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Suppression of Rhizoctonia solani in potato fields. II. Effect of origin and degree of infection with Rhizoctonia solani of seed potatoes on subsequent infestation and on formation of sclerotia

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Abstract

The seed potatoes used in these experiments had been grown in a slightly acid pleistocene sandy soil or in a marine, holocene sandy loam. They were free of sclerotia of *R. solani* or lightly or moderately speckled with them. Seed potatoes from the sandy soil produced plants that suffered less from *Rhizoctonia* than plants from seed potatoes that had been grown on the marine sandy loam. Similarly harvested tubers had, in a non-conducive soil and in conducive soils with a (very) low inoculum density of *R. solani,* fewer sclerotia when they came from seed potatoes grown in an acid sand.

In each soil, the degree of infestation of the crop not only depended on the severity of infection of the seed potatoes, but also on their origin.

With regard to sclerotia production on tubers, three types of soil were distinguished: suppressive, conducive with a high, and conducive with a very low inoculum density of *R. solani*.

The differences in infestation and in the amounts of sclerotia on tubers between the crop grown from seed potatoes from the sandy soil and that from seed potatoes from the marine sandy loam soil, is attributed to a richer load of antagonists on the former and possibly to a larger proportion of saprophytic *Rhizoctonia* strains among their sclerotia.

The antagonists seem to be inhabitants of the subterranean parts of the plant and to function independently of the soil. This implies possibilities for their use in biological control.

Additional keywords: antagonism, conducive and suppressive soil, *Verticillium biguttatum.*

Introduction

In previous papers on this subject (Jager and Velvis, 1980, 1983) we tentatively concluded that suppression of *R. solani* in a potato field would be conditioned by a combination of two factors:

1. the abundance of soil-borne antagonists which can also thrive and multiply in the soil and on the surface of the subterranean parts of the potato plant, and
2. the 'load' of antagonists already present on the skin and in and on sclerotia of the seed potato before planting and compatible with the microflora of the soil site and contributing to the suppression.

The most common antagonistic fungi belonged to the *'Gliocladium-Verticillium* complex' (Jager and Velvis, 1983). In 1977 Jager et al. (1979) considered *Gliocladium roseum* as the most important antagonist as they isolated this fungus as the most numerous one from stolons in the warm and dry summer of 1977. Earlier in the season of that year some isolations of a *Verticillium* species were made. When compared with *G. roseum* on agar, an isolate of this fungus from a sclerotium was, neither a very impressive mycoparasite nor an antibiont. Later on, in normal (moist) years, we isolated the *Verticillium* species as the most common inhabitant of subterranean parts of the potato plant and of sclerotia. The species was named *V. biguttatum* by Gams and Van Zaayen (1982). The fungus was able to kill sclerotia (Velvis and Jager, 1983) and hyphae. The reason for our difficulty in distinguishing between *G. roseum* and *V. biguttatum* will be discussed later (Jager and Velvis, in prep.). In 1980, field experiments were set up to find out whether the antagonists are typical soil inhabitants or belong to the microflora which normally lives on the subterranean parts of the potato plant.

Materials and methods

Seed potatoes of the variety Bintje grown on a pleistocene sandy soil ('sand seed') or on a holocene sandy loam ('clay seed') were planted on four fields on each of the two soil types, viz. sandy soils and marine loam soils. Some properties of the soils are given in Table 1.

The seed potatoes were visually divided into three categories, viz., clean, and lightly and moderately speckled with sclerotia of *R. solani*, according to Bernelot Moens (1973). A study of the viability of the sclerotia, estimated by germination on water agar, showed that 42% of the sclerotia of the 'sand seed' and 12% of those of the 'clay seed' failed to germinate (Table 2). It was unknown which proportion of the sclerotia on the seed potatoes of each origin was pathogenic to the potato plant.

