989b) and cotton (Huisman and Ashworth, 1976) and when the above-ground stem parts of these crops remain in the field after harvest, the inoculum level of *V.dahliae* in soil increases greatly. Levels of inoculum in soil decrease when monocotyledonous crops or sugar beet are grown, on which the fungus produces few, if any, microsclerotia. This could explain why the inoculum levels detected in soil by the bioassay were lowest in MSBBP, and lower in MP and SP than in P (Table 4).

Huisman and Ashworth (1976) found that the inoculum level of *V.dahliae* in soil increased rapidly after cotton, but once soils were infested, the rate of inoculum decrease, even in the presence of non-host crops, was very low.

In my experiment, 83 days after planting, 12 % of the stems of cv. Element were infected with *V.dahliae* on those plots cropped with potato in 1986 for the first time since 1977, following one year of rye and seven years of barley. On the same day the percentage infected stems in the MSBBP and SP rotations were 29 and 43 %, respectively. Thus, soil infestation with *V.dahliae* decreased if plants had been grown that were poor hosts or non-host, but the rate of attrition of its propagules under non-hosts appeared low. However, there is a disagreement about whether monocotyledonous plants may be considered strictly as nonhosts (Krikun and Bernier, 1987; Malik and Milton, 1980; Mathre, 1986).

The rate and level of infection of a crop with *V.dahliae* may depend not only on the inoculum level in the soil. Thus, although treatments SP and MP had similar soil infestation levels (Table 4), early in the growing season the number of infected plants was much higher in SP than in MP (Table 1). Application of nematicides evidently retarded the infection of plants (Table 1) and Hoyman and Dingman (1967) found similar results with aldicarb when applied to a field heavily infested with *V.dahliae* and the root-knot nematode *Meloidogyne hapla*. A synergistic relationship between *V.dahliae* and endoparasitic nematodes has been proved for *Globodera* spp. (Evans, 1987; Corbett and Hide, 1971), *Meloidogyne hapla* (Jacobsen et al., 1979), *Pratylenchus thornei* (Siti et al., 1979) and *Pratylenchus penetrans* (Rowe et al., 1985). *V.dahliae* is able to penetrate unwounded roots easily, but most hyphae fail to penetrate deeper than the epidermal layers (Perry and Evert, 1983). Nematodes assist *V.dahliae* to evade the natural defences of the root by opening an invasion channel for the fungus (Storey and Evans, 1987) and/or inducing physiological changes in the host (Riedel, 1988).

Before the potato crops were planted, population densities of root-knot nematodes (*Meloidogyne* spp.) were much higher in soil of SP than in MP (Leijdens and Hofmeester, 1986). Possibly, therefore the greater numbers of nematodes in SP stimulated infection in this rotation so that although the levels of soil infestation with *V.dahliae* propagules were equal, there were initially more infected stems in SP than in MP. Thus, the decrease in level of stem infection when nematicides had been applied to the soil was probably caused by the reduction of *Meloidogyne* populations. However, the reduction of *Pratylenchus* populations, mainly *P.crenatus* (70 %), but also *P.penetrans* (15 %), *P.neglectus* and *P.fallax* (Leijdens and Hofmeester, 1986), may also have contributed to this phenomenon. Riedel et al. (1985) showed that *P.penetrans*, but not *P.crenatus*, promoted infection by *V.dahliae*.

Although Evans and McKeen (1975) obtained a considerable reduction in the number of viable microsclerotia of *V.dahliae* by growing a non-host or by fallow inoculum densities in MP and SP were high after the potato crops. It is possible that the crop following potato (maize in MP and sugar beet in SP) may have selected for strains that differ in pathogenicity to potato because Krikun and Bernier (1987), Zilberstein et al.(1983) and Isaac and Rogers (1974) obtained isolates specific to certain host plants. Also, Tjamos (1981) found that the degree of pathogenicity of *V.dahliae* to tomato depended on the previous cropping history. Thus, the sugar beet crop may have selected for strains that are more pathogenic for potato than did maize, assuming that *V.dahliae* can reproduce on maize.

Positive correlations were found between the percentage stems infected by *V.dahliae* and plant weight (Table 5) but it seems unlikely that the growth of plants is stimulated by *V.dahliae* infection. When I grew potatoes in soil artificially infested with *V.dahliae* there was no difference between their weights and those of control plants at the time when symptoms of wilt appeared (unpublished results). One explanation could be that rapidly growing plants with an extensive root system are more likely to encounter propagules of *V.dahliae* and to become infected than slow-growing plants.

Nematicides did not affect stem infection by *C.coccodes*; no relationship was found between the cropping frequency of potatoes and the number of stems infected (Table 1) and at the end of the growing season all the stems in each rotation were infected. There was only a very weak relation between the number of stems infected and the number of stems with wilt symptoms. So it seems unlikely that *C.coccodes* was responsible for wilt symptoms early in the growing season. Emmond and Ledingham (1972) obtained similar results and this absence of a relationship may be because tuber-borne inoculum also acted as an infection source since seed tubers are often severely infested with *C.coccodes* (Komm and Stevenson, 1978; Mooi, 1956).

Conclusions

1. Increasing the frequency of potato cropping on the same field results in an increase in infection of stems by *V.dahliae* early in the growing season, but has no effect on the *C.coccodes* infection of stems.
2. Cropping sequence affects the number of stems infected with *V.dahliae* early in the growing season, because of different numbers and species of endoparasitic nematodes in the soil.
3. Application of the granular nematicides aldicarb and oxamyl results in a

marked decrease in *V.dahliae* infection of potato stems early in the growing season but has no effect on the infection of stems by *C.coccodes*. At the end of the growing season, soil infestation with *V.dahliae* microsclerotia is the same in untreated and nematicide-treated soils.

4. The number of potato stems infected with *V.dahliae* depends greatly on the cultivar grown.

5. There is a close relationship between number of *V.dahliae* infected stems and the occurrence of wilt symptoms, but there is no such relationship for *C.coccodes*.

6. There is a close positive relationship between the level of *V.dahliae* infection and the size of the potato plant early in the growing season.

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CHAPTER 8

SYNERGISTIC INTERACTIONS BETWEEN *RHIZOCTONIA SOLANI*, *VERTICILLIUM DAHLIAE*, *MELOIDOGYNE* SPP. AND *PRATYLENCHUS NEGLECTUS* IN POTATO

K. Scholte and J.J. s'Jacob

Summary

Samples of a sandy soil and a marine clay soil sterilized by steam were put in 55-l containers insulated with polystyrene and placed outdoors on a brick pavement. Sandy soil was infested singly or in all possible combinations with root-knot nematodes (*Meloidogyne* spp.) and the fungi *Rhizoctonia solani* and *Verticillium dahliae*, and the marine clay soil was infested with the root-lesion nematode *Pratylenchus neglectus* and the same fungi to evaluate the effects of these organisms on the yield of potato. The experiments were carried out from 1983 to 1986.

Tuber yield was reduced by single infestations of the *Meloidogyne* spp. and *V.dahliae* but not significantly by *R.solani* or *P.neglectus*. A three-factor interaction: nematode * *R.solani* * *V.dahliae* was found in both experiments. *R.solani* and *V.dahliae* showed significant synergistic effects when soil was infested with the *Meloidogyne* spp. or *P.neglectus*.

Introduction

Two experiments were initiated in 1979 to study the effects of short rotations on the yield of potato and on the development of its pests and diseases. In both experiments yield decreased (Scholte, 1989d; Scholte and s'Jacob, 1989b) and the population density of soil-borne pathogens increased with increasing frequency of cropping potato (Scholte, 1987 and 1989c; Leijdens and Hofmeester, 1986).

Pathogens affect the growth and yield of potato but their effects are influenced by the way they interact with each other, with non-pathogenic components of the soil flora and fauna, and with the environment.

To elucidate some of the effects and interactions, two container experiments were carried out from 1983 to 1986. In one experiment, the interactions between root-knot nematodes, *Meloidogyne chitwoodi* and *M.hapla*, and the pathogenic fungi *Rhizoctonia solani* and *Verticillium dahliae* were investigated. These organisms occurred together in a crop rotation experiment on a sandy soil (Scholte, 1987, 1989c; Leijdens and Hofmeester, 1986). In the other experiment, the interactions between the same fungi and the root-lesion nematode *Pratylenchus neglectus* were studied, organisms that occurred together in a crop rotation experiment on a marine clay soil (Scholte and s'Jacob, 1989b).

Materials and methods

Experiment 1

For this experiment a quantity of a light sandy soil, containing 2.8 % organic matter and with a pH-KCl of 5.2, was sieved on 14 December 1982, thoroughly mixed and sterilized with steam at 100 °C for one hour. Plastic containers of 94 x 34 x 23 cm (l x w x h) with drainage holes near the bottom were placed outdoors on a brick pavement and each was filled with about 55 l of the soil. The containers were insulated with 2-cm thick polystyrene sheets on all vertical sides.

On 26 April 1983 root-knot nematodes, *Meloidogyne hapla* and *M.chitwoody*, were introduced in half the number of the containers and to increase the population, red clover (cv. Barfiola) was grown during the summer and peas (cv. Finale) during the autumn: in winter, winter rye (cv. Dominant) was grown to provide soil cover.

On 25 April 1984 inoculum of *Rhizoctonia solani* and *Verticillium dahliae* was mixed with the soil. Each species was used singly or in combination with each other and with the *Meloidogyne* spp.. When a given organism was omitted from a treatment an equal volume of a sterilized culture of that organism was added instead. Control containers consisted of soil with killed inoculum of both fungi.

The experiment was set out as a randomized complete block design with 8 replications. The cultivar used was Element which was also used in the crop rotation experiment on sandy soil.

Experiment 2

A quantity of a marine clay soil, containing 6.7 % organic matter and with a clay fraction (< 2 μm) of 30 % and a pH-KCl of 7.4, was treated in the same way and on approximately the same dates as the sandy soil in Experiment 1.

On 26 April 1983 the nematode *Pratylenchus neglectus* was introduced in half the number of the containers and to increase the population, maize (cv. Dorina) was grown during the summer and wheat (cv. Arminda) during the autumn and winter.

On 25 April 1984 inocula of *R.solani* and *V.dahliae* were mixed with the soil as was done in Experiment 1.

The experiment was set out as a randomized complete block design with 4 replications. The cultivar used was Hertha which was also used in the crop rotation experiment on marine clay soil.

Experimental procedure

On 26 April 1984 and 1985 and on 24 April 1986 six 20 g single-sprouted tubers, visibly free from black scurf and previously disinfected by immersion for 5 minutes in ethyl mercury bromide (AArdisan, AAgrunol, Haren, 4 % a.i., 0.3 % solution) to kill superficial mycelium of *R.solani*, were planted 9 cm deep in each container. After emergence the plants were watered once or twice daily depending on the weather.

Each year the following quantities of nutrients were applied to each container, apportioned over five applications from planting date to 12 weeks after planting : 27.2 g N, 4.4 g P, 35.5 g K, 2.5 g Mg and 57 ml of a trace element solution containing 20 g $MnSO_4 \cdot H_2O$, 30 g H_3BO_3, 5 g $ZnSO_4 \cdot 7H_2O$, 1 g $CuSO_4 \cdot 5H_2O$ and 1 g $Na_2MoO_4 \cdot 2H_2O$ per litre of water.

During the growing season *Phytophthora infestans* was controlled by regular sprayings of chlorothalonil (Daconyl 2787, AAgrunol, Haren, 73 % a.i.) at the manufacturers recommended rates.

Before harvest the tops of the plants were collected, cut into small pieces and mixed with the upper 10 cm of the soil of the containers from which they originated. In 1985 and 1986, 4 weeks before planting, soil was turned over in each container.

Nematode inoculation

For Experiment 1, soil was taken on 10 December 1982 from plots continuously cropped with potato in a rotation experiment near Wageningen on sandy soil (Scholte, 1987: Experiment 1), sieved and put into 16-1 plastic trays. Seeds of Pot Marigold (*Calendula officinalis*) were sown in the soil to trap nematodes consisting of a mixed population of *M.hapla* and *M.chitwoodi*. The trays were placed in a glasshouse at 22 °C.

On 11 Januari 1983 plants were dug out, rinsed in tap water, the roots surface sterilized in 2 % NaOCl for one minute and again rinsed in tap water. They were replanted into 16-l plastic trays that had been filled with sandy soil sterilized with steam at 100 °C. On the same day, seeds of Pot Marigold were sown near the disinfected replanted seedlings and the containers again placed in the glasshouse. Examination of the roots of the seedlings showed that no endoparasitic nematodes other than the *Meloidogyne* spp. were present.

On 25 April 1983, aerial parts of the Pot Marigold plants were removed from the trays, and the soil and roots in the trays mixed and incorporated into the soil in the containers on the brick pavement. Half the number of the containers received 2 l of soil infested with *Meloidogyne* spp.; the others received 2 l soil containing Pot Marigold roots without the nematodes spp. After inoculation, red clover (cv. Barfiola) was sown in all the containers to increase the nematode population during the summer of 1983. On 15 August 1983, the aerial parts of clover were removed and on 2 September 1983 a mixture of pea (cv. Finale) and winter rye (cv. Dominant) was sown. The rye was killed on 4 April 1984 with paraquat (Gramoxone, ICI Holland, Rotterdam, 20 % a.i., 5 ml per l water).

For Experiment 2, soil was taken on 7 December 1982 after a wheat crop from plots alternately cropped with potato and wheat in a rotation experiment in the East Flevoland Polder on a calcareous marine clay (Scholte, 1987: Experiment 2), sieved and put into 16-l plastic trays. Seeds of maize (cv. Dorina) were sown in the soil to trap *P.neglectus* and the trays placed in a glasshouse at 22 °C.

On 11 Januari 1983 the plants were dug out, and disinfected in the same way as was done with Pot Marigold in Experiment 1, and replanted to 16-l trays filled with steam (100 °C) sterilized marine clay soil. Seeds of maize were sown near the transplanted seedlings which were cut off above soil level on 21 Januari 1983.

On 26 April 1983 the maize plants were decapitated, the soil and finely chopped roots mixed in the trays, and then incorporated into the soil in the containers on the brick pavement. Half the number of these containers received 2 l of soil infested with *P.neglectus*, the others received 2 l of uninfested soil. After the inoculation, maize (cv. Dorina) was sown to increase the population of *P.neglectus*.

On 18 August 1983 the maize plants were cut off above soil level and wheat (cv. Arminda) was sown. The wheat was killed with paraquat on 4 April 1984.

R.solani and V.dahliae inoculum

Potato tubers with black scurf from plots continuously cropped with potato in the crop rotation experiments on sandy soil near Wageningen and on marine clay soil in the East Flevoland Polder were planted in moist perlite. After 4 weeks portions of infected stems were plated on water agar. Hyphal tips were isolated from the plates and transferred to plates of malt-biotone medium (Jager et al., 1979). From these isolates, 3 mm mycelial disks, taken from the 1 cm outer edge, were placed in 300 ml Erlenmeyer flasks on perlite wetted with 200 ml of a solution containing 15 g malt extract/l + 1 g biotone/l. The flasks were incubated for four weeks at 20 °C. When dead inoculum was needed, culture flasks were sterilized twice, within two days, at 120 °C for 30 minutes.

On 25 April 1984, inoculum of *R.solani* obtained from sclerotia from the crop rotation experiment on sandy soil was mixed with the soil in the containers of Experiment 1 in a 1:160 ratio (volume/volume). Similarly, inoculum obtained from sclerotia from the crop rotation experiment on marine clay soil was mixed with soil in the containers of Experiment 2.

V.dahliae inoculum, prepared as described by Scholte et al. (1985), was added to the soil as described under Experiment 1 in a 1:250 ratio (volume/volume).

Observations

Plant emergence and senescence were recorded. In 1985 and 1986 the date of maturity was taken as the day on which all plants within a container had no green leaves and plants were harvested at least two weeks later. Tubers were weighed fresh and their dry matter content determined by drying samples at 105 °C for 16 h.