Disinfected seed potatoes were included to get an idea about the *Rhizoctonia* infection from the soil. Before they were planted in sandy soils, seed potatoes produced in a loam soil were disinfected. Likewise, seed potatoes grown in a sandy soil were disinfected before they were planted in loam and clay loam soils. Seed potatoes grown in a soil similar to the one in which they would be planted thus kept their population of antagonists intact. We supposed that antagonists present on tubers would thrive better in a soil where they belonged than in an alien soil. For disinfection the tubers were dipped into a diluted formaldehyde solution (0.3%) at about 52 °C for 4 min (Butler and Jones, 1955). All seed potatoes (three categories of infestation and each from two soil types) were sprouted in daylight in a greenhouse and planted in the field in eight replicate plots. Each field thuis had 48 plots, each consisting of six to eight rows of five plants of one origin and category. At regular intervals during the growing season a number of plants was sampled from the plots to estimate the degree of infestation of stems and stolons (on the first date only of stems). Infestation was rated as healthy, very light, light, moderate, heavy and very heavy. A disease index (d.i.) was calculated by multiplying the number of plants of each class by a certain factor as follows:

Table 1. Properties of the soil of the experimental fields.

Field	pH-KCl	Coarse sand (210-2000 μm) (%)	Silt (2-50 μm) (%)	Clay (<2μm) (%)	Humus (%)	K_2O (mg kg^{-1})	MgO (mg kg^{-1})	$CaCO_3$ (%)	Pwater (mg l^{-1})
Sandy soil									
Haren	4.1	11.4	37.1	—	5.7	110	42	—	15
Borger	5.0	36.0	11.8	—	6.5	140	89	—	37
Zeijerveld	4.4	17.5	42.7	—	6.8	190	95	—	42
Blijham	5.2	17.5	20.3	—	19.3	240	207	—	68
Marine soils									
Kloosterburen	5.1	1.7	30.8	6.1	1.9	80	—	0.0	50
Zuurdijk	7.3	0.2	45.2	22.8	2.0	180	—	8.8	55
Kimswerd	6.5	0.3	53.7	24.4	3.9	200	—	0.2	27
Bellingwolde	6.5	1.3	47.9	40.7	3.6	320	—	0.2	43

Tabel 1. Eigenschappen van de grond van de proefvelden.

Table 2. Viability of sclerotia of *R. solani* detached from seed potatoes grown in a sandy soil ('sand seed') and in a sandy loam soil ('clay seed').

Origin of sclerotia	Sclerotia (%) with indicated numbers of germination hyphae		
	0	1-10	>10
Sand seed	42	25	33
Clay seed	12	35	53

Tabel 2. Verschil in levenskracht van sclerotiën van R. solani van pootgoed afkomstig van zand- en kleigrond.

$$\text{d.i.} = \frac{\text{healthy} \times 0 + \text{very light} \times \frac{1}{2} + \text{light} \times 1 + \text{moderate} \times 1\frac{1}{2} + \text{heavy} \times 3 + \text{very heavy} \times 5}{\text{total number of plants sampled}/100}$$

Three weeks before harvest stems and leaves were desiccated chemically. During these three weeks the production of sclerotia reaches a maximum (Mulder et al., 1979). Seed potatoes were harvested in early August and potatoes for consumption in mid-September. According to the number and size of sclerotia the tubers were classified as clean (without sclerotia), and lightly, moderately and heavily speckled. The sclerotium index was calculated by multiplying the weight of each class by its factor as follows:

$$\text{s.i.} = \frac{\text{clean} \times 0 + \text{light} \times 3\frac{1}{2} + \text{moderate} \times 5 + \text{heavy} \times 6}{\text{total weight of all classes}}$$

The factors used were chosen more or less arbitrarily. The values of the sclerotium index are used for mutual comparison of the effects of the degree of infection and the origin of the seed potatoes on the formation of sclerotia in the different soils. This index is different from the rating we used earlier (Jager and Velvis, 1980, 1983).

The presence of sclerotia inhabiting fungi was determined by incubating sclerotia on moist perlite for 4 weeks at 20 °C. From each plot 100 sclerotia, detached from tubers, were used.

Results

The disease indices of stems and stolons in the course of the growing season are given in Fig. 1. The result for only four of the eight fields are presented, those for the other fields not being essentially different.