Black scurf on each tuber was scored as: 0 = no sclerotia, 1 = slight to moderate cover of sclerotia, and 2 = moderate to extensive cover of sclerotia. A black scurf index (BSI) was calculated using the formula:

$$BSI = 100 \times (0 \times n_0 + 0.5 \times n_1 + n_2) / n_{total},$$

where n = the number in each category 0-2 and total.

Endoparasitic nematodes were extracted from the roots by the funnel-spray method (extraction time six days; Oostenbrink, 1960) and nematode densities in the soil were estimated by extracting them with an Oostenbrink elutriator (Oostenbrink, 1960).

Results

The high numbers of nematodes of both *Meloidogyne* spp. and *P.neglectus* per 100 ml soil show that the inoculation technique was successful (Table 1). No other plant-parasitic nematodes were detected.

In Experiment 1 the three-factor interaction *Meloidogyne* * *V.dahliae* * *R.solani* tended to statistical significance ($P \leq 0.10$). Synergism between *R.solani* and *V.dahliae* was absent in soil without *Meloidogyne* spp., but when these nematodes were present, there was a significant ($P \leq 0.01$) interaction between them (Table 2). Tuber yield was depressed by *Meloidogyne* spp. and by *V.dahliae* but not by *R.solani* when soil was infested with each of these organisms alone.

In Experiment 2 the three-factor interaction *P.neglectus* * *V.dahliae* * *R.solani* was very highly significant ($P \leq 0.001$). There was no interaction between *R.solani* and *V.dahliae* in soil without *P.neglectus*, but the interaction was again significant in soil infested with this nematode (Table 2). Tuber yield was depressed by *V.dahliae*, and, less markedly, by *P.neglectus* and *R.solani* when soil was infested with each of these organisms alone.

In both experiments the growing period was significantly shortened by nematodes and very significantly so by *V.dahliae* (Table 3) causing early dying. *R.solani* shortened the growing period only in Experiment 2. There was no evidence that synergistic interaction shortened the growing period. Infection by *V.dahliae* decreased ($P \leq 0.001$) the dry matter content of the tubers (data not shown).

In 1984, but not in 1985 and 1986, plants emerged irregularly in the containers infested with *R.solani*. The weight percentage of misshapen tubers was increased by this pathogen in 1984 and in 1985 in Experiment 1 ($P \leq 0.001$) and Experiment 2 ($P \leq 0.01$), but not in 1986 (data not shown). Black scurf was found only on tubers from containers infested with *R.solani* (Table 4).

Discussion

The experimental procedures reported here differ in many ways from inoculation experiments done by others. Four months before inoculation, the soil was sterilized to eliminate soil organisms introduced by previous crops. One year was used to increase populations of plant-parasitic nematodes. Thereafter, inocula of *R.solani* and *V.dahliae* were added to the soil and potato

Table 1. Numbers of *Meloidogyne* spp. and *P.neglectus* per 100 ml soil in two experiments on different dates.

Date	Experiment 1		Experiment 2	
	Control	*Meloidogyne* spp.	Control	*P.neglectus*
7 - 05 - 1984	0	1705	0	370
16 - 12 - 1985	0	1925	0	1720
20 - 05 - 1986	0	1520	0	370
15 - 12 - 1986	0	4040	0	2200

Table 2. The dry matter yield of tubers in containers infested with *R.solani* and *V.dahliae* and *Meloidogyne* spp. (Experiment 1) or *P.neglectus* (Experiment 2), averaged over 1984 to 1986.

	Experiment 1				Experiment 2			
	Control		*Meloidogyne* spp.		Control		*P.neglectus*	
V.dahliae	*R.solani*		*R.solani*		*R.solani*		*R.solani*	
	-	+	-	+	-	+	-	+
-	100[a]	99	93	93	100[a]	95	97	98
+	91	88	88	82**	93	91	94	86**

[a] 100 = 1452 g (Exp. 1) and 1343 g (Exp. 2) dry matter per container.

** The interaction between *R.solani* and *V.dahliae* is significant at $P \leq 0.01$ under *Meloidogyne* spp. (Exp. 1) and *P.neglectus* (Exp. 2), but is absent in the control in both experiments.

Table 3. Duration of the growing period (number of days), averaged over 1985 and 1986, for the treatments in Experiments 1 and 2.

Experiment	Treatment[a]							
	C	N	R	V	NR	NV	RV	NRV
1	137	130	133	122	134	122	121	121
2	132	128	126	127	129	122	123	121

[a] C = control, N = nematodes: *Meloidogyne* spp. in Exp. 1 and *P.neglectus* in Exp. 2; R = *R.solani*; V = *V.dahliae*.

The growing period was significantly shortened by the nematodes ($P \leq 0.05$) and *V.dahliae* ($P \leq 0.001$) in both experiments, and by *R.solani* ($P \leq 0.01$) in Experiment 2.

Table 4. Black scurf index (0-100) of tubers, averaged over 1984 to 1986, for the treatments in Experiments 1 and 2.

Experiment	Treatment[a]							
	C	N	R	V	NR	NV	RV	NRV
1	0	0	58	0	56	0	51	53
2	0	0	59	0	60	0	58	58

[a] For explanation: see Table 3.

was grown for three consecutive years without adding more inoculum. It was assumed that the potato plant, as a host, would maintain sufficient levels of the pathogens. After harvest the foliage was incorporated into the soil because *V.dahliae* forms numerous microsclerotia in the aerial parts of the potato. The advantage of these methods is that the soil infestations corresponds better with field conditions than do infestations obtained by the simple addition to soils or plants of laboratory inocula.

Requirements for succes of the technique used are that the infestation levels be maintained and that the soil does not become infested with unwanted pathogens. The experiments satisfied both requirements. Counts of the numbers and species of nematodes confirmed that none were present, other than those introduced. During the three year duration of the experiments, high levels of black scurf were found on tubers from containers infested with *R.solani*, whereas tubers from the uninfested containers were always free from black scurf. Similarly numerous microsclerotia of *V.dahliae* were found in the foliage of plants from infested containers.

During the experimental period the population densities of parasitic nematodes were high (Table 1). However, such levels contrast with some found in the field, because in pot or container experiments the root/soil ratios are mostly higher than those found in the field.

Infection by *V.dahliae* is promoted by nematodes which assist it to evade the natural defences of the root by opening invasion channels (Storey and Evans, 1987; Perry and Evert,1983) and/or inducing physiological changes in the host (Riedel, 1988). This effect is proven for *M.hapla* (Jacobsen et al., 1979), *Pratylenchus thornei* (Siti et al., 1979) and *P.penetrans* (Rowe et al., 1985). Indirect evidence for this effect is provided by Scholte (1989c) who showed that the rate of infection by *V.dahliae* was markedly decreased in a crop rotation experiment when granular nematicides were applied to the soil. *Meloidogyne* spp. and *Pratylenchus* spp. (mainly *P.crenatus*) were the predominant endoparasitic nematodes.

The effects of *P.neglectus* on infection by *V.dahliae* are unknown. However, Scholte and s'Jacob (1989b) found in a crop rotation experiment on marine clay soil, where *P.neglectus* was the only endoparasitic nematode, that the percentage of infected stems and the percentage of plants with wilt symptoms was significantly decreased ($P \leq 0.05$) when the nematicide ethoprophos was applied to plots continuously cropped with potato.

In Experiments 1 and 2 there was no significant interaction between *Meloidogyne* spp. or *P.neglectus* and *V.dahliae*. In experiments carried out in clay drain tiles, 25 cm diameter, Martin et al. (1982) proved that a synergistic interaction between *P.penetrans* and *V.dahliae* took place only at low initial densities of fungus inoculum, but at high levels of inoculum the effects of both pathogens were only additive. Coosemans (1975) obtained similar results in pot experiments. Scholte (1989c) concluded that plants with an extensive root system had a greater chance of being infected with *V.dahliae* than plants with a small root system. In pot and container experiments the root/soil ratio is much higher than in the field. The high level of *Verticillium* inoculum and the relatively high root density probably explains the absence of synergism between nematodes and *V.dahliae* in Experiments 1 and 2. However, Scholte (1989c) showed that in field plots continuously cropped with potato (thus with high levels of *V.dahliae* inoculum), the application of nematicides retarded the rate of stem infection.

In Experiments 1 and 2 there was no significant interaction between the nematodes and *R.solani*. Thus, the interaction between *R.solani* and *V.dahliae* in the presence of endoparasitic nematodes in the soil was the only, albeit very interesting interaction. The mechanism of this interaction is difficult to explain. Perhaps *R.solani* and *V.dahliae* mutually reinforce each others' infectivity, a relationship suggested by Khoury and Alcorn (1973). They found that *R.solani* significantly increased the percentage of cotton plants (seedlings) infected by *V.dahliae*. They supposed that the type of injury caused by *R.solani* might also increase plant susceptibility by providing avenues of ingress in those areas usually penetrated by *V.dahliae*. However, *V.dahliae* penetrates the plant via the roots whereas *R.solani* attacks underground stem parts, stolons and tubers, at a time when the roots are still white. Mutual stimulation of infection therefore appears unlikely, unless *V.dahliae* can also infect via stem parts already infested with *R.solani*. As infection by *V.dahliae* was not promoted by nematodes in Experiments 1 and 2, it is unlikely that *R.solani* increases it. The interaction on yield cannot therefore be attributed to enhanced mutual infection.

The differences in the length of the growing period between the treatments did not entirely account for the differences in yield. For instance, the duration of the growing season was reduced just as much whether *V.dahliae* was present alone or in combination with nematodes and *R.solani*. Yet, the yield reduction was larger when the three pathogens were present together (Table 2). This indicates that three pathogens jointly exert a larger influence on growth processes than each of them alone.

The three pathogens attack the plant in different ways. Severe attacks by *R.solani* partly destroy the phloem and xylem vessels of stems. *V.dahliae* invades the xylem vessels and may block them, partly by its mycelium and partly by the formation of tyloses and gums thus inhibiting the transport of water and nutrients. Moreover, *V.dahliae* produces toxins that evoke wilt symptoms in leaves (Harling et al, 1986). Endoparasitic nematodes invade the roots and affect their activities.

Our results do not fully agree with those described by Kotcon et al. (1985) who investigated interactions between *P.penetrans*, *R.solani*, *V.dahliae* and *Colletotrichum coccodes*. In two experiments, using fresh inoculum, they found that *V.dahliae* reduced tuber yield not at all and by 12 %: there was a greater effect when potatoes were grown two years in succession on the same plots without re-inoculation in the second year. Moreover, in the latter experiment there was an interaction between *P.penetrans* and *R.solani*. Similarly, in our experiments the effects were smallest in the year that both fungi were added to the soil and they were very pronounced in the following years.

Conclusions

1. Tuber yield decreases markedly by *Meloidogyne* spp. and *V.dahliae* and is hardly affected by *P.neglectus* and *R.solani* when each of the pathogens is present in the soil alone.
2. *R.solani* and *V.dahliae* interacts synergistically when soil is also infested with *M.hapla* and *M.chitwoodi* or *P.neglectus*.

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CHAPTER 9

CAUSES OF DIFFERENCES IN GROWTH PATTERN, YIELD AND QUALITY OF POTATOES IN SHORT ROTATIONS ON SANDY SOIL AS EFFECTED BY CROP ROTATION, CULTIVAR AND APPLICATION OF GRANULAR NEMATICIDES

K. Scholte

Summary

From 1979 to 1986 a crop rotation experiment was carried out on a light sandy soil to study the effects of the cropping frequency of potato on the yield and the development of soil-borne diseases in that crop.

Tuber yield decreased markedly with increasing cropping frequency of potato, but also depended on what crops were grown in rotation with the potato. In the short rotations plant growth was already reduced during the early part of the growing season and the duration of the growing period was also shortened. The fungi *Verticillium dahliae* and *Rhizoctonia solani* and root-knot nematodes (*Meloidogyne* spp.) were the most important yield reducing pathogens. Rotation effects depended on the cultivar used in the experiment.

The fresh weight percentage of misshapen tubers increased with increasing cropping frequency of potato and after application of granular nematicides, but the incidence of common scab (*Streptomyces scabies*) on tubers was not affected by these factors.

Introduction

From 1979 to 1986 a field experiment was carried out on sandy soil to study the effects of short rotations on the yield of potato and on the development of soil-borne diseases in that crop.

Earlier reports described the effects of various rotations and granular nematicides on the incidence of *Rhizoctonia solani* (Scholte, 1987) and *Verticillium dahliae* and *Colletotrichum coccodes* (Scholte, 1989c) in this experiment. Leijdens and Hofmeester (1986) reported on the effects of the rotations on population densities of parasitic nematodes. This paper will discuss the effects of rotations on the growth pattern, yield and tuber quality of potato, and the causes of reduced yields in short rotations.

Material and methods

Crop rotation experiment

This experiment has been described in an earlier paper (Scholte, 1987: Experiment 1). It was laid out near Wageningen in 1979 on light sandy soil containing 2.6 % organic matter and with a pH-KCl of 5.2. In the experiment four rotations with potato (including continuous cropping) were compared:

P = continuous cropping of potato
MP = maize - potato
SP = sugar beet - potato
MSBBP = maize - sugar beet - barley - barley - potato

They were compared on untreated plots and on plots treated annually with a granular nematicide even when a crop other than potato had been grown. The nematicide was always broadcast one day before planting and then incorporated into the soil with a spring-tine cultivator. Oxamyl (Vydate 10G, Shell Nederland Chemie, Den Haag, 10 % a.i., 50 kg ha^{-1}) was applied from 1979 to 1984 and aldicarb (Temik 10G, Union Carbide Benelux, Maarssen, 10 % a.i., 30 kg ha^{-1}) in 1985 and 1986.

The experiment was laid out in a randomized complete block design with four replications; every crop in a rotation was grown in each year. For example, for the MSBBP rotation there were five untreated and five treated plots in each replication. The potato cultivar used was Element.

In 1986 the crop rotation experiment was carried out for the last year. This made it possible to change the original concept of the experiment. Therefore, in 1986 each potato plot was split into two: half of the plot was planted with cv. Element (as in the years before) and the other with cv. Mirka. Mirka was included in the experiment, because of its high tolerance to *Verticillium dahliae* (Scholte et al., 1985).

The experiment also contained plots continuously cropped with barley since 1979 (preceding crops: rye in 1978 and potato in 1977). In 1986, these barley plots were planted with potatoes for the first time since 1979. This cropping system is designated as RBBBBBBBP.

Observations

At the beginning of the growing season the number of emerged plants per plot was counted every 2 or 3 days. The duration of the growing period was calculated in number of days from planting until maturity. Maturity was defined as the stage when ca. 90 % of the plants had lost their green leaves.

From 1981 to 1986 18 plants were harvested from each plot ca. 74 days after planting. The plants that were harvested were regularly distributed over the whole net plot. Fresh and dry matter yields and dry matter contents of tops and tubers and main stems (stems sprouting directly from the seed tuber) and tuber numbers were determined yearly. The dry weight of roots was also assessed from 1983 to 1985. To do this the roots were dug out to ca. 20 cm depth and after washing carefully in tap water cut off from stems and stolons. Samples for dry matter determination were dried in a forced ventilated oven at 105 °C for at least 18 hours. The occurrence of galls on roots, caused by root-knot nematodes (*Meloidogyne hapla* and *M.chitwoodi*) was assessed visually in 1983 and 1985. The number of root galls was scored using four classes: 0 = no root galls, 1 = slight occurrence of root galls, 2 = moderate occurrence of root galls, 3 = a large number of root galls. From these figures a root gall index (RGI) was calculated using the formula:

$$RGI = 100 \times (0 \times n_0 + 0.33 \times n_1 + 0.67 \times n_2 + n_3)/n_{total},$$

where n = the number in each category 0-3 and total.

At final harvest 30 m^2 per plot was harvested (4 rows at 0.75 m distance with a length of 10 m). Fresh and dry weights and dry matter content of tubers were determined. Common scab on tubers was assessed on a sample of 100-150 tubers per plot. Common scab on each tuber was scored using four classes: 0 = tuber free from scab, 1 = tuber slightly covered with scab (< 20 %), 2 = tuber moderately covered with scab (20-50 %) and 3 = tuber severely covered with scab (> 50 %). From these figures a common scab index was calculated using the same formula as that for calculating the root gall index.

Only in 1983 were tubers found with galls caused by *Meloidogyne chitwoodi*. The percentage of tubers with galls was assessed for each plot. In 1985 and 1986 the fresh weight percentage of misshapen tubers (elongated and knobby tubers with protruding eyes) was determined on samples of 100-150 tubers.

Soil pathogens

Earlier papers showed the effects of crop rotation on soil-borne pathogens in this experiment. Soil infestation with pathogens prior to planting the potato crop in spring are summarized in the present paper on the basis of analyses carried out in the period 1981 to 1986. Soil infestation with *Verticillium dahliae* is based on the percentage of infected plants in the field, the rate of infection and the results of a bio test on soil infestation. Soil infestation with *R.solani* is based on percentage and severity of infected plants in the field, whereas soil infestation with parasitic nematodes is based on their numbers per 100 ml soil.

Multiple linear regression analyses are used to find out the relative importance of each pathogen for final tuber yield and calculations are made to estimate the contribution of *R.solani* to the yield depression in the short rotations.

Results

Crop parameters at the periodic harvest 74 days after planting

Complete emergence was observed on all plots each year. The rate of emergence was not affected by the rotation or nematicide treatment (data not shown).

Application of nematicides increased haulm and tuber weight in all rotations, but the increase was not equal for all rotations (Table 1). In MP there was only a slight increase but there was a strong increase in P and SP. So, the order in which the rotations were ranked for yield attributes was changed by the application of nematicides. This is clearly shown for the total dry matter yield. The ranking order from a high to a low yield was MSBBP = MP > SP > P in untreated plots and MSBBP > MP = SP > P in treated plots.

In untreated plots the dry haulm weight did not differ between the rotations MSBBP and MP, but it was considerably lower in SP and very much lower in P. In untreated plots the tuber weight (fresh and dry matter) differed significantly between all the rotations, in the order MSBBP > MP > SP > P.

In untreated plots the root weight increased in the order MSBBP, MP, P and SP. A close positive linear relationship was found between the root weight and the root gall index ($r = 0.99$, $P \leq 0.001$). The root gall index was highest in the rotation SP. After application of nematicides the differences in root weight between rotations disappeared completely.

Table 1. Effect of crop rotation and nematicide treatment (N) on different crop parameters at the periodic harvest ca. 74 days after planting, averaged over 1981 to 1986.

Crop parameter[a]	N[b]	Rotation[c] P	MP	SP	MSBBP	Mean
Relative total dry weight	-	73	95	84	100	88
	+	91	102	104	114	103
Total dry weight (g/m^2)	-	225 c	292 a	258 b	308 a	271
	+	279 c	315 b	320 b	350 a	316***
Tubers fresh weight (g/m^2)	-	549 c	750 b	646 bc	879 a	706
	+	713 c	856 b	896 b	1014 a	870***
Tubers dry weight (g/m^2)	-	99 c	131 ab	118 bc	152 a	125
	+	122 c	144 b	154 ab	167 a	147***
Haulm dry weight (g/m^2)	-	127 c	161 a	140 b	157 a	146
	+	157 c	171 ab	166 bc	182 a	169***
Root dry weight (g/m^2)[d]	-	5.19 b	4.80 b	6.07 a	4.63 b	5.17
	+	4.39 a	4.26 a	4.40 a	4.26 a	4.33***
Dry matter content of tubers (%)	-	16.0 a	15.8 a	15.9 a	15.7 a	15.9
	+	15.6 a	15.5 a	15.6 a	15.3 a	15.5***
Dry matter content of haulm (%)	-	10.3 a	9.9 bc	10.0 b	9.7 c	10.0
	+	9.9 a	9.4 b	9.5 b	9.1 c	9.5***
Main stem number/m^2	-	16.9 a	18.2 a	17.5 a	17.4 a	17.5
	+	17.4 b	18.4 b	18.7 ab	20.1 a	18.6***
Tuber number/m^2	-	55.5 a	58.9 a	61.5 a	62.1 a	59.5
	+	65.8 b	68.3 b	67.2 b	76.3 a	69.4***
Root gall index (0-100)[e]	-	40 b	25 bc	68 a	13 c	36
	+	12 a	4 a	4 a	0 a	5***

[a] For each parameter: different letters indicate that differences between rotations within a nematicide treatment are significant at $P \leq 0.05$ (according to the Studentized range test of Tukey).

[b] - = control, + = plots yearly treated with a granular nematicide.

[c] P = continuous cropping of potato; MP = maize - potato; SP = sugar beet - potato; MSBBP = maize - sugar beet - barley - barley - potato.

[d] Averaged over 1983 to 1985.

[e] Averaged over 1983 and 1985.

*** Indicate significant effects of the nematicide treatment at $P \leq 0.001$.

The dry matter content of the haulm reflected the growing conditions of the crop. The best growing crops showed the lowest dry matter content. Therefore, the dry matter content of MSBBP plants was lower than that of plants grown in P, with intermediate levels for MP and SP plants. In all cases, dry matter content was lower when nematicides were applied.

No significant differences in dry matter content of the tubers were found between rotations, but it was significantly lower in all rotations if nematicides were applied.

Application of nematicides increased the number of main stems and tubers. No significant differences in the number of main stems and tubers were found between rotations in untreated plots. However, in treated plots the highest stem and tuber numbers were found in the rotation MSBBP and the lowest in plots continuously cropped with potato (P). The rotations MP and SP showed intermediate numbers.

Crop parameters at final harvest

At final harvest, fresh and dry tuber yield varied greatly between rotations (Table 2). Application of nematicides increased tuber yield in all rotations, but the extent depended on the rotation. The highest relative increase was found in SP and P and the lowest in MP. The ranking order of the rotations in terms of dry matter yield of tubers was MSBBP >> MP >> SP >> P in untreated plots and MSBBP >> MP ≥ SP >> P in treated plots. The relative differences between rotations were much greater at final harvest than at the periodic harvest 74 days after planting (Tables 1 and 2).

The dry matter content of the tubers increased with increasing cropping frequency of potato in untreated plots, but there were no differences between rotations in plots treated with nematicides (Table 2).

The duration of the growing season decreased in the order MSBBP, MP, SP and P and increased in all rotations after application of nematicides (Table 2).

Yield attributes of cvs Element and Mirka in 1986

In 1986 the potato yield was higher in RBBBBBBBP than in MSBBP (Table 3). The difference in yield between these two cropping systems was much greater for cv. Element than for cv. Mirka. The tuber yield of both cultivars increased after application of nematicides, both in the MSBBP rotation and in the cropping system with potato after eight years of cereals (RBBBBBBBP). However, in the short rotations the cultivars responded differently to the application of nematicides. In P, MP and SP the tuber yield of cv. Element

Table 2. Effect of crop rotation and nematicide treatment (N) on different crop parameters at final harvest, averaged over 1981 to 1986.

Parameter[a]	N[b]	Rotation[c]				Mean
		P	MP	SP	MSBBP	
Tubers relative dry weight	-	65	88	74	100	82
	+	82	99	94	117	98
Tubers dry weight (g/m^2)	-	675 d	920 b	773 c	1043 a	853
	+	852 c	1035 b	980 b	1225 a	1023***
Tubers fresh weight (g/m^2)	-	2819 d	3872 b	3294 c	4462 a	3612
	+	3572 c	4335 b	4085 b	5188 a	4295***
Dry matter content of tubers (%)	-	24.0 a	23.7 ab	23.5 bc	23.3 c	23.6
	+	23.8 a	23.9 a	23.9 a	23.6 a	23.8*
Fraction of tubers with galls (%)	-	5.8 yz	12.1 x	8.6 xy	1.1 z	6.9
	+	2.5 x	1.3 x	0.3 x	0 x	1.0***
Number of growing days	-	126 d	135 b	131 c	139 a	133
	+	132 d	140 b	136 c	145 a	138***

[a] For each parameter: different letters indicate significant differences between rotations within a nematicide treatment at $P \leq 0.10$ (letters x to z) or at $P \leq 0.05$ (letters a to d) (according to the Studentized range test of Tukey).

[b] and [c] For explanation: see Table 1.

* and *** Indicate significant effects of the nematicide treatment at $P \leq 0.05$ and $P \leq 0.001$, respectively.

increased appreciably, whereas the tuber yield of cv. Mirka did not react at all to the application of nematicides in the rotations.

Tuber quality at final harvest

The effects of rotations and nematicide treatment on the occurrence of common scab and misshapen tubers are only given for 1986 (Table 4), because this was the year for which the results of the cropping system with potato after eight years of cereals were available. Neither the cropping frequency of potato (the rotational effects) nor the application of nematicides showed any effect on the incidence of common scab on tubers. This was also found for cv. Element in the preceding years. Averaged over 1981 to 1986 the common scab index ranged between 36 and 41, irrespective of rotation and nematicide treatment.

Table 3. Effect of crop rotation and nematicide treatment (N) on dry weight (g/m^2) of tubers at final harvest, for cultivars Element and Mirka in 1986.

Cultivar[a]	N[b]	Rotation[c]					Mean
		P	MP	SP	MSBBP	RBBBBBBBP[d]	
Element	-	754 d	1111 b	894 c	1077 b	1403 a	1048
	+	815 d	1242 b	1065 c	1283 b	1580 a	1197***
Mirka	-	1022 c	1496 a	1326 b	1534 a	1613 a	1398
	+	1019 d	1435 c	1318 c	1681 b	1842 a	1459*

[a], [b] and [c] For explanation: see Table 1.

[d] RBBBBBBBP = rye in 1978, barley from 1979 to 1985 and potato in 1986.

* The nematicide effect is significant in MSBBP and RBBBBBBBP ($P \leq 0.05$) and not in the other rotations.

*** Indicate significant effects of the nematicide treatment at $P \leq 0.001$.

Table 4. Effect of crop rotation and nematicide treatment (N) on common scab index (0-100) of tubers and on the fraction of misshapen tubers (fresh weight basis) in 1986, averaged over two cultivars.

Parameter[a]	N[b]	Rotation[c]					Mean
		P	MP	SP	MSBBP	RBBBBBBBP[d]	
Common scab index	-	57	55	45	58	57	54
	+	54	52	52	47	48	50
	Mean	55 a	53 a	49 a	52 a	52 a	
Weight % of mis-shapen tubers	-	8.6	3.3	3.3	2.8	1.1	3.8
	+	21.5	8.4	5.1	2.2	2.4	7.9**
	Mean	15.1 a	5.9 b	4.2 b	2.5 b	1.7 b	

[a], [b] and [c] For explanation: see Table 1.

[d] For explanation: see Table 3.

** The nematicide effect is significant in P and MP ($P \leq 0.05$) and not in the other rotations.

The nematicide treatment increased the fresh weight percentage of misshapen tubers. However, this increase was only significant ($P \leq 0.05$) in the rotations P and MP. The weight percentage of misshapen tubers was high in P and much lower in the other rotations. In 1985 similar results were obtained

Table 5. Soil infestation with different soil pathogens prior to planting date of the potato in various crop rotations. +, ++, +++, ++++ and +++++ indicate a low, moderate, high, severe and very severe soil infestation, respectively.

Pathogen	Rotation[a]			
	P	MP	SP	MSBBP
V.dahliae[b]	+++++	++++	++++	++
R.solani[c]	+++++	+++	+++	+
Meloidogyne spp.[d]	+++++	++	++++	++
Pratylenchus spp.[d]	+	+++	+	+++
Tylenchorhynchus dubius[d]	+	+++	+	++++
Rotylenchus robustus[d]	++	+	+++	+
Paratylenchus projectus[d]	+	+	+++	+

[a] For explanation: see Table 1.

[b] Scholte (1989c).

[c] Scholte (1987).

[d] Leijdens and Hofmeester (1986).

Table 6. The total decreases (%) in dry tuber yield in the rotations P, MP and SP compared with the rotation MSBBP for cvs Element (averaged over 1981 to 1986) and Mirka (1986), and the estimated contribution of *R.solani* to these yield decreases.

Rotation[a]	Element				Mirka			
	Control		Nematicide		Control		Nematicide	
	Total	*R.solani*	Total	*R.solani*	Total	*R.solani*	Total	*R.solani*
P	35	4	30	10	33	22	39	25
MP	12	2	16	5	3	4	15	14
SP	26	3	20	4	14	3	22	14

[a] For explanation: see Table 1.

(data not shown in tables). In that year the weight percentage of misshapen tubers increased significantly in P, from 15.1 % in the control to 24.9 % in the nematicide treatment, and in MP from 2.8 to 9.3 %. Levels in the other rotations were low and not affected by the nematicide.

In 1983 at final harvest many tubers showed galls resulting from *M.chitwoodi*. This was the only year in which these tuber galls occurred; they were probably promoted by the special weather conditions in that year (a cool and very wet spring was followed by high temperatures during summer). Most tubers with galls were found in the rotation MP, fewer were found in SP and fewest in MSBBP (Table 2). The application of nematicides greatly reduced the number of tubers with galls.

Effects of soil pathogens on yield

Soil infestation with pathogens prior to planting the potato crop in spring is summarized in Table 5 on the basis of analyses carried out in the period 1981 to 1986. Soil infestation with *V.dahliae* and *R.solani* increased with increasing cropping frequency of potato, whereas population densities of nematodes also depended on the host crop suitability of the other crops grown in rotation with potato.

Multiple linear regression analysis showed that *V.dahliae*, *Meloidogyne* spp. and *R.solani* accounted for 91 % ($P \leq 0.01$) of the total variation in dry tuber weight for cv. Element (averaged over 1981 to 1986) at final harvest. *V.dahliae* accounted for by far the greatest variation and *R.solani* the least. The same pathogens explained 88 % ($P \leq 0.01$) of the total variation for cv. Mirka (used only in 1986), but in this case *R.solani* accounted for by far the greatest variation. When *C.coccodes* was included in the regression analysis models of both cultivars, it did not increase the percentage variation that could be explained for both cultivars.

From 1981 to 1986 *R.solani* attacks of stems and stolons were assessed. They are reported in a summarized form by Scholte (1987). Scholte (1989b) also assessed the effects of stem and stolon attacks of *R.solani* on final tuber yield. So, the contribution of *R.solani* to the tuber yield depressions in the short rotations could be calculated (Table 6). Only a limited part of the yield depressions in the short rotations could be ascribed to *R.solani* for cv. Element from 1981 to 1986. However, the contribution of *R.solani* to the yield depression of Mirka in 1986 was high.

Discussion

Yields decreased with increasing cropping frequency of potato. Differences in growth between the short rotations and the five-year rotation MSBBP were already occurring during the early part of the growing season. Growth of potatoes was particularly reduced in P and SP. Initially, the main cause of the reduced growth of potato in these short rotations was the attack of roots by root-knot nematodes. The root-knot nematodes were the most dominant nematodes in this experiment (Leijdens and Hofmeester, 1986). They occurred in all rotations but the highest population densities were found in P and SP. Population densities were much lower in MP than in P and SP and the yield reduction in MP was initially low compared with MSBBP. The higher dry matter content in the haulm in the short rotations and on untreated plots was a consequence of a reduced uptake of water. In 1986, uptake of minerals was also reduced (data not shown) but the mineral content of plants in the short rotations was the same as in MSBBP.

A small part of the reduced growth in the short rotations in the first part of the growing season must be ascribed to *R.solani*, especially in P. Severe attacks of stems and stolons by this fungus reduce plant growth (Scholte, 1989b).

In the second half of the growing season yield depressions increased in the short rotations, mainly because of the fast development of wilt symptoms in the leaves, caused by *V.dahliae* (Scholte,1989c). This resulted in a lower level of light interception (data not shown) and a shortening of the growing season. Multiple linear regression analyses showed that *V.dahliae* was the most yield-reducing factor for cv. Element in the short rotations, followed by *Meloidogyne* spp.. *R.solani* accounted for a small part of these yield reductions. This fact was confirmed by calculations about the contribution of *R.solani* to the yield depressions (Table 6).