The disease indices of plants from 'sand seed' were always lower than those from 'clay seed' of the same infection class. Very often the disease index of plants from moderately infected 'sand seed' was lower than that of plants from lightly infected 'clay seed'. Thus the amount of sclerotia present on seed potatoes is not necessarily a measure of infestation of the crop.

Fig. 1. Disease indices during the course of the growing season of plants growing from seed potatoes that originated from a neutral sandy loam ('clay seed') or from an acid sand ('sand seed').
•———• clean seed potatoes; •———0 disinfected seed potatoes; ×———× slightly infected seed potatoes; +———+ moderately infected seed potatoes;
Points in the curves, obtained after harvest of the seed potatoes are connected with dotted lines. Points obtained when the plants were already starting to die – and lost their resistance – are not connected to the preceding points.

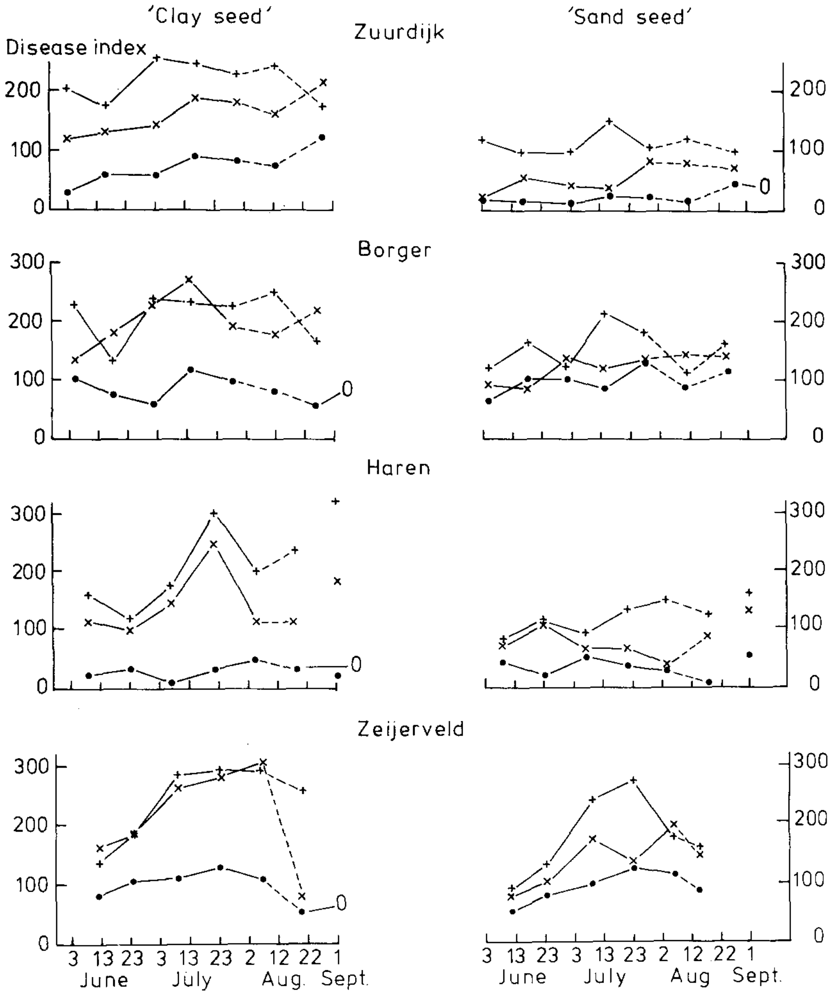

Fig. 1. Aantastingsindices gedurende het groeiseizoen van planten gegroeid uit pootgoed afkomstig van de klei ('clay seed') of van het zand ('sand seed').
•———• schoon pootgoed; •———0 ontsmet pootgoed; ×———× licht besmet pootgoed; +———+ matig besmet pootgoed
Na de oogst van het pootgoed zijn de punten in de figuur met stippellijnen verbonden met de voorgaande punten. Punten verkregen van een gewas dat begon af te sterven – en z'n weerstand begon te verliezen – zijn niet verbonden met de voorafgaande punten.