Potatoes yielded less in the five-year rotation MSBBP than when they were grown after eight years of cereals (RBBBBBBBP). This difference in tuber yield should mainly be ascribed to the different levels in soil infestation with *V.dahliae* (Scholte, 1989c). Therefore, in 1986 the difference in yield between the two cropping systems was greater for cv. Element (which is very susceptible to *V.dahliae*) than for cv. Mirka (which is highly tolerant to *V.dahliae*). The positive effect of the application of nematicides in MSBBP and RBBBBBBBP is probably mainly caused by the control of root-knot nematodes, in MSBBP accompanied by a retardation of the *V.dahliae* infection and in RBBBBBBBP possibly by a control of the high population density of *Tylenchorhynchus dubius*. The population of root-knot nematodes occurring in RBBBBBBBP was probably virtually a monopopulation of *M.chitwoodi*, because barley is a non-host for *M.hapla* and a suitable host for *M.chitwoodi*.

Mirka appeared to be very susceptible to *R.solani* (Scholte 1989b). This explains why the application of nematicides had no positive effect on the yield of this cultivar in P, MP and SP in 1986 (Table 3). Application of the nematicides greatly increased the *R.solani* attack of stems and stolons. The positive effect of nematode control by the nematicides was completely cancelled by the increase of *R.solani*. *R.solani* contributed highly to the yield depressions of cv. Mirka in the short rotations (Table 6 and results of multiple linear regression analyses).

The stimulatory effect of granular nematicides on *R.solani* led Hofman (1988) to study this aspect. He found that the increase of *R.solani* was primarily caused by a reduced grazing of the mycophagous soil fauna (nematodes, springtails and mites) on the pathogen in nematicide-treated fields.

So, nematicides reduced nematode attack and increased stem and stolon canker caused by *R.solani*. However, another effect of nematicides was observed in this experiment. The application of nematicides retarded the *V.dahliae* infection (Scholte, 1989b). Endoparasitic nematodes, such as *M.hapla* promote the rate of infection by *V.dahliae*. So, the increased duration of the growing season after application of nematicides can be explained at least partly by the retarding effect of the *V.dahliae* infection.

Another synergistic interaction between soil pathogens may have occurred in the experiment. Scholte and s'Jacob (1989a) showed a synergistic interaction between *V.dahliae* and *R.solani* in the presence of *Meloidogyne* spp. All these pathogens occurred in high densities in the experiment.

Thus, high cropping frequencies of potato resulted in considerable yield losses. But tuber quality was also affected. Short rotations showed an increase in misshapen tubers, because of the higher *R.solani* attack in these rotations (Scholte, 1989b).

Tuber quality was also affected by common scab caused by *Streptomyces scabies*. However, there was no relation between the cropping frequency of potato and the incidence of common scab. Common scab differs in this aspect from netted scab (Scholte, 1989a; Scholte and Labruyère, 1985). The results indicate that common scab survives for several years in soil and/or the pathogen has a wide host range. The latter seems to be the most plausible explanation for the occurrence of common scab at similar levels in rotations with different cropping frequencies of potato.

Different crops in a rotation select differently on *Meloidogyne* sp. The host crop ranges of *M.hapla* have been studied by Faulkner and McElroy (1964) and those of *M.chitwoodi* by O'Bannon et al. (1982) and Mojtahedi et al. (1988). Host crop suitability also depends on the cultivar used, but in general the potato is an excellent host for both *M.hapla* and *M.chitwoodi*. Sugar beet is considered as a moderate host for both nematode species, whereas maize is a non-host for *M.hapla* and a suitable host for *M.chitwoodi*. Thus, maize enhances *M.chitwoodi* and therefore this nematode met less competition with *M.hapla* in MP than in P and SP. The optimum temperature for *M.chitwoodi* is lower than for *M.hapla* (O'Bannon and Santo, 1984) and consequently it completes more generations within a season. These facts explain why in 1983 the percentage of tubers with galls was higher in MP than in the other short rotations.

Conclusions

1. On sandy soils the yield of potato depends greatly on the cropping frequency of that crop and also on the crops grown in rotation with the potato.
2. *V.dahliae*, *R.solani* and *Meloidogyne* spp. are very important yield-reducing pathogens in short rotations on sandy soils.
3. The cultivars used in a crop rotation experiment greatly influence the results of that experiment.
4. Root galls induced by root-knot nematodes increase the root weight.
5. The incidence of common scab on tubers is not affected by the cropping frequency of the potato or the application of granular nematicides.
6. The fresh weight percentage of misshapen tubers increases with increasing cropping frequency of potato and after application of granular nematicides.

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CHAPTER 10

EFFECTS OF CROP ROTATIONS, CULTIVAR AND GRANULAR NEMATICIDES ON GROWTH AND YIELD OF POTATO IN SHORT ROTATIONS ON A MARINE CLAY SOIL

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Summary

High cropping frequencies lead to an increase of problems with soil-borne diseases and pests. From 1979 to 1985 a crop rotation experiment was carried out on a marine clay soil to study the effects of the cropping frequency of potato on its yield and on the development of soil-borne diseases.

Tuber yield decreased markedly with increasing cropping frequency of potato. Compared with the rotation wheat-sugar beet-oats-potato, yields of cv. Hertha were reduced by 27 % in continuous cropping of potato and by ca. 15 % in the wheat-potato and sugar beet-potato rotations. However, a pot experiment showed that the yield depression in the short rotations depended on the cultivar used.

Crop growth was unaffected in the early part of the growing season, but declined in the second part. The senescence of crops accelerated as cropping frequency of potato increased. *Verticillium dahliae* was the most important yield-reducing factor. Root infection by this fungus was stimulated by the root-lesion nematode *Pratylenchus neglectus*.

Introduction

Soil infestation with cyst nematodes (*Globodera* spp.) increases when potato is grown in short rotations. However, other soil-borne pathogens may also increase in such rotations and affect the growth and yield of potato. Therefore, from 1979 to 1985 a field experiment was carried out on a marine clay soil to study the effects of short rotations on the yield of potato and on the development of soil-borne diseases and pests, other than cyst nematodes, in that crop.

An earlier report described the effect of various rotations and granular nematicides on the incidence of *Rhizoctonia solani* (Scholte, 1987) in this experiment. This paper will discuss the effects of rotations on the growth pattern and yield of potato, and the causes of reduced yields in short rotations.

The effects of short rotations on yield and quality of potato on sandy soil have already been described (Scholte, 1989d). *Rhizoctonia solani*, *Verticillium dahliae* and root-knot nematodes (*Meloidogyne* spp.) were the most important yield-reducing pathogens on a sandy soil.

Material and methods

Experiment 1 (crop rotation experiment)

This experiment, described earlier (Scholte, 1987: Experiment 2) was laid out in the East Flevoland polder on a calcareous marine clay containing 3.1 % organic matter and a clay fraction (<2 μm) of 27 % and with a pH-KCl of 7.3. Potato had been grown only once (1974) on the trial field since the polder had been reclaimed from the sea in 1957. The crop in 1978 (the year preceding the start of the experiment) was oats. The experiment comprised four rotations:

P = continuous cropping of potato
WP = wheat - potato
SP = sugar beet - potato
WSOP = wheat - sugar beet - oats - potato.

These were compared on untreated plots and on plots treated annually with a granular nematicide even when crops other than potato were grown. Nematicide was always broadcast one day before planting and incorporated into the soil with an oscillating harrow. In 1979 oxamyl (Vydate 10G, Shell Nederland Chemie, Den Haag, 10 % a.i., 50 kg ha^{-1}) was applied, from 1980 to 1984 ethoprophos (Mocap 20G, Duphar, Amsterdam, 20 % a.i., 50 kg ha^{-1}) and in 1985 aldicarb (Temik 10G, Union Carbide Benelux, Maarssen, 10 % a.i., 30 kg ha^{-1}).

The experiment was laid out in a randomized complete block design with two replications; every crop in a rotation was grown in each year. For example, for the WSOP rotation there were four untreated and four treated plots in each replicate. Each plot was 40x6=240 m^2. The potato cultivar used was Hertha.

The experiment had to be terminated in 1985 because the soil was contaminated with potato cyst nematodes (*Globodera* spp.).

Observations

At the beginning of the growing season the number of plants that had emerged per plot was counted every two or three days. The duration of the growing period was calculated in number of days from planting until maturity. Maturity was defined as the stage when 90 % of the plants had lost their green leaves.

From 1981 to 1985, 30 plants regurlarly distributed over the whole net plot were harvested from each plot ca. 61 and 108 days after planting (but not on day 108 in 1982). Fresh and dry matter yields and dry matter contents of tops and tubers and main stem (stems sprouting directly from the seed tuber) and tuber numbers were determined. The dry weight of roots was also assessed. Roots were dug out to ca. 20 cm depth and after washing carefully in tap water cut off from stems and stolons. Samples for dry matter determination were dried in a forced ventilated oven at 105 °C for at least 18 hours.

At final harvest 40x3=120 m^2 per plot were harvested (4 rows, 0.75 m apart, 40 m long). Fresh and dry weights and dry matter content of tubers were determined. The fresh weight fraction of misshapen tubers was also determined.

Assessment of soil pathogens

Endoparasitic nematodes were extracted from the roots by the funnel-spray method (extraction time six days; Oostenbrink, 1960) and nematode densities in the soil were ascertained by extracting them with an Oostenbrink elutriator (Oostenbrink, 1960).

In 1983 and 1984 at each periodic harvest, four stems of each plant were checked for *V.dahliae* and *C.coccodes* infection, as described earlier by Scholte (1989c).

Multiple linear regression analyses were used to ascertain the relative importance of each pathogen for final tuber yield.

Experiment 2 (pot experiment with cultivars)

In October 1985, soil was taken from the field of Experiment 1, viz. from P plots that had been continuously cropped with potato for 7 years (P soil), and from WSOP plots (oats plots), where potato should be planted in the following year (WSOP soil). During winter the soil was stored outdoors in wooden containers covered with plastic sheeting. The soil was used for a pot experiment in 1986. On 10 April each lot of soil was sieved and thoroughly mixed. One week before planting part of each lot of soil was sterilized by gamma irradiation with 25 kGy (a medical sterile dosage) to eliminate soil-borne plant pathogens.

Black plastic pots (5.8 l) were filled with unsterilized or sterilized soil and placed in white enamel pots. The pots were placed outdoors in a randomized complete block design with six replications.

On 24 April a 20 g single-sprouted tuber, visibly free from black scurf and previously disinfected against *R.solani* with validamycine (Solacol, AAgrunol, Haren, 30 g/l a.i., 3 % solution), was planted in each pot.

Three different cultivars were used. Hertha, always used in Experiment 1, was planted in unsterilized soil and in sterilized soil. To investigate the role of *V.dahliae* as a yield-reducing factor in the crop rotation experiment, Element, which is very susceptible to this pathogen (Scholte, 1989d), and Mirka, which is highly tolerant (Scholte et al., 1985), were planted in unsterilized soil.

From the date of emergence until 12 weeks after planting the following total amounts of nutrients were applied per pot, apportioned over 8 applications: 4928 mg N, 1240 mg P, 7176 mg K, 576 mg Mg and 16 ml of a trace element solution containing 20 g $MnSO_4 . 1H_2O$, 30 g H_3BO_3, 5 g $ZnSO_4 . 7H_2O$, 1 g $CuSO_4 . 5H_2O$ and 1 g $Na_2MoO_4 . 2H_2O$ per litre of water.

Observations

During the growing period the incidence of wilt symptoms was scored. At final harvest the fresh and dry yields of tubers were assessed.

Results

Presentation of the results (Experiment 1)

Tubers were normally planted in mid-April, but in 1983, wet fields caused planting to be delayed until 8 June; as a result, the plants did not die off naturally and therefore the haulm was killed by chemical spraying (Scholte, 1987). However, yields remained low and the rotation effects were much smaller than in the other years. Therefore, the results of that year have been presented separately, whereas those of 1981 and 1982 and those of 1984 and 1985 have been averaged.

Effects on yield (Experiment 1)

In the first half of the growing season the total dry matter yield was not affected by the rotations (Table 1). However, yield was initially reduced by

Table 1. Effect of crop rotation and nematicide treatment (N) on total dry weight (g/m^2) at the periodic harvest 61 days after planting. Experiment 1.

Year	N[a]	Rotation[b] P	WP	SP	WSOP	Mean
1981/1982	-	236	246	273	275	257
	+	206	227	233	202	217*
	Mean[c]	223 a	236 a	253 a	238 a	
1983	-	135	107	141	117	125
	+	118	131	126	110	121
	Mean[c]	127 a	119 a	134 a	114 a	
1984/1985	-	201	217	206	248	218
	+	192	217	183	217	202
	Mean[c]	196 a	217 a	194 a	232 a	

[a] - = control (untreated), + = plots treated yearly with a nematicide.

[b] P = continuous cropping of potato; WP = wheat-potato; SP = sugar beet-potato; WSOP = wheat-sugar beet-oats-potato.

[c] Different letters indicate that differences between rotations are significant at $P \leq 0.05$ (according to the multiple range test of Student-Newman-Keuls).

* Indicate significant effects of the nematicide treatment at $P \leq 0.05$.

the nematicide in all rotations, except in WP in 1983 and 1984/1985. Tubers were affected more than the haulms (data not shown).

Differences in dry tuber weight at final harvest occurred already in 1981/1982, but they were not affected by the nematicide treatment (Table 2). The lowest yield was obtained in continuous cropping and the highest yield in the WSOP rotation, with intermediate levels in WP and SP. The differences in yield between the two rotations WP and SP were very small. In later years the yield differences between the short rotations and WSOP increased in the untreated plots. However, in those years the nematicide influenced yield positively in the short rotations, but not in WSOP. So, the yield depression in the short rotations was much greater in untreated plots than in treated plots.

The effects on fresh tuber yield (data not shown) were the same as for

Table 2. Effect of crop rotation and nematicide treatment (N) on dry tuber weight (g/m^2) at final harvest. Experiment 1.

Year	N[a]	Rotation[b]				Mean
		P	WP	SP	WSOP	
1981/1982	-	991	1030	1056	1224	1075
	+	960	1096	1108	1163	1082
	Mean[c]	975 c	1063 b	1083 b	1194 a	
1983	-	711	770	773	753	752
	+	669	737	727	774	727
	Mean[c]	690 b	754 a	750 a	763 a	
1984/1985[d]	-	1096 c	1254 b	1298 b	1501 a	1288
	+	1157 b	1404 a	1420 a	1472 a	1363*

[a], [b] and [c] For explanation: see Table 1.

[d] Different letters indicate that differences between rotations within a nematicide treatment are significant at $P \leq 0.05$ (according to the multiple range test of Student-Newman-Keuls).

* The nematicide effect is significant in WP and SP ($P \leq 0.05$) and not in the other rotations.

Table 3. Effect of crop rotation and nematicide treatment (N) on the duration (number of days) of the growing period. Experiment 1.

Year	N[a]	Rotation[b]				Mean
		P	WP	SP	WSOP	
1981/1982	-	112	123	123	125	120
	+	115	120	122	126	121
	Mean[c]	113 b	121 a	122 a	125 a	
1984/1985[d]	-	123 c	130 b	134 b	149 a	134
	+	126 c	136 b	138 b	147 a	137*

[a], [b] and [c] For explanation: see Table 1.

[d] For explanation: see Table 2.

* The nematicide effect is significant in WP ($P \leq 0.05$) and not in the other rotations.

Table 4. Effect of crop rotation and nematicide treatment (N) on numbers of *P.neglectus* per 10 g roots. Experiment 1.

Year	N[a]	Rotation[b]				Mean
		P	WP	SP	WSOP	
1981/1982[c]	-	483 a	215 a	370 a	448 a	379
	+	99 a	47 a	85 a	103 a	83***
1983[c]	-	425 c	745 b	390 c	1090 a	663
	+	290 c	545 b	335 c	815 a	496**
1984/1985[c]	-	118 b	370 a	196 b	533 a	1551
	-	13 a	108 a	63 a	135 a	761***

[a] and [b] For explanation: see Table 1.

[c] Different letters indicate that differences between rotations within a nematicide treatment are significant at $P \leq 0.05$ (according to the multiple range test of Student-Newman-Keuls).

** and *** Indicate significant effects of the nematicide treatment at $P \leq 0.01$ and $P \leq 0.001$, respectively.

dry tuber yield, because dry matter content of tubers was not influenced by the rotations or the nematicide treatment.

At the periodic harvest 108 days after planting the differences in yields between the rotations anticipated those obtained at the final harvest (data not shown).

Effects on the duration of the growing period (Experiment 1)

In 1981/1982 the duration of the growing period was not affected by the nematicide, but it was shorter in P than in the other rotations (Table 3). However, in 1984/1985 the growing period was slightly prolonged by the nematicide in the short rotations but not in WSOP. There were considerable differences between the rotations. The growing period was shortest for continuous cropping (P) and longest for WSOP. There were no significant differences between both the 1:2 rotations (WP and SP). In 1983 the haulms were killed chemically in all rotations on 27 September.

Effects on other growth parameters (Experiment 1)

The rate of emergence, number of main stems, number of tubers and root weight were not affected by rotations or by nematicide treatment (data not shown).

Table 5. Effect of crop rotation and nematicide treatment (N) on percentage potato stems infected with *V.dahliae* and *C.coccodes* 89 (1983) and 125 (1984) days after planting and the percentage of plants with wilt symptoms (% wilt) in 1983 109 days after planting. Experiment 1.

Parameter	Year	N[a]	Rotation[b]				Mean
			P	WP	SP	WSOP	
V.dahliae	1983	-	48	8	15	0	18
		+	25	5	12	4	12*
		Mean[c]	37 a	7 bc	14 b	2 c	
	1984	-	73	55	48	30	52
		+	67	47	47	38	50
		Mean[c]	70 a	51 b	48 b	34 b	
C.coccodes	1983	-	8	5	3	0	4
		+	5	7	3	8	6
		Mean[c]	7 a	6 a	3 a	4 a	
	1984	-	67	75	60	72	68
		+	62	75	65	75	69
		Mean[c]	64 a	75 a	63 a	73 a	
Wilt (%)	1983	-	54	12	18	1	21
		+	30	4	7	3	11*
		Mean[c]	42 a	8 b	12 b	2 b	

[a], [b] and [c] For explanation: see Table 1.

* The nematicide effect is significant in P ($P \leq 0.05$) and not in the other rotations.

Effects on soil pathogens (Experiment 1)

Pratylenchus neglectus was the only endoparasitic nematode in this field until 1985. In all years the numbers in the roots were greatly decreased by the nematicide application (Table 4). The nematicide effect was smallest in 1983. In that year the wet spring delayed the planting time and was followed by a dry and warm summer. In 1981/1982 there were no clear differences between the rotations, but from 1983 onwards the highest numbers in potato roots were found in WSOP and WP. In these rotations the potato crop was preceded by a cereal. Population densities of other parasitic nematodes were

Table 6. Dry weight of tubers (g/pot) at final harvest and percentage wilt in the leaves on 16/6 in relation to rotation (WSOP = wheat-sugar beet-oats-potato, P - continuous cropping of potato), cultivar and soil treatment. Experiment 2.

Soil treatment	Cultivar	Dry tuber weight (g/pot)		% wilt in leaves on 16/6	
		WSOP	P[a]	WSOP	P
Untreated	Hertha	263	236 (90)*	1	11
Untreated	Element	210	174 (83)*	26	42
Untreated	Mirka	262	271 (103)	0	0
Sterilized[b]	Hertha	293	314 (107)	0	0

[a] Values in parentheses are relative yields of P compared with WSOP.

[b] Sterilized with gamma irradiation.

* P differs significantly from WSOP at $P \leq 0.05$.

very low.

The highest percentage of stems infected by *V.dahliae* was found in P, intermediate levels in WP and SP and lowest levels in WSOP (Table 5). The percentage of plants with wilt symptoms in 1983 showed the same trends. In 1983 the nematicide treatment significantly reduced the percentage of stems infected by *V.dahliae* and the percentage of plants with wilt symptoms in P.

The level of *C.coccodes* infection in stems was not affected by the rotations or by the nematicide (Table 5). However, the level of infection was very low in 1983.

Regression analyses (Experiment 1)

Multiple linear regression analyses showed that *V.dahliae* accounted for 88 % ($P \leq 0.05$) of the total variation in dry tuber weight at final harvest. Including *R.solani*, *C.coccodes* or *P.neglectus* in the regression analysis models did not increase the percentage variation that could be explained.

Effects in Experiment 2

The dry tuber yield of cv. Hertha was 10 % lower in P soil than in WSOP soil (Table 6). When cv. Element was grown, there was a much larger yield depression in P soil; no rotation effect was observed when cv. Mirka was grown. When sterilized soil was used, the differences between the two rotations disappeared completely.

The dry matter content of the tubers of Element and Hertha from unsterilized P soil was statistically significantly lower than that of tubers from unsterilized WSOP soil. Tubers of Mirka showed no such effect, and neither did tubers of Hertha from sterilized soil (data not shown).

On 16/6 wilt symptoms were more serious in P soil than in WSOP soil for cvs Hertha and Element (Table 6). No wilt occurred in cv. Mirka, or in cv. Hertha grown in sterilized soil. Wilt symptoms were also observed in cv. Element in WSOP soil. Unilateral wilting of leaves indicated that *Verticillium* was the cause.

Discussion

An increased frequency of potato cropping resulted in lower yields. These effects were greater in 1984/1985 than at the beginning of the experiment. Because a potato crop had only been grown once in the soil before the experiment was started in 1979, it may be expected that soil contamination with specific potato pathogens was low or even absent. Thus, differences in results between 1981/1982 and 1984/1985 may indicate a trend. Therefore it is debatable if the maximum yield depressions in the short rotations had already been reached in 1984/1985. This was only likely for continuous cropping.

When soil was sterilized, the yield capacity of soil from plots that were continuously cropped with potato (P soil) was as high as that of soil from WSOP plots. This suggests that microbial agents are responsible for the lower yield capacity of the soil in the short rotations.

The stem and stolon attack by *R. solani* was relatively high in the short rotations and very low in WSOP (Scholte, 1987). When *R.solani* is responsible for the reduced yields then yield reductions can already be observed early in the growing season (Scholte, 1989b). But in the experiment described here, no such early yield reductions were found. Thus, the lower yields in the short rotations cannot directly be attributed to *R.solani*.

Numbers of *Pratylenchus neglectus* were not high. In 1984/1985 the application of nematicides increased yields in the short rotations, but not in WSOP, whereas the highest numbers of *P.neglectus* occurred in this rotation. Therefore, a direct effect of this nematode species on yield is unlikely.

The yield depressions in the short rotations are probably associated with early senescence of the haulms, indicating that *V.dahliae* plays an important role. This is supported by the results of the multiple regression analyses and by the results of the pot experiment. When cv. Element (very susceptible to *V.dahliae*) was grown, the yield depression increased, whereas when cv. Mirka (highly tolerant to *V.dahliae*) was grown the yield depression in P disappeared completely.

The results of the current experiment are in full agreement with those obtained by Hoekstra (1989a) and Lamers (1989). They also observed decreasing yields with increasing cropping frequency of potato on the same type of soil. In their experiments *V.dahliae* was also by far the most important yield-reducing factor (Bollen et al., 1989; Lamers et al., 1989).

In the current field experiment, netted scab can be excluded as a yield-reducing factor because cv. Hertha is immune to this disease.

Early senescence increased with increasing cropping frequency of potato, but the specific symptoms of Verticillium wilt, unilateral chlorosis and necroses of leaves, were only observed in the warm summer of 1983 and in the pot experiment, although a high percentage of stems were infected by the fungus in 1984. At low temperatures the symptoms are difficult to distinguish from normal senescence and may initially only involve reduced growth (Isaac and Harrison, 1968), a reduced photosynthetic efficiency of green leaves of infected plants is also observed (Bowden and Rouse, 1987). So, the adverse effect on crop growth by *V.dahliae* is not exclusivily associated with the occurrence of wilt symptoms.

The positive effect on yield of the nematicide could not be attributed to a direct effect of nematode control. The only important parasitic nematode was *P.neglectus* and the highest population densities occurred in WP and WSOP. In these rotations potato was preceded by a cereal, and cereals are good hosts for *P.neglectus* (Loof, 1978). But in 1984/1985, the nematicide increased yield significantly in WP (by 12 %) and decreased yield in WSOP by 2 % (not significant). This difference in nematicide effect between the two rotations is probably caused by a retardation in the *V.dahliae* infection in WP (and also in P and SP). Root-lesion nematodes facilitate the *V.dahliae* infection. This has been proved for *P.penetrans* (Rowe et al., 1985) and *P.thornei* (Siti et al., 1979; Scholte, 1989a). As the soil infestation with *V.dahliae* was low in 1981/1982, no positive effect on yield could be obtained with the nematicide.

Scholte and s'Jacob (1989a) proved that *P.neglectus*, *R.solani* and *V.dahliae* showed a synergistic effect. Therefore, *R.solani* and *P.neglectus*, may have contributed indirectly to the yield depression in the short rotations.

The incidence of *Colletotrichum coccodes* depended on the weather. Low levels of the fungus were found in stems in the dry summer of 1983, but much more were found in the wet summer of 1984. The same trend was observed by

Bollen et al. (1989) and Stevenson et al. (1976). In the present field experiment, no relation was found between the fraction of infected stems and the cropping frequency of potato. That is in agreement with the findings of Scholte (1989c) and Emmond and Ledingham (1972). Thus, it is unlikely that *C.coccodes* contributed directly to the yield depression in the short rotations. Scholte (1989c) suggested that the absence of the relationship between the cropping frequency of potato and the percentage of stems infected by *C.coccodes* was caused by the tuber-borne inoculum also acting as a source of infection. However, Bollen et al. (1989) observed that the number of infected stems depended on the cropping frequency of potato. In their experiment, seed tubers were not disinfected, whereas in the current experiment and in the experiment described by Scholte (1989c), seed tubers were disinfected against *R.solani*. Langerfeld (1987) found indications that *C.coccodes* increased in the progeny tubers when the mother tubers were disinfected with chemicals and their importance as infection source obviously increased.

Hoekstra (1989a) observed lower yields when the potato was preceded by sugar beet. In the current experiment this negative effect of sugar beet was not found: tuber yields reached the same levels in both the 1:2 rotations WP and SP. However, sugar beet tops were always removed from the fields, whereas in the experiment described by Hoekstra the tops were left on the field.

Conclusions

1. On marine clay soils the tuber yield of potato depends greatly on its cropping frequency.
2. *Verticillium dahliae* is the main cause of the reduced yield in short rotations on marine clay soil in the absence of *Globodera* spp.
3. The nematode *Pratylenchus neglectus* very probably facilitates the infection process of *V.dahliae*, thereby indirectly affecting potato yield.
4. *Colletotrichum coccodes* does not directly contribute to the yield depression in short rotations.

CHAPTER 11

OVERVIEW AND GENERAL DISCUSSION

Effects of rotations on tuber yield

An increasing cropping frequency of potato leads to an increasing tuber yield reduction even in the absence of potato cyst nematodes. In a crop rotation experiment on sandy soil with cultivar Element, a 1:1 rotation (continuous cropping of potato) and 1:2 (potato once every two years) rotations yielded respectively 35 % and 12-24 % less than potato cropped in a 1:5 rotation (potato on the same field only once per five years). However, even a 1:5 rotation resulted in a yield loss. In 1986, tuber yield was substantially lower in this 1:5 rotation than in a rotation in which potato was grown after 8 years of cereals. Frequent cropping of potato also reduced tuber quality.

In a crop rotation experiment on clay soil with cv. Hertha, tuber yields when potato was cropped continuously and in 1:2 rotations were 27 % and ca. 15 % lower compared with potato in a 1:4 rotation. However, in this experiment the yield reductions were probably not at their maximum.

Large effects of the cropping frequency of potato were also found in pot experiments with river clay but depended on the cultivar used.

Greater tuber yield reductions with increasing cropping frequency of potato in the absence of *Globodera* spp. have also been found by other researchers, such as Hoekstra (1989), Lamers (1989) and Roth et al. (1981).

Soil pathogens and the susceptibility of cultivars

Disinfecting the soil with methylbromide and gamma irradiation or pasteurization with steam at 60 °C for 30 minutes eliminated the rotation effect on yield completely, suggesting that it was caused by microbial pathogens.

The soil pathogens that caused the greatest yield reductions were *Streptomyces* spp. (causing netted scab), *Rhizoctonia solani*, *Verticillium dahliae* and, but only on sandy soil, root-knot nematodes (*Meloidogyne*) spp. On clay soil the root lesion nematodes *Pratylenchus thornei* and *P.neglectus* were also included in the complex. *Colletotrichum coccodes* appeared only to contribute under special conditions, whereas *Fusarium tabacinum*, frequently isolated from potato roots, showed no negative effect on plant growth.

In the crop rotation experiment on sandy soil, tuber yields of cvs Element and Mirka decreased similarly with increasing cropping frequency of potato, but the causes were different. The yield decrease of Element was mainly caused by an infection of *V.dahliae* and to a small extent by an attack of *R.solani*. For Mirka the reverse was the case. Both cultivars are immune to netted scab, so that in the crop rotation experiment on sandy soil yield depressions in the short rotations were not caused by *Streptomyces* spp. A test showed that the majority of cultivars grown in the Netherlands are immune to netted scab caused by *Streptomyces* spp..

In the pot experiments with river clay the highest yield depressions occurred in cultivars that were susceptible to netted scab as well as to *V.dahliae*. Within the cultivars large differences in tolerance to *V.dahliae* were observed. Mirka was very tolerant.

So, the effects obtained in crop rotation experiments largely depended on the cultivar used in the experiment. Because of the magnitude of the yield reductions in short rotations it is very important to collect data about the susceptibility and tolerance of cultivars to important soil pathogens.

Streptomyces

Netted scab appeared to be an important disease of the potato. It is caused by *Streptomyces* spp.. Netted scab, formerly known as 'russet scab' in English, occurs in Europe, and differs in many ways from 'russet scab' in the USA and from 'common scab'.

All the experiments showed that the levels of contamination of soil with the *Streptomyces* spp. causing netted scab are greatly increased by planting a susceptible cultivar. The subsequent decline in yield of a susceptible potato crop is much more serious than the effects of netted scab on tuber quality. The pathogens attack the root system of young plants. The resulting decrease in growth rate led to fewer tubers per plant and finally to substantially lower yields. Plant senescence was not enhanced.

The application of nematicides did not affect tuber infection by netted scab or by common scab. Therefore, tuber infections by scab pathogens seem to be independent of nematodes.

There was no relation between the cropping frequency of potato and the incidence of common scab (*S.scabies*) on tubers, indicating that this pathogen has a wide host crop range. Cereals are probably host crops, because after cropping rye for one year and barley for seven years, tuber attack was as high as after 8 years of continuous cropping of potato. Often, severe infection of netted scab occurred on potatoes grown on fields that had been permanent grassland in previous years. In the Netherlands this disease was therefore also called 'grassland scab'. This indicates that *Streptomyces* spp. that are able to attack the potato plant also have *Graminaceae* as host crop.

When netted scab and common scab occur together in a field and potato cultivars susceptible to both diseases are grown continuously, netted scab suppresses common scab. However, many cultivars are immune to netted scab.

Rhizoctonia solani

Stem and stolon attacks caused by soil-borne *R.solani* were strongly increased by an increase of the cropping frequency of potato both on sandy soil and on clay soil. The frequency of cropping potato has a greater effect on the incidence of *R.solani* than the type of preceding crop. The stem and stolon attack was of similar level in the 1:2 rotations sugar beet-potato, maize-potato and wheat-potato.

The effects of cropping frequency are more clearly expressed by the levels of infection of the stems and the stolons of the potato plant than in the occurrence of black scurf (sclerotia of *R.solani*) on progeny tubers. Stem and stolon infection and black scurf development are different processes, the former being greatly influenced by the density of the inoculum in the soil at the beginning of the growing season. During crop growth the fungus multiplies because the potato plant is an excellent host and initial differences in density of the fungus tend to level out as the growing season proceeds. Even when the initial density of the inoculum is low there is ample time for the fungus to multiply. Sclerotia usually form at the end of the growing season when the haulms are dying. However, black scurf level was moderate in the 1:4 or 1:5 rotations because soil infestation at the beginning of the growing season was very low in these rotations.