The infestation of plants from disinfected seed potatoes was caused by *Rhizoctonia* inoculum from the soil. A slight infestation from the soil was found on only one pleistocene soil (Haren) and on three holocene soils (Zuurdijk, Kloosterburen and Kimswerd). Bellingwolde showed a higher infestation. This field was very wet, due to heavy rains. In the other fields on pleistocene soils (Borger and especially Blijham and Zeijerveld) the infestation from the soil was more severe. In holocene soils, the infestation of plants from non-disinfected, clean (sclerotia-free) 'clay seed' was generally more severe than the infestation of plants from lightly infected 'sand seed'. Although no sclerotia had been found on clean 'clay seed', the possibility exists that hyphae or monilioid cells had been present near the buds. On pleistocene soils, plants from non-disinfected clean 'sand seed' showed little or no more infestation than plants from disinfected 'clay seed' (Haren, Zeijerveld).

Relatively low values for the disease index of plants from 'sand seed' were found at Haren, Zuurdijk and Kimswerd.

The sclerotium indices of tubers harvested for seed or consumption from plants growing from each type of seed potatoes on four of the eight fields are presented in Fig. 2. When these data are compared with the degree of infestation of stems and stolons during the season, as presented in Fig. 1., information is obtained about (1) the type of *Rhizoctonia* strains that was most frequently involved (pathogenic or saprophytic strains), (2) the incoculum density of *Rhizoctonia* in the soil in the case of disinfected seed, and (3) the presence of active antagonists.

Fig. 2. Sclerotium indices of harvested seed potatoes (P) and potato tubers for consumption (C) from four experimental plots. Tubers were harvested from plants growing from seed potatoes that originated from a neutral sandy loam ('clay seed'), or from an acid sand ('sand seed'). 'Clay seed' and 'sand seed' had been used disinfected (a_0) or non-disinfected clean (a_1), or lightly (b) or moderately (c) infected with *R. solani* sclerotia (dashes indicate extreme values).

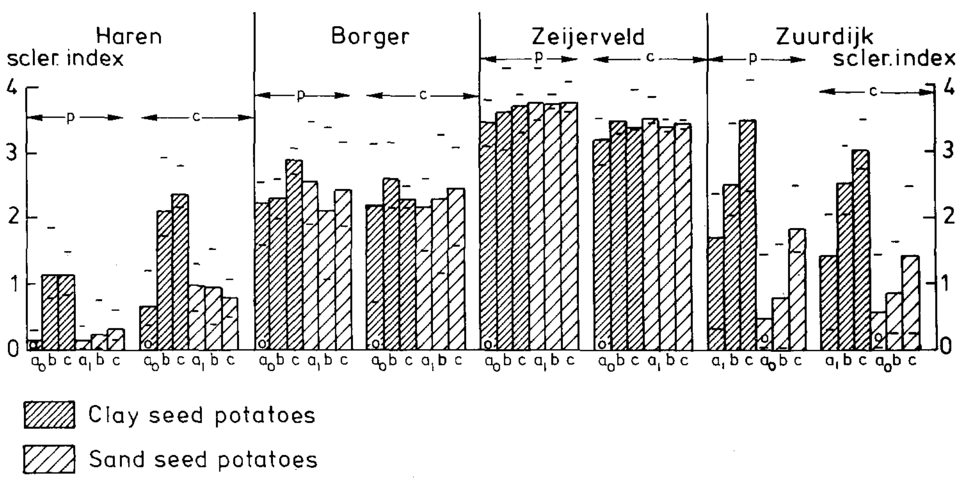

Fig. 2. Sclerotiumindices van geoogst pootgoed (P) en consumptieaardappelen (C) van vier verschillende proefvelden. De knollen zijn geoogst van planten gegroeid uit pootgoed van het zand ('sand seed') of van de klei ('clay seed'). Het gebruikte pootgoed was schoon en wel ontsmet (a_o) of niet ontsmet (a_1), of licht (b) of matig (c) bezet met sclerotiën van R. solani (extreme waarden zijn in de figuur aangeduid met –).

Based on the production of sclerotia on tubers in different soils, three types of soils were distinguished, viz. suppressive soil and two types of conducive soils.