The hyperparasite *Verticillium biguttatum* occurred in the crop rotation experiment on sandy soil. The highest inoculum densities on stolons were found in continuous cropping; levels were intermediate in the 1:2 rotations and low in the 1:5 rotation. Notwithstanding the presence of *V.biguttatum* sufficient viable *R.solani* inoculum remained in the soil of continuously cropped plots to enable a severe stem infestation of the potato plants to develop. In spring, *V.biguttatum* cannot adequately hinder infection. Temperature seems to be an important factor, because whereas *R.solani* can grow vigorously at low temperatures, *V.biguttatum* is ineffective when the temperature falls below 12 °C (Jager and Velvis, 1985).

Only severe and very severe attacks of stems and stolons by soil-borne *R.solani* decreased yield and the dry matter content of tubers and increased the proportion of deformed and small tubers. The attack increased during the growing period. Severe and very severe stem and stolon attacks reduced fresh tuber yield by 16-21 % and dry tuber yield by 20-29 %.

Cultivars differed greatly in susceptibility to stem and stolon attacks caused by *R.solani*. The contribution of *R.solani* to the total tuber yield depression in short rotations was much greater for cv. Mirka than for cv. Element.

A higher proportion of misshapen tubers occurred in rotations with a high cropping frequency of potato. This effect must be ascribed to the high attack of plants by *R.solani*.

The application of granular nematicides (aldicarb, oxamyl and ethoprophos) greatly increased the attack of stems and stolons, both on sandy soil and on clay soil. This stimulatory effect of granular nematicides on *R.solani* was primarily caused by reduced grazing of the mycophagous soil fauna on the pathogen in nematicide-treated fields (Hofman, 1988).

Verticillium dahliae

V.dahliae is one of the most important yield-reducing fungi when potato is grown in short rotations. The fungus produces large numbers of microsclerotia in tissues of dying potato plants, especially in the haulm. Therefore, soil contamination increases strongly after each potato crop. A biotest revealed that differences in inoculum level were caused by differences in the cropping frequency of potato. Early in the growing season, the percentage of stems infected by *V.dahliae* increased with an increasing cropping frequency of potato. Later in the growing season almost all the stems of the crop were infected in fields with a high cropping frequency of potato. In the crop rotation experiment on sandy soil a close correlation was found between the number of infected stems in mid-June and the incidence of wilt symptoms in leaves two weeks later.

However, the rate of stem infection not only depended on the inoculum level in the soil, but also on the activity of endoparasitic nematodes. *Globodera* spp. (Evans,1987; Corbett and Hide, 1971), *Meloidogyne hapla* (Jacobsen et al., 1979), *Pratylenchus penetrans* (Rowe et al., 1985) and *P.thornei* (Siti et al., 1979) stimulate the infection process of *V.dahliae*. In all my experiments granular nematicides retarded the infection. In the crop rotation experiment on sandy soil this effect was very probably because the nematicide controlled the root-knot nematodes. This assumption is based on the fact that potato stems in the sugar beet-potato rotation were infected more rapidly than in the maize-potato rotation. In the former rotation the population density of *Meloidogyne* spp. was much greater than in the latter rotation, whereas the biotest showed no differences in inoculum density of *V.dahliae*. Moreover, the population density of other endoparasitic nematodes, especially that of *P.crenatus*, was much higher in the maize-potato rotation than in the sugar beet-potato rotation. However, this nematode species does not seem to be very effective in stimulating the infection of *V.dahliae* (Riedel et al., 1985).

The soil contamination with both *V.dahliae* and root-knot nematodes was lower in the sugar beet-potato rotation than under continuous cropping of potato. Nevertheless, the level of infection of the crop with *V.dahliae* was as high in this 1:2 rotation as under continuous cropping. The activity of the root-knot nematodes was much greater in the sugar beet-potato rotation than in continuous cropping. This appeared from the greater numbers of galls on roots and from the higher densities of *Meloidogyne* larvae in roots during the growing season. These facts also point to the stimulating effect of the root-knot nematodes on the infection by *V.dahliae*.

Other endoparasitic nematodes can also play a role on the infection of potato roots by *V.dahliae* in the Netherlands. The application of nematicides to the soil retarded the appearance of Verticillium wilt in a pot experiment with river clay. Two-thirds of the nematodes in this soil were *P.thornei* and one-third were *P.neglectus*. Siti et al. (1979) have proved that *P.thornei* facilitates the infection process of *V.dahliae*. There have been no reports that *P.neglectus* does likewise. However, in the crop rotation experiment on clay soil in 1983, the percentage of stems infected by *V.dahliae* was statistically significantly lower in plots treated with the nematicide ethoprophos than in untreated plots. The percentage of plants with wilt symptoms was also lower in treated plots. The application of ethoprophos increased tuber yield in the short rotations, but not in the 1:4 rotation. *P.neglectus* was the only endoparasitic nematode in this experiment and the highest population densities occurred in the 1:4 rotation. So, the positive effect of ethoprophos on tuber yield could not be ascribed to the control of nematodes, but it can be attributed to an indirect effect on *V.dahliae* infection. *V.dahliae* was the most important yield-reducing factor in this experiment. Single inoculations of *P.neglectus* hardly affected tuber yield. Schepers et al. (1986) also observed positive effects of granular nematicides on tuber yield of potato in the absence of well-known yield-reducing nematodes. *P.neglectus* was the only endoparasitic nematode that occurred in their experiments. However, they found no relation between the nematode density and the positive effects on tuber yield of the nematicides. Earlier (1985) I proved that granular nematicides did not have any positive effect on plant growth in soils free of nematodes or other pathogens.

The rate at which *V.dahliae* infects the potato plants seems to depend on the size of the root system. A close linear relationship was found between the weight of haulm and tubers and the percentage of infected stems per plant early in the growing season. The heavier the plant, the higher the level of infection with *V.dahliae*. It may be expected that rapidly growing plants have a more extensive root system, and therefore have a greater chance of encountering a *V.dahliae* propagule in the soil than slow-growing plants. The importance of the extent of the root system for the infection with *V.dahliae* was confirmed in a pot experiment. With susceptible cultivars a serious root attack by netted scab resulted in a less extensive root system. On average, symptoms of Verticillium wilt in leaves occurred 10 days later in three cultivars whose roots had been severely attacked by netted scab than in three cultivars immune to netted scab. This also explains why the application of a nematicide to soil with a high cropping frequency of potato had a less positive effect on the yield of a cultivar susceptible to netted scab than on the yield of a cultivar immune to netted scab. Of course, it cannot be excluded that the presence of *Streptomyces* spp. on and in roots directly affects the chance of the roots being infected by *V.dahliae*, or that the fungus penetrates the plant less easily if the root tissue has already been attacked by another pathogen.

Inoculation experiments proved that *V.dahliae* can reduce tuber yield substantially, but these experiments also revealed differences between cultivars in tolerance to the fungus. Mirka appeared to be highly tolerant.

Once a soil is severely infested with *V.dahliae* it takes many years before the infestation level falls below the damage threshold of susceptible cultivars. In the crop rotation experiment on sandy soil more than 50 % of the stems in the 1:5 rotation were infected, though the fungus could not produce large quantities of microsclerotia on the other crops in the rotation (maize, sugar beet, barley, barley). In this experiment weeds were always effectively controlled, so that the fungus could not multiply on these plants. Therefore, the positive effect of the nematicides in the 1:5 rotation must at least partly be ascribed to a retardation of the *V.dahliae* infection. This also explains why the nematicide effect in this rotation was greater for the susceptible cultivar Element than for the tolerant cultivar Mirka.

Colletotrichum coccodes

There is much controversy at to whether the fungus *C.coccodes* is an important potato pathogen. The fungus is thought to belong to the complex of pathogens that causes the early dying disease in potato.

In inoculation experiments the fungus showed no important effect on plant growth if it was inoculated singly. In one experiment, leaf senescence was somewhat accelerated but tuber yield was not affected. No synergism was found with other pathogens, except when potato plants of a cultivar that was very susceptible to *V.dahliae* suffered heavily from the latter pathogen. Wet soil conditions promoted *C.coccodes*.

In the crop rotation experiments on sandy soil and on clay soil no significant relation was found between the cropping frequency of potato and the number of stems infected with *C.coccodes*. In the second half of the growing season all stems in each rotation of the experiment on sandy soil, including the 1:5 rotation, appeared to be infected. Clearly, there is a close relation between the cropping frequency of potato and the soil infestation with *C.coccodes*, because the fungus produces large quantities of microsclerotia on dying potato tissues. However, seed tubers are mostly also infested and disinfecting them with organo-mercury compounds or other chemicals is unsuccessful (Mooi, 1956; Langerfeld, 1987). So, as well as the soil, the seed tuber is also an important infection source for the potato plant. This explains why no close relation was observed between the cropping frequency of potato and the percentage of stems infected with *C.coccodes*. There was also a weak relation between the number of infected stems and the appearance of wilt symptoms in the leaves. Moreover, the percentage variation in tuber yield that could be explained in regression analysis models did not increase when *C.coccodes* was included. Therefore, it can be concluded that effects of the cropping frequency of potato on tuber yield are not caused by a direct effect of *C.coccodes*.

Fusarium tabacinum

F.tabacinum was very frequently isolated from potato roots, but inoculation experiments demonstrated that the fungus did not cause root lesions or lower yields.

Nematodes

In the crop rotation experiment on sandy soil a great variety of parasitic nematodes was observed. Of these nematode species, *Meloidogyne hapla* and *M.chitwoodi* accounted for a great part of the variation in tuber yield.

Early in the growing season many galls were observed on potato roots, depending on the rotation: high numbers were especially found in the sugar beet-potato rotation and in continuous cropping of potato. The galls increased the total root weight, but the activity of the roots decreased. There was a positive correlation between the number of galls on roots and the dry matter content of the haulm early in the growing season. A higher dry matter content in the haulm points to a reduced uptake of water by the crop.

An inoculation experiment showed a direct effect of root-knot nematodes on growth and yield of the potato crop. But root-knot nematodes also have an indirect effect on the yield of potato. In the crop rotation experiment on sandy soil very strong indications were obtained that these nematodes facilitate the infection of the fungus *V.dahliae*. Moreover, in a pot experiment with the same type of soil, *Meloidogyne* spp. showed a synergistic three-factor interaction with the fungi *R.solani* and *V.dahliae*, resulting in a substantial tuber-yield loss. A similar synergistic three-factor interaction between these two fungi and the nematode *Pratylenchus neglectus* was found on clay soil.

Thus, root-knot nematodes appeared to be an important yield-reducing factor on sandy soil, both directly and indirectly. Because *Meloidogyne* spp. has a wide host crop range, their yield-reducing effect does not depend solely on the cropping frequency of potato. Moreover, their activity seemed to be affected by the kind of crops in the rotation or by the density of their population. Notwithstanding that before planting the potato the soil contamination was lower in the sugar beet-potato rotation than in continuous cropping, the negative effect of these nematodes was greater in the former rotation than in continuous cropping.

Under certain weather conditions *M.chitwoodi* may reduce tuber quality on sandy soil by the formation of galls.

Interactions between soil organisms

Lower yields in short rotations usually cannot be ascribed to a single pathogen, but are the consequence of a complex of harmful organisms. In addition, all kinds of interactions may occur, e.g. between soil pathogens, and also between soil pathogens and the non-pathogenic soil flora and fauna.

In the experiments described in this thesis strong indications were found that the endoparasitic nematodes *Meloidogyne* spp., *P.thornei* and *P.neglectus* facilitate the infection of the plant root by *V.dahliae*. On the other hand, a severe root attack by *Streptomyces* spp., causing netted scab, delayed the infection by *V.dahliae*. *Meloidogyne* spp., *V.dahliae* and *R.solani* showed a distinct synergistic effect on sandy soil. Both fungi showed the same synergistic interaction with *P.neglectus* on clay soil.

C.coccodes showed a synergistic interaction with *V.dahliae*, but only in cultivars that were very susceptible to the latter fungus.

Granular nematicides/insecticides increased the stem and stolon attack by *R.solani* on sandy soil and on clay soil. The nematicides not only eliminated parasitic nematodes but also mycophagous nematodes, mites and springtails (Hofman, 1988), so that *R.solani* was less inhibited than in untreated plots. In short rotations on sandy soil the hyperparasite *V.biguttatum* was unable to prevent severe stem and stolon infections by *R.solani* early in the growing season, but the formation of viable sclerotia on tubers was reduced at the end of the growing season. So, it is likely that this hyperparasite reduces the inoculum potential in soil, though rarely to such low levels that the next potato crop is sufficiently protected.

It is not clear why the *Meloidogyne* nematodes were much more active in fields after sugar beet in the sugar beet-potato rotation than in fields continuously cropped with potato. Possibly, the high population density of these nematodes stimulated the incidence of antagonists under continuous cropping of potato, or mutual competition decreased the number of successful penetrations of roots.

General conclusions

Streptomyces spp. (causing netted scab), *Rhizoctonia solani*, *Verticillium dahliae* and *Meloidogyne* spp. (the latter only on sandy soil) strongly reduce the growth and yield of the potato crop. Soil infestation with these pathogens greatly increases with increasing cropping frequency of potato. The yield reduction caused by these pathogens in short rotations depends greatly on the susceptibility and tolerance to these pathogens of the cultivar grown.

Pratylenchus thornei, *P.neglectus*, and (but only under special conditions) also *Colletotrichum coccodes* indirectly affect the growth and yield of the potato. *Fusarium tabacinum* does not reduce the growth of the potato plant. *Streptomyces scabies* (common scab) is not affected by the cropping frequency of potato.

Thus, the ultimate yield depressions with high cropping frequency of potato depend on a complex of organisms. The complexity increases because of mutual interactions between these organisms and the interactions of the organisms with potato cultivars and with the environmental conditions. Therefore, using soil samples to predict the yield decrease does not seem to be a feasible proposition.

Even in 1:5 rotations yields of potato were not the highest possible, because cropping frequency of potato alone does not determine its final yield, also the crop species within the rotation play a role. Other species may act as hosts for potato pathogens and pathogens may survive more than four years in situ.

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SUMMARY

Introduction

In the Netherlands the potato is grown frequently in the same field. Ultimately a high cropping frequency mostly leads to the soil being contaminated with potato cyst nematodes (*Globodera* spp.), resulting in lower yields. Much research has already been done on these noxious nematodes. To prevent further infestations of healthy fields, the cropping frequency of potato on the same field is limited by law.

However, it is important to know whether other soil organisms harmful to the potato, are also encouraged by high cropping frequency. This thesis describes research on these organisms and their relative importance.

Two crop rotation experiments were carried out to investigate the effects of various rotations that differed in the cropping frequency for potato and in the crops grown with potato in the rotation. To study the effect of different soil types, one crop rotation experiment was laid out on sandy soil and the other on clay soil. In these experiments the effects of crop rotations on growth pattern, yield and quality of potato and on the development of soil-borne diseases and pests were assessed.

To find explanations for the effects occurring in the two crop rotation experiments supplementary field, pot and container experiments were carried out. The soil used in these experiments was from the two crop rotation experiments, from other crop rotation experiments in the Netherlands and from farmers' fields. Inoculation experiments were carried out with pathogens derived from diseased plant material to investigate their effect on plant growth and to study the interactions between different pathogens and between pathogens and other factors.

Effects of rotations on the potato crop

In the crop rotation experiment on sandy soil the dry tuber yield of cultivar Element was 35 % lower in plots continuously cropped with potato than the yield of potato grown in a 1:5 rotation (maize-sugar beet-barley-barley-potato). Compared with the 1:5 rotation the 1:2 sugar beet-potato rotation yielded 24 % less and the 1:2 rotation maize-potato 12 % less. The difference between the two 1:2 rotations largely disappeared after application of granular nematicides. The nematicides increased the yield in all rotations, but the relative yield depressions in the short rotations were hardly affected.

In the short rotations plant growth was already reduced in the beginning of the growing season, especially in continuous cropping of potato and in the sugar beet-potato rotation. Later in the growing season the differences increased and the duration of the growing season was also shortened. At the end of June or early in July wilt symptoms usually occurred in the leaves, most severely and abundantly in the short rotations.

Even in the 1:5 rotation, tuber yields were not maximum. In 1986, the potato yielded less in this five-year rotation than when they were grown after eight years of cereals.

In the short rotations tuber quality was also reduced by an increased weight percentage of misshapen tubers and, only in one year, by an increased number of tubers with galls.

In the crop rotation experiment on clay soil, by comparison with potato grown in the 1:4 rotation wheat-sugar beet-oats-potato, continuous cropping of potato yielded 27 % less, the 1:2 rotation wheat-potato 17 % less and the 1:2 rotation sugar beet-potato 14 % less. Reduced plant growth in the short rotations developed mainly in the second part of the growing season. No differences were observed in tuber quality.

In pot experiments with soil from other crop rotation experiments and from farmers' fields, the yields when potato was frequently grown on the same field were also very much lower compared with potato growing in rotations with potato once per four or five years.

The lower yields in these experiments in the short rotations (including continuous cropping) were obtained in the absence of potato cyst nematodes.

Causes of reduced growth in short rotations

Disinfecting the soil with methylbromide and gamma irradiation or pasteurization with steam at 60 °C for 30 minutes eliminated the rotation effect on yield completely, suggesting that it was caused by microbial pathogens.

The most important yield-reducing soil pathogens were *Streptomyces* spp. (causing netted scab), *Rhizoctonia solani*, *Verticillium dahliae* and, but only on sandy soil, root-knot nematodes (*Meloidogyne hapla* and *M.chitwoodi*). On clay soil the nematodes *Pratylenchus thornei* and *P.neglectus* were also included in the complex. *Colletotrichum coccodes* appeared only to contribute under special conditions, whereas *Fusarium tabacinum*, frequently isolated from potato roots, did not show any negative effect on plant growth.

Streptomyces

Streptomyces spp., causing netted scab, attack on the root system of young plants and reduced their growth rate at emergence, leading to fewer tubers per plant and finally to substantially lower yields. Plant senescence was not enhanced.

Soil infestation with netted scab increased greatly with increasing cropping frequency of susceptible potato cultivars. However, the incidence of common scab (*S.scabies*) was not affected by the cropping frequency of potato. When netted scab and common scab occurred together and potato cultivars susceptible to both diseases were grown continuously, netted scab suppressed common scab. However, a large number of cultivars appeared to be immune to netted scab.

Rhizoctonia solani

Stem and stolon attacks caused by soil-borne *R.solani* depended greatly on the cropping frequency of potato. Levels were high in continuous cropping and low in rotations with potato once per four or five years, and levels were intermediate in 1:2 rotations. The frequency of cropping potato had a greater effect on the incidence of *R.solani* than which crop preceded the potato. The effects of cropping frequency were more clearly expressed by the levels of infection of the stems and stolons of the potato plant than in the occurrence of black scurf on progeny tubers. Stem and stolon infection and black scurf development may be considered as different processes.

With a high cropping frequency of potato the antagonist *Verticillium biguttatum* was unable to inhibit stem and stolon infection sufficiently, notwithstanding its presence in great density in sandy soil.

The application of granular nematicides such as aldicarb, oxamyl and ethoprophos resulted in a marked increase of the infection of potato stems and stolons by *R.solani*.

Severe and very severe attacks of stems and stolons of soil-borne *R.solani* decreased the tuber yield and the dry matter content of tubers, increased the proportion of deformed and small tubers, but had a negligible effect on haulm yield and stem number. The attack increased during the growing period. Severe and very severe stem and stolon attacks reduced fresh tuber yield by 16-21 % and dry tuber yield by 20-29 %.

Potato cultivars differed in susceptibility to a stem and stolon infection by *R.solani*.

Verticillium dahliae

Inoculum levels in the soil increased with increasing cropping frequency of potato. However, the level of stem infection of potato plants not only depended on the inoculum level in the soil, but also on the population density, activity and species of endoparasitic nematodes in the soil. The application of granular nematicides retarded stem infection. This was very probably because the nematicides controlled root-knot nematodes (*Meloidogyne* spp.) on sandy soil and root lesion nematodes (*Pratylenchus thornei* and *P.neglectus*) on clay soil.

Once a soil was severely infested with *V.dahliae* it seemed to take many years before the infestation level had fallen to below the damage threshold for susceptible potato cultivars. In a 1:5 rotation for potato more than 50 % of the stems were infected, though the fungus could not produce large quantities of microsclerotia on the other crops in the rotation (maize, sugar beet,barley, barley). Weeds were effectively controlled in this experiment.

In inoculation experiments *V.dahliae* caused substantial yield losses, but these experiments also revealed differences between cultivars in tolerance to the fungus. Mirka appeared to be very tolerant.

A close positive correlation was found between the level of *V.dahliae* infection and the size of the potato plant early in the growing season. The heavier the plant, the higher the level of infection. Rapidly growing plants are likely to have a more extensive root system, and therefore a greater chance of encountering a *V.dahliae* propagule in the soil than slow-growing plants.

Colletotrichum coccodes

In inoculation experiments the fungus showed no important effect on plant growth if it was inoculated singly. In one experiment, leaf senescence was somewhat enhanced, but tuber yield was not affected. No synergism was found with other soil pathogens, except in the case of potato plants of a cultivar suffering very severely from a *V.dahliae* infection. The proportion of stems infected by *C.coccodes* was much greater in wet years than in dry years.

In crop rotation experiments no relation was found between the cropping frequency of potato and the number of infected stems, probably because in addition to soil-borne inoculum, tuber-borne inoculum also acts as infection source. At the end of the growing season all stems in each rotation were infected. Only a weak relation was found between the number of infected stems and the appearance of wilt symptoms in the leaves. Application of nematicides had no effect on the infection of stems. In regression analysis models the percentage of variation in tuber yield that could be explained did not increase when the stem infection of *C.coccodes* was included in the model.

Nematodes

Root-knot nematodes (*Meloidogyne hapla* and *M.chitwoodi*) explained much of the variation in tuber yield in the crop rotation experiment on sandy soil. Early in the growing season a great number of galls on potato roots were observed, with the highest numbers being in the sugar beet-potato rotation and in continuous cropping of potato. The galls increased the total root weight, but the activity of the roots decreased. There was a positive correlation between the number of galls on roots and the dry matter content of the haulm early in the growing season, suggesting a reduced uptake of water by the crop.

An inoculation experiment showed a direct effect of root-knot nematodes on tuber yield of the potato crop. But root-knot nematodes also have an indirect effect on the yield of potato. Strong indications were obtained that these nematodes facilitate the infection of roots by the fungus *V.dahliae*. Moreover, in a pot experiment with the same type of soil, *Meloidogyne* spp. showed a synergistic three-factor interaction with the fungi *R.solani* and *V.dahliae*, resulting in a substantial tuber yield loss. A similar synergistic three-factor interaction between these two fungi and the nematode *Pratylenchus neglectus* was found on clay soil. There were also indications that both *P.thornei* and *P.neglectus* stimulated the infection of roots by *V.dahliae*.

Root-knot nematodes appeared to be an important yield-reducing factor on sandy soil, both directly and indirectly. However, their population densities depended not only on the cropping frequency of potato but also on the other host crops in the rotation. Moreover, the activity of these microorganisms seemed to be affected by the type of crops in the rotation or by the densities of their populations. The negative action of these nematodes was greater in the sugar beet-potato rotation than in continuous cropping of potato, notwithstanding a lower soil contamination before planting the potato.

It appeared that under certain weather conditions *M.chitwoodi* may cause loss of tuber quality on sandy soil by inducing gall formation.

Interactions between soil organisms

Lower yields in short rotations could not only be ascribed to a single pathogen, but were also the consequence of a complex of harmful organisms. These organisms showed many interactions, with each other and with other factors.

Strong indications were found that the endoparasitic nematodes *Meloidogyne* spp., *P.thornei* and *P.neglectus* facilitated the infection of the plant root by *V.dahliae*. On the other hand, a severe root attack by *Streptomyces* spp., causing netted scab, delayed the infection by *V.dahliae*. *Meloidogyne* spp., *V.dahliae* and *R.solani* showed a distinct synergistic effect on sandy soil. Both fungi also showed the same synergistic interaction with *P.neglectus* on clay soil.

C.coccodes showed a synergistic interaction with *V.dahliae*, but only in cultivars that were highly susceptible to the latter fungus.

Granular nematicides/insecticides increased the stem and stolon attack by *R.solani*, suggesting that they eliminated not only parasitic nematodes but also mycophagous nematodes, mites and springtails. In short rotations on sandy soil the hyperparasite *V.biguttatum* was unable to prevent severe stem and stolon infections by *R.solani* early in the growing season, but fewer viable sclerotia had formed on tubers at the end of the growing season.

Netted scab suppressed common scab when cultivars susceptible to both diseases were grown.

General conclusions

In the Netherlands, in the absence of *Globodera* spp., lower yields of potato in short rotations seemed to be mainly caused by *Streptomyces* spp. (causing netted scab), *Rhizoctonia solani*, *Verticillium dahliae* and *Meloidogyne* spp. and only indirectly by *Pratylenchus thornei*, *P.neglectus* and, under special conditions, also by *Colletotrichum coccodes*. The susceptibility and tolerance of potato cultivars to these pathogens largely determine the ultimate yield depression in the short rotations.

SAMENVATTING

EFFECTEN VAN VRUCHTWISSELING OP HET OPTREDEN VAN BODEMPATHOGENEN EN DE GEVOLGEN VOOR DE PRODUCTIE VAN AARDAPPELEN

Doelstelling en opzet van het onderzoek

De aardappel wordt in Nederland met hoge frequentie op eenzelfde perceel geteeld. Een hoge teeltfrequentie leidt op de langere duur bijna altijd tot een bodembesmetting met aardappelcysteaaltjes (*Globodera rostochiensis* en *G.pallida*), resulterend in lagere opbrengsten. Er is reeds veel onderzoek verricht naar deze zeer schadelijke nematode. Om de uitbreiding ervan tegen te gaan is de teeltfrequentie van aardappelen in Nederland zelfs wettelijk geregeld.

De vraag is evenwel of aardappelcysteaaltjes in Nederland de enige belangrijke bodempathogenen zijn die de groei van een aardappelgewas hinderen bij een hoge teeltfrequentie. Zijn er nog andere bodempathogenen die ook een negatief effect hebben op het groeipatroon, de opbrengst en de kwaliteit van dat gewas en waarvan de populatiedichtheid samenhangt met de teeltfrequentie van de aardappel? Het proefschrift is op deze bodempathogenen gericht.

Om effecten van de teeltfrequentie van de aardappel op de groei, opbrengst en kwaliteit van dat gewas in relatie tot het optreden van bodempathogenen te onderzoeken werd in 1979 een onderzoeksproject gestart. Er werden twee vruchtwisselingsproeven aangelegd met verschillende rotaties. De rotaties verschilden in teeltfrequentie van de aardappel. Daarnaast waren er rotaties met gelijke teeltfrequentie van de aardappel, maar verschillend in de gewassen waarmee de aardappel werd afgewisseld. Om effecten van de teeltfrequentie op verschillende grondsoorten te onderzoeken werd een vruchtwisselingsproef aangelegd op een humusarme zandgrond in de omgeving van Wageningen en één op zeeklei in Oostelijk-Flevoland.

Om verklaringen te vinden voor in de vruchtwisselingsproeven opgetreden effecten werden aanvullende veldproeven en pot- en containerproeven uitgevoerd. In deze proeven werden specifieke behandelingen aangebracht welke er op waren gericht bodempathogenen op te sporen en het relatieve effect ervan vast te stellen. In de pot- en containerproeven werd gebruik gemaakt van grond die afkomstig was van de beide vruchtwisselingsproefvelden, van vruchtwisselingsproefvelden elders in Nederland en van praktijkpercelen. Bovendien werden inoculatieproeven uitgevoerd met pathogenen welke uit ziek plantemateriaal van vruchtwisselingsproeven waren geïsoleerd. De inoculatieproeven waren bedoeld om effecten van pathogenen op het aardappelgewas beter te kunnen bestuderen en om interacties tussen pathogenen onderling en met andere factoren op te sporen.

Effecten van rotaties op een aardappelgewas

In de vruchtwisselingsproef op humusarme zandgrond was de droge-stofopbrengst aan knollen van het ras Element gemiddeld over 1981 tot en met 1986 bij continuteelt 35 % lager dan de opbrengst bij de teelt van aardappelen in een 1:5 rotatie (éénmaal per vijf jaar aardappelen op hetzelfde veld). De 1:2 rotatie suikerbieten-aardappelen bracht 24 % en de 1:2 rotatie snijmais-aardappelen 12 % minder op dan in de 1:5 rotatie. De opbrengst werd dus niet alleen beïnvloed door de teeltfrequentie van aardappelen, maar ook door de gewassen waarmee de aardappel werd afgewisseld.

Het onderlinge verschil tussen de beide 1:2 rotaties verdween grotendeels bij toepassing van granulaire nematiciden. De nematiciden hadden in alle rotaties een positief effect op de opbrengst. De relatieve opbrengstverschillen tussen de nauwe rotaties en de 1:5 rotatie veranderden echter nauwelijks door nematicidetoepassing.

In de nauwe rotaties trad al meteen vanaf de opkomst een verminderde groei op, vooral in de continuteelt en in de rotatie suikerbieten-aardappelen. De verschillen in gewasgroei namen in de loop van het groeiseizoen verder toe. Meestal begonnen eind juni verwelkingsverschijnselen op te treden, het eerst in de nauwe rotaties. De gewassen stierven sneller af naarmate de teeltfrequentie van aardappelen hoger was. In de 1:2 rotatie suikerbieten-aardappelen was de levensduur van het gewas korter dan in de 1:2 rotatie mais-aardappelen.

Zelfs in de 1:5 rotatie bleken de opbrengsten niet maximaal. In 1986 waren ze namelijk aanzienlijk lager dan die in een teeltsysteem, waarbij aardappelen op een veld werden geteeld na 8 jaar graan.

In de nauwe rotaties was ook de kwaliteit van de knollen geringer door een groter percentage misvormde knollen.

In de vruchtwisselingsproef op zeeklei bleef de droge-stofopbrengst aan knollen bij continuteelt 27 % en bij 1:2 teelt in de rotaties tarwe-aardappelen en suikerbieten-aardappelen respectievelijk 17 en 14 % achter bij die van 1:4 teelt.

In de potproeven werden eveneens grote effecten van de teeltfrequentie van aardappelen op de knolopbrengst gevonden.

Oorzaken van rotatie-effecten

In potproeven bleek, dat door sterilisatie van grond met methylbromide of gammastraling of door pasteurisatie bij 60 °C met stoom gedurende een half uur alle rotatieverschillen in opbrengend vermogen verdwenen. Dit wees op het voorkomen van schadelijke bodemorganismen bij hoge teeltfrequenties van de aardappel.

De belangrijkste opbrengstbeïnvloedende bodemorganismen bleken te zijn: actinomyceten die netschurft veroorzaken (*Streptomyces* spp.), de schimmels *Rhizoctonia solani* en *Verticillium dahliae* en op zandgrond ook wortelknobbelaaltjes (*Meloidogyne hapla* en *M.chitwoodi*). Op kleigrond bleken de nematoden *Pratylenchus thornei* en *P.neglectus* een indirect effect te hebben door synergistische interacties met andere bodempathogenen. De schimmel *Colletotrichum coccodes* bleek alleen onder bijzondere omstandigheden schade te veroorzaken, terwijl de schimmel *Fusarium tabacinum* geen enkel negatief effect vertoonde.

Streptomyces

Netschurft bleek een belangrijke ziekte voor de aardappel. Een toenemende teeltfrequentie van dit gewas leidde tot een sterke toename van de bodembesmetting met netschurft. Na drie pauzejaren voor de aardappel (1:4 teelt) bleek netschurft nog zeer sterk in de grond aanwezig, hoewel minder dan bij hogere teeltfrequenties.