A. Suppressive soils. The field at Haren was the only with a suppressive soil: the sclerotium index of the tubers was strongly reduced compared with that of the seed potatoes used and of tubers from other fields; disinfected seed produced a nearly clean crop. The suppression was most evident in the case of tubers harvested as seed potatoes. The tubers harvested for consumption carried more sclerotia. The antagonism seems to be reduced here towards the end of the season. Remarkable was also the difference between the crop from 'sand seed' with a low sclerotium index and that from 'clay seed' with a higher index.

B_1. Conducive soils, with a high inoculum density of R. solani, Such soils are a source of much *Rhizoctonia* infection. The sclerotium production on the crop was about the same for all treatments, irrespective of origin and degree of infection of the seed potatoes. The values of the sclerotium index seem to be more or less characteristic for each soil (Borger, Blijham, Kloosterburen and Zeijerveld).

In addition to pathogenic strains, saprophytic strains of *R. solani* were always present. Antagonists were present – sometimes even in relatively large numbers –, but they did not suppress *R. solani.* The reason for their apparent antagonistic inability is not yet clear.

B_2. Conducive soils, with a (very) low inoculum density of R. solani. These soils are principally conducive, but they usually have low inoculum densities of *R. solani* and presumably have a weak antagonistic ability. The degree of infection of the planted seed potatoes is reflected by the sclerotium indices of tubers harvested on the different plots (Zuurdijk, Kimswerd). The soils were holocene, marine soils with a pH-KCl of 6.5 and higher. The differences between 'sand seed' and 'clay seed' with regard to infestation and the formation of sclerotia were very pronounced.

Infection of sclerotia by antagonists. Sclerotia of *R. solani* on potato tubers can be infected by different kinds of antagonists (Jager et al., 1979, Jager and Velvis, 1980, 1983). The composition of the soil microflora appears to determine the degree of infection and the kind of infecting organisms, which are usually fungi. Streptomycetes are often present (Jager et al., 1979; Jager and Velvis, 1980, 1983). Antagonistic fungi grow slowly on sclerotia and can sporulate abundantly. They kill the cells and consume their contents. Killed sclerotia are soft in a moist condition and can be easily fragmented between the fingers. Up to now many mycoparasites have been found as killers of sclerotia. *V. biguttatum* proved to be the most common parasite. Table 3 gives the percentages of sclerotia from tubers of the fields infected with different mycoparasites and microorganisms of unknown character (epiphytes). The percentage of uninfected sclerotia is also given. Fig. 3 shows the colonization of a sclerotium by *V. biguttatum.* The whole sclerotium is overgrown by the parasite. Fig. 4 illustrates the colonization by *Streptomycetes,* which is restricted to isolated patches.

Rhizoctonia-conducive soils (Zeijerveld, Kloosterburen and Borger) had a high percentage of sclerotia infected with *V. biguttatum,* whereas the suppressive soil at Haren had the highest percentage of uninfected sclerotia. An abundant presence of

Table 3. Percentage of sclerotia from potato tubers infected with various hyperparasites.

Field	Vert.[1]	Glio.	Horm.	Pen.	Strept.	Others	Uninfected
Estimated in October							
Haren	59	1	0	6	46	2	21
Borger	65	0	0	0	54	5	7
Zeijerveld	76	2	3	3	26	31	8
Blijham	26	1	0	0	75	2	8
Kloosterburen	72	1	2	0	49	2	3
Zuurdijk	38	0	0	0	80	0	12
Kimswerd	0	0	0	5	97	2	3
Bellingwolde	54	0	0	1	81	0	3
Estimated in April after storage at 4 °C (washed tubers)							
Haren	5	0	0	5	57	7	31
Borger	9	0	0	3	46	0	46
Zeijerveld	14	1	0	2	28	1	56
Blijham	12	0	1	1	50	4	39
Kloosterburen	12	0	0	5	47	2	34
Zuurdijk	1	1	0	0	53	4	40
Kimswerd	0	0	0	16	82	28	5
Bellingwolde	0	0	0	0	93	1	7

[1] Vert. = *Verticillium biguttatum;* Glio. = *Gliocladium (roseum)*; Horm. = *Hormiactis fimicola*; Pen. = *Penicillium* spp.; Strept. = *Streptomyces* spp.

Tabel 3. Het percentage sclerotiën van de oogst van de proefvelden, dat geïnfecteerd is met verschillende hyperparasieten.

sclerotia increases the chance of infection. In the suppressive soil of Haren only very few sclerotia were formed and a relatively large part of these escaped parasitism.

The washed tubers with sclerotia were stored during winter at 4 °C. In April the sclerotia were again examined for the presence of antagonists (Table 3). The decrease of *V. biguttatum* is striking. *V. biguttatum* does not grow at a temperature of 4 °C. Its minimum temperature is slightly lower than 15 °C (Van den Boogert and Jager, in prep). A high relative humidity is necessary for good growth. This condition exists in normally moist field soil and on wetted perlite in a petri dish. Up to now we never found *V. biguttatum* growing on sclerotia of potato tubers in a dry soil. The reasons for the decrease of *V. biguttatum* in sclerotia during storage are not exactly known. Lack of survival structures, and activity of antagonists and predators (mites) at the subminimal temperature for *V. biguttatum* may account for its decline.

The percentage of sclerotia with streptomycetes was still high. Their effect on the pathogen is not clear. The colonies were small and grew very slowly; they were often present on dead hyphae and not on the sclerotium.

Presumably they are not important as killers of sclerotia. There was an increase in the percentage of sclerotia infected with a *Penicillium* sp. which could grow under the

Fig. 3. A sclerotium of *R. solani* overgrown with a parasitizing *V. biguttatum.*

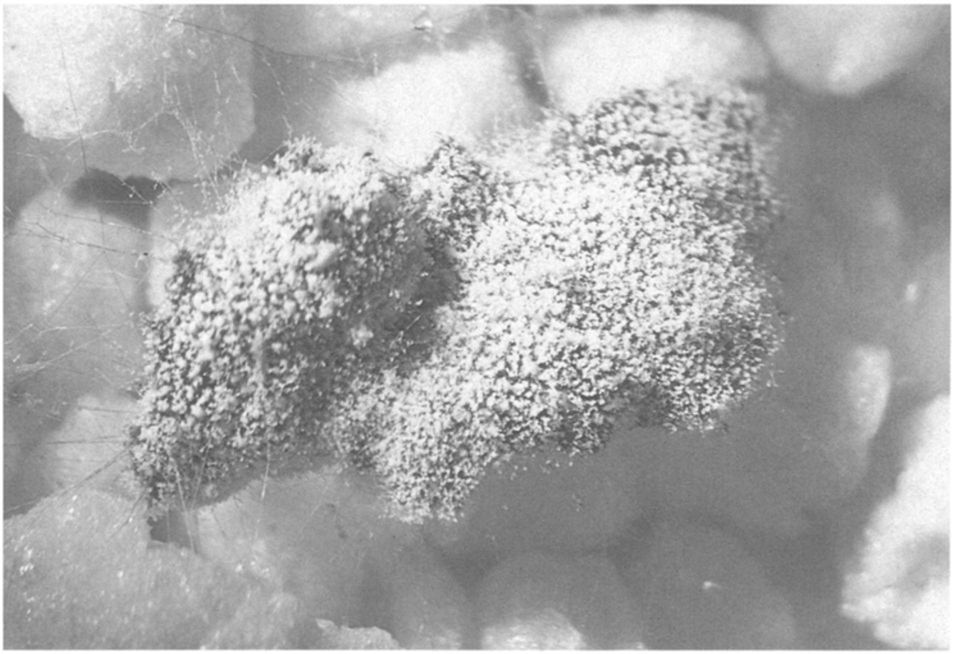

Fig. 3. Een sclerotium van R. solani overgroeid met een parasiterende V. biguttatum.

cold and dry conditions of storage. The increase in the percentage of sclerotia which was not, or no longer, infected was obvious. The assumption that these sclerotia would be dead proved not to be valid (Table 4). A decrease in viability seemed to occur amongst the sclerotia of Kimswerd, where an increase in *Penicillium* on the sclerotia was observed (Table 3). There was no change in viability of the sclerotia from the other fields. This means that no antagonists were present there that could grow on sclerotia under the conditions of storage.