Netschurft bleek naast de knollen in het bijzonder de wortels van de aardappelplant aan te tasten. De wortelaantasting vond al tijdens de opkomstfase van de plant plaats. Bij een hoge besmettingsgraad van de grond werd de plantegroei sterk geremd, resulterend in een geringer aantal knollen per plant en uiteindelijk in een aanzienlijke lagere opbrengst. De levensduur van de plant werd niet verkort.

Er bleek geen enkele relatie tussen de teeltfrequentie van aardappelen en het voorkomen van gewone schurft, veroorzaakt door *Streptomyces scabies*. Uit het onderzoek bleek, dat wanneer gewone schurft en netschurft samen voorkomen in een veld en er worden bij voortduring rassen geteeld welke vatbaar zijn voor beide ziekten, netschurft de gewone schurft verdringt.

Rhizoctonia solani

De mate van een stengel- en stoloonaantasting van een gewas door de schimmel *Rhizoctonia solani* bleek op zandgrond en op kleigrond zeer sterk afhankelijk van de teeltfrequentie van aardappelen. Continuteelt van aardappelen leidde tot zware stengel- en stoloonaantastingen. Het aantastingsniveau daalde duidelijk wanneer niet vaker dan eenmaal per twee jaar aardappelen op hetzelfde veld werden geteeld. Het percentage planten met een zware aantasting van stengels en stolonen als gevolg van een bodeminfectie bleek bij een teeltfrequentie van 1:4 of 1:5 verwaarloosbaar. De teeltfrequentie van de aardappel had een veel belangrijker effect op de mate van de stengel- en stoloonaantasting dan de gewassen waarmee de aardappel in een rotatie werd afgewisseld.

De teeltfrequentie bleek een geringer effect te hebben op het voorkomen van lakschurft (sclerotiën van *R.solani*) op de knollen aan het einde van het groeiseizoen. Op zeeklei werd geen enkel verschil in lakschurft aangetroffen tussen continuteelt van aardappelen en 1:2 teelt, terwijl op zandgrond als gevolg van de aanwezigheid van de hyperparasiet *Verticillium biguttatum* bij continuteelt zelfs een geringer aantal sclerotiën werd gevormd. Wel werden altijd minder sclerotiën gevormd bij 1:4 en 1:5 teelt dan bij 1:2 teelt.

Alleen zware en zeer zware stengel- en stoloonaantastingen hadden een negatieve invloed op de knolopbrengst. De aantasting van planten door *R.solani* nam tijdens het groeiseizoen voortdurend toe. Doordat een Rhizoctonia-aantasting een negatief effect had op het droge-stofgehalte van de knollen was het effect van *R.solani* groter op de droge- dan op de verse-knolopbrengst. Zwaar tot zeer zwaar door *R.solani* aangetaste planten gaven op basis van versgewicht 16-21 % en op basis van drooggewicht 20-29 % lagere opbrengsten.

In rotaties met een hoge teeltfrequentie van aardappelen werden meer misvormde knollen aangetroffen dan in ruime rotaties. Dit effect moet worden toegeschreven aan de verhoogde aantasting door *R.solani*. Een toenemende graad van aantasting ging namelijk gepaard met een toegenomen gewichtspercentage misvormde knollen. Het aantal kleine knollen nam hoofdzakelijk toe bij zeer zwaar aangetaste planten (krielplanten).

De toepassing van granulaire nematiciden/insecticiden leidde tot een zeer sterke toename van de stengel- en stoloonaantasting, zowel op zandgrond als op kleigrond.

Verticillium dahliae

In een biotoets werd een sterke relatie gevonden tussen de teeltfrequentie van aardappelen en de bodembesmetting met *V.dahliae*. In het veld werden bij een hoge teeltfrequentie van de aardappel vroeg in het groeiseizoen meer geïnfecteerde stengels aangetroffen dan bij een lage teeltfrequentie. Bij hoge teeltfrequenties raakten uiteindelijk vrijwel alle stengels van een gewas geïnfecteerd. Er werd een zeer nauwe correlatie aangetroffen tussen het aantal met *V.dahliae* geïnfecteerde stengels op ca. 15 juni en het optreden van verwelkingsverschijnselen in de bladeren twee weken later.

In alle proeven werd een vertraagde infectie van de stengels aangetroffen na toepassing van gegranuleerde nematiciden. Het kon aannemelijk worden gemaakt dat dit nematicide-effect in de vruchtwisselingsproef op lichte zandgrond veroorzaakt werd door bestrijding van wortelknobbelaaltjes (*Meloidogyne hapla* and *M.chitwoodi*), in de vruchtwisselingsproef op zeeklei door bestrijding van *Pratylenchus neglectus* en in een potproef met rivierklei door bestrijding van *P.thornei* en *P.neglectus*.

De snelheid waarmee planten geïnfecteerd kunnen raken met *V.dahliae* lijkt mede af te hangen van de omvang van het wortelstelsel. Vroeg in het groeiseizoen werd een zeer nauwe correlatie gevonden tussen het gewicht van de totale individuele plant en het aantal geïnfecteerde stengels per plant. Planten met een groter totaal gewicht hebben waarschijnlijk ook een omvangrijker wortelstelsel en hoe omvangrijker het wortelstelsel hoe groter de kans dat de plant een *V.dahliae* ziektekiem ontmoet.

Inoculatieproeven toonden aan dat een infectie door *V.dahliae* tot aanzienlijke opbrengstdervingen kan leiden.

Wanneer een grond eenmaal flink besmet is geraakt met *V.dahliae* duurt het vrij lang voordat de besmettingsgraad van de grond zodanig is afgenomen dat vatbare rassen zonder merkbare schade geteeld kunnen worden. In de vruchtwisselingsproef op zandgrond raakte bij een 1:5 teeltfrequentie van de aardappel nog een aanzienlijk deel van de planten geïnfecteerd (meer dan 50 %), hoewel de schimmel op de andere gewassen in de rotatie (gerst, mais en suikerbieten) geen belangrijke hoeveelheden microsclerotiën kan produceren. Onkruiden werden in deze proef altijd adequaat bestreden, zodat deze niet als overlevingsbron voor de schimmel hebben kunnen fungeren.

Colletotrichum coccodes

In de vruchtwisselingsproeven op lichte zandgrond en op zeeklei werd geen duidelijke relatie tussen de teeltfrequentie van de aardappel en het verloop van het aantal geïnfecteerde stengels waargenomen. In de tweede helft van het groeiseizoen raakten in de proef op zandgrond alle stengels in alle rotaties, dus ook bij de 1:5 teelt van de aardappel, geïnfecteerd. Dit werd toegeschreven aan het feit, dat naast de bodem ook de moederknol vrijwel altijd als infectiebron optreedt.

C.coccodes wordt wel in verband gebracht met het optreden van de verwelkingsziekte in aardappelen. In de veldproeven bleek er geen relatie te bestaan tussen het aantal door *C.coccodes* geïnfecteerde stengels en het aantal planten met vroegtijdige verwelkingsverschijnselen in het loof. Bij multiple lineaire regressieanalyses met de knolopbrengst als de te verklaren variabele voegde *C.coccodes* geen enkel extra verklarend effect toe.

In inoculatieproeven toonde de schimmel geen belangrijk effect op de plantegroei. In één proef werd aan het eind van het groeiseizoen een iets versnelde afsterving van de oudste bladeren waargenomen. Dit had evenwel geen enkel effect op de knolopbrengst. Indien *C.coccodes* samen met andere pathogene organismen in de grond was gebracht trad geen synergisme op, behalve bij een ras dat zeer vatbaar was voor *V.dahliae*. In dat geval veroorzaakte *C.coccodes* een toename van de schade die werd veroorzaakt door *V.dahliae*. In een nat jaar werden aanzienlijk meer stengels geïnfecteerd dan in een droog jaar.

Fusarium tabacinum

F.tabacinum kon zeer dikwijls van aardappelwortels worden geïsoleerd, maar door middel van inoculatieproeven werd aangetoond dat de schimmel wortellesies noch opbrengstreducties veroorzaakte.

Nematoden

In de vruchtwisselingsproef op lichte zandgrond werd een breed scala aan parasitaire nematoden waargenomen. Van deze nematodensoorten bleken *Meloidogyne* spp. een belangrijk deel van de variatie in knolopbrengst te kunnen verklaren. De *Meloidogyne* populatie was een mengpopulatie van *M.hapla* en *M.chitwoodi*. Vroeg in het groeiseizoen werd al een groot aantal gallen op de wortels van aardappelplanten waargenomen, met name in de rotatie suikerbieten-aardappelen en bij continuteelt van aardappelen. Door de gallen werd het totale wortelgewicht verhoogd, maar er waren duidelijke aanwijzingen, dat dat ten koste ging van het functioneren van het wortelsysteem. Er bleek een positieve correlatie te bestaan tussen het aantal gallen op de wortels en het droge-stofgehalte van het loof in de eerste helft van het groeiseizoen. Een hoog droge-stofgehalte in het loof wijst op een verminderde vochtopname door het gewas.

Behalve een direct effect op de groei en opbrengst van een aardappelgewas bleken wortelknobbelaaltjes ook een indirect effect op die groei en opbrengst te hebben. In de veldproef op lichte zandgrond werden zeer sterke aanwijzingen verkregen dat deze aaltjes een stimulerend effect hebben op het infectieproces van de schimmel *V.dahliae*. In een potproef met eenzelfde grond werd bovendien gevonden dat *Meloidogyne* aaltjes een synergistische interactie vertoonden met de schimmels *R.solani* en *V.dahliae*, resulterend in een versterkte afname van de knolopbrengst. Eenzelfde synergistische interactie werd in een potproef met kleigrond gevonden tussen deze beide schimmels en de nematode *Pratylenchus neglectus*.

De activiteit van *Meloidogyne* larven lijkt beïnvloed te worden door de soort van de gewassen in de rotatie of door de dichtheid van de populatie. Ondanks een lagere bodembesmetting voor het poten van de aardappelen in de rotatie suikerbieten-aardappelen vergeleken met continuteelt van aardappelen was de negatieve werking van deze nematoden in eerstgenoemde rotatie groter dan in de continuteelt.

M.chitwoodi was er de oorzaak van dat in 1983, waarschijnlijk door de bijzondere weersomstandigheden in dat jaar, een groot aantal gallen op aardappelknollen werd aangetroffen.

Interacties tussen organismen

De lagere opbrengsten van aardappelen in nauwe rotaties waren niet het gevolg van één enkel pathogeen maar van een complex van schadelijke organismen. Daarbij bleken allerlei interacties op te treden tussen bodempathogenen onderling. Zo werden er sterke aanwijzingen gevonden dat de endoparasitaire nematoden *Meloidogyne* spp., *Pratylenchus thornei* en *P.neglectus* de infectie van de plantewortel door *V.dahliae* bevorderen. Een heftige wortelaantasting door *Streptomyces* spp. (netschurft) vertraagde daarentegen de infectie door *V.dahliae*. *R.solani* *V.dahliae* en *Meloidogyne* spp. vertoonden een duidelijk synergistisch effect op zandgrond. Beide schimmels vertoonden ditzelfde synergistisch effect ook op kleigrond, maar dan in aanwezigheid van de nematode *P.neglectus*.

Er werden aanwijzingen gevonden dat *C.coccodes* alleen schade aan de opbrengst van een aardappelgewas toebrengt, wanneer het gewas door een andere oorzaak, zoals een zware aantasting door *V.dahliae* in een voor deze schimmel zeer vatbaar ras, heftig staat te lijden. Vochtige bodemomstandigheden verhogen de infectie van een gewas door *C.coccodes*.

Gewone schurft (*Steptomyces scabies*) werd in hoge mate verdrongen door netschurft (*Streptomyces* spp.) wanneer bij voortduring een ras werd geteeld, dat voor beide ziekten vatbaar is.

Effecten van rassen

Binnen het beschikbare rassenassortiment bleken grote verschillen in vatbaarheid voor bodempathogenen voor te komen. Door gebruik te maken van deze geconstateerde verschillen bleken rassen een hulpmiddel om de belangrijkheid van bepaalde bodempathogenen te onderzoeken.

Het bleek dat slechts 8 van de 95 rassen die opgenomen waren in de 57e Beschrijvende Rassenlijst voor Landbouwgewassen 1982 vatbaar waren voor netschurft. Twee qua areaal belangrijke rassen, Bintje en Désirée, bleken tot de vatbare rassen te behoren. Verder bleken er duidelijke verschillen tussen rassen te bestaan in vatbaarheid voor een stengel- en stoloonaantasting door *R.solani*. Inoculatieproeven met *V.dahliae* brachten rasverschillen in tolerantie aan het licht. Het ras Mirka bleek erg tolerant. Dit ras reageerde niet met een opbrengstdaling waar andere rassen dat wel deden.

Als gevolg van deze verschillen tussen rassen in vatbaarheid en tolerantie voor schadelijke bodempathogenen bleken de verschillen tussen rotaties als gevolg van verschillen in teeltfrequentie zeer sterk rasafhankelijk.

Conclusies

Streptomyces spp. (netschurft), *Rhizoctonia solani*, *Verticillium dahliae* en *Meloidogyne* spp. zijn pathogenen van de aardappel die voor een zeer groot deel teeltfrequentie-effecten van dit gewas onder Nederlandse omstandigheden verklaren bij afwezigheid van *Globodera* spp. De teeltfrequentie-effecten hangen in hoge mate af van de vatbaarheid en de tolerantie van het ras voor de betreffende ziekten. Het niveau van opgetreden schade hangt ook sterk af van onderlinge interacties tussen de pathogenen.

Colletotrichum coccodes veroorzaakt alleen schade onder zeer bijzondere omstandighedenen en *Fusarium tabacinum* in het geheel niet. De teeltfrequentie van de aardappel heeft geen invloed op de aantasting door *Streptomyces scabies* (gewone schurft).

CURRICULUM VITAE

Klaas Scholte werd geboren op 19 oktober 1938 te Garminge (gemeente Westerbork). Van 1952 tot 1956 bezocht hij de Lagere Landbouwschool te Westerbork en van 1956 tot 1958 de Rijks Middelbare Landbouwschool te Assen. Tevens volgde hij in die laatste periode de cursus Aardappelselecteur, welke georganiseerd werd door de Keuringsdienst Drenthe van de Nederlandse Algemene Keuringsdienst (NAK). Van al deze opleidingen werd het diploma met lof behaald.

Vanaf 1958 was hij werkzaam op het gemengde landbouwbedrijf van zijn ouders met de teelt van pootaardappelen als belangrijkste inkomensbron. Als hobby hield hij zich bezig met het kweken van nieuwe aardappelrassen. In 1963 slaagde hij voor het examen Mulo B via een schriftelijke cursus bij de Leidsche Onderwijsinstellingen (LOI).

Op 15 juni 1964 werd hij aangesteld als assistent van de bedrijfsleider van het proefbedrijf van de afdeling Landbouwplantenteelt en Graslandcultuur van de Landbouwhogeschool te Wageningen, met als taak de verzorging van akkerbouwproeven. Vanaf 1964 bezocht hij de Rijks Avond Hogere Landbouwschool te Ede, waarvan in 1967 het diploma werd behaald. Vanaf eind 1967 werd hij aangesteld als assistent van Ir. L.J.P. Kupers (lector in de landbouwplantenteelt, later hoogleraar). Nadien werden nog talrijke cursussen gevolgd, zoals Programmeren in Fortran IV (1968), Plantenfysiologie (Heterosiscursus 1972, met lof), de PAO-cursussen Schriftelijk rapporteren (1973), Statistiek-deel I (1976), -deel II (1977) en -deel III (1978) en Remote sensing (teledetectie) in landbouw en natuurbeheer (1982), en de computercursussen SPSS (1977) en Genstat (1985).

Na het doorlopen van diverse rangen werd hij in 1985 aangesteld als universitair docent bij de vakgroep Landbouwplantenteelt en Graslandkunde van de Lanbouwuniversiteit te Wageningen.