Discussion

Seed potatoes produced on a slightly acid pleistocene sand soil gave rise to plants that suffered less from *Rhizoctonia* than plants from seed potatoes produced on a holocene, about neutral, marine soil and the amounts of sclerotia on the harvested tubers were smaller, except for conducive soils with much *Rhizoctonia.*

These phenomena were probably due to two factors: first, differences in the amount and kind of antagonists on the surface of the seed potatoes and on and in the sclerotia, and secondly, differences in the proportion of sclerotia of saprophytic strains among those on the seed potatoes. The presence of saprophytic strains of *R. solani* among sclerotia on the tubers and in the soil was already reported by Person (1945), Flentje and Saksena (1957), Bolkan and Wenham (1973) and Jager and Velvis (1980). The se-

Fig. 4. Small colonies of *Streptomycetes* on a sclerotium of *R. solani*.

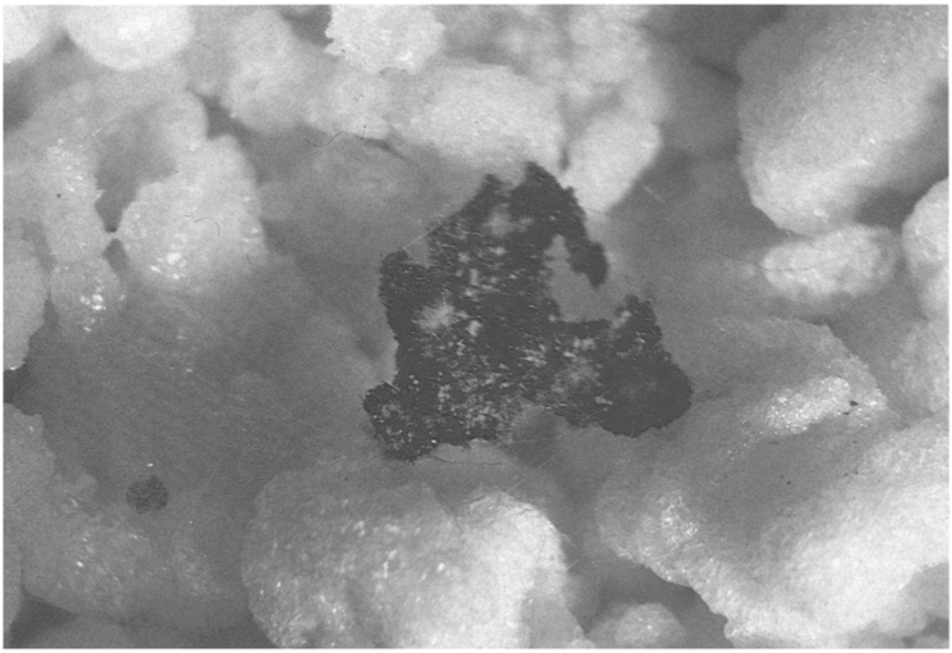

Fig. 4. Kleine streptomyceetkolonies op een sclerotium van R. solani.

Table 4. Viability of sclerotia of *R. solani* detached from tubers shortly after harvest (October) and after storage (April).

Field	Sclerotia (%) with indicated numbers of germination hyphae							
	October				April			
	0	0-10	10-25	25	0	0-10	10-25	25
Haren	1	24	31	45	2	23	28	47
Borger	0	1	21	78	0	10	15	75
Zeijerveld	0	13	12	75	0	3	12	85
Blijham	0	0	8	92	0	6	17	77
Kloosterburen	0	2	4	94	0	6	3	91
Zuurdijk	0	3	18	79	0	11	6	83
Kimswerd	1	17	12	70	5	32	26	37
Bellingwolde	0	10	11	79	0	11	14	75

Tabel 4. Levenskracht van sclerotiën van R. solani, verkregen van aardappelknollen kort na de oogst (oktober) en na bewaring (april).

cond factor cannot be used to explain the difference in the amount of sclerotia on tubers from 'sand seed' and 'clay seed', as saprophytic strains also form many sclerotia.

Antagonists that reduce the infestation and the formation of sclerotia probably are the major factor. They contributed to the suppressive ability of the soil in the field at Haren, but also led to a reduced infestation of plants from 'sand seed' and a low production of sclerotia in Zuurdijk and Kimswerd. Sclerotia from sandy soils proved to be less viable (Table 2) and more frequently infected by antagonistic fungi that those from holocene soils, on average 73 and 25%, respectively (Jager and Velvis, 1980).

From Table 3 it is clear that sclerotia produced in conducive soils with much *Rhizoctonia* (Zeijerveld, Borger and Kloosterburen) were most severely infected by *V. biguttatum* and other mycoparasites.

This paradoxal situation may be explained by the fact that the population of *V. biguttatum* started to grow and to spread late, so that it failed to destroy *R. solani*, and by the fact that the population of *V. biguttatum* in these soils consisted of strains that are less effective antagonists, at least against living hyphae. It seems to be much easier for antagonists to kill metabolically inactive sclerotia than metabolically active hyphae. Some species growing on sclerotia do not show parasitism against hyphae (*H. fimicola*, some *Penicillium* spp., most *Streptomyces* spp.). Even within the species *V. biguttatum* there are members which are hardly or not active against living hyphae. We isolated from infected sclerotia some strains of *V. biguttatum* which were completely inhibited by *R. solani* on agar during at least two weeks. The proportion of similar strains in a natural population of *V. biguttatum* in soil is unknown; presumably it varies among fields and also within a field.

The antagonists present on the 'sand seed' were found to be active not only in the sandy soils but also in the other soils (Fig. 1; Fig. 2, except in conducive soils with much *Rhizoctonia*). It is concluded that the antagonist(s) presumably belong to the natural inhabitants of the surfaces of stems, stolons and roots of the potato plant and thus are largely independent of the soil itself. If this is true, there may be prospects for biological control of *R. solani* with these antagonists. This will be further investigated.

Samenvatting

Onderdrukking van Rhizoctonia solani in aardappelpercelen. II. Invloed van herkomst en mate van bezetting van pootaardappelen met Rhizoctonia solani op de resulterende aantasting en de vorming van sclerotia

Gebleken is, dat het gebruikte pootgoed afkomstig van zandgrond – of het nu vrij is van sclerotiën van *Rhizoctonia solani* of licht of matig hiermee bezet – een minder sterke aantasting geeft van het gewas (Fig. 1) en vaak een geringere sclerotiumproduktie op de geoogste knollen (Fig. 2) dan overeenkomstig pootgoed van de klei.

De mate van aantasting van de plant hangt af van de mate van besmetting van de pootknol (Fig. 1), tenzij een sterke besmetting vanuit de grond optreedt.

Drie categorieën van gronden werden onderscheiden. Op *Rhizoctonia-dragende* gronden met veel *Rhizoctonia* was de hoeveelheid sclerotiën op de oogst ongeveer gelijk voor zand- en kleipootgoed, ongeacht de mate van besmetting. Het niveau van sclerotiënbezetting is daar afhankelijk van de grond. In een *Rhizoctonia-werende*

grond is het niveau van sclerotiënproduktie op de oogst, vergeleken met die op het pootgoed, laag.

Bij *Rhizoctonia-dragende* gronden met zeer weinig *Rhizoctonia* (zavel- en kleigrond) bepaalt de mate van besmetting van het pootgoed de sclerotiënbezetting van de oogst.

Het verschil in gedrag tussen het gebruikte pootgoed van de klei en van het zand t.a.v. de aantasting van de plant door *R. solani* en de sclerotiënvorming op de oogst wordt toegeschreven aan een rijkere bezetting van het zandpootgoed met antagonisten. Tevens is het mogelijk dat saprofytische (niet of weinig ziekteverwekkende) stammen van *R. solani* in de sclerotiën op het zandpootgoed sterker vertegenwoordigd zijn.

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