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FOOT ROT OF *CUCURBITA FICIFOLIA*, THE ROOTSTOCK OF CUCUMBER, CAUSED BY *NECTRIA HAEMATOCOCCA* VAR. *CUCURBITAE*[1]

Een voetziekte van Cucurbita ficifolia, *de onderstam van komkommers, veroorzaakt door* Nectria haematococca *var.* cucurbitae

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In 1962 in the Netherlands a foot rot due to *Nectria haematococca* Berk. & Br. var. *cucurbitae* (Snyd. & Hans.) Dingley occurred in *Cucurbita ficifolia*, the rootstock of grafted cucumber grown in glasshouses. The Dutch isolates of the pathogen proved to be identical with ones isolated from abroad. *C. ficifolia* seedlings grown in infested soil showed a foot rot at the base of the hypocotyl when about two weeks old, after which the plants soon died off completely. Though the fungus could grow from the rootstock into the cucumber graft, it never showed systemic growth in still living stems. If soil-infestation was only slight, *C. ficifolia* plants became attacked at a later stage of development. This was in agreement with the dying off of mature cucumbers in the glasshouses at the commencement of cropping. All Cucurbitaceae which were grown in infested soil finally succumbed to the disease. No resistant substitute for the *C. ficifolia* rootstock was found. Other crops appeared to be resistant. The seed-borne character of the pathogen was demonstrated by injecting fruits with a spore suspension at different developmental stages. When the surviving fruits were harvested, only those inoculated when three to five weeks old contained viable seeds, some of which were infected superficially as well as internally. The use of seeds from bruised and infected fruits might have introduced the pathogen into the greenhouses of holdings specializing in selling grafted plants and cucumber seedlings, thousands of which are daily sent all over the country, thus spreading the disease. In recent years this has been avoided by using only seeds from non-damaged fruits and by regularly steaming the soil in which the seedlings are grown.

INTRODUCTION

Cucumbers have been cultivated under glass in the Netherlands for very many years. As crop rotation is impossible, soil-borne diseases are inevitable in all crops grown under glass and, especially in cucumbers, several *Fusarium* species have been a serious menace in the past (RIETBERG, 1940; Proeftuin "Zuid-Hollandsch Glasdistrict" te Naaldwijk, Jaarverslagen 1943 en 1944). Formerly steam sterilisation was the only method of preventing an attack of these fungi. In 1945 grafting of cucumbers onto rootstocks of *Cucurbita ficifolia* which are resistant to certain *Fusarium* species, was introduced (MAAN, 1946) and this method has since been extensively applied in practice. Grafting was first carried out bij the growers themselves, but later on some growers started specializing in the production of these grafts. At present practically all grafting is performed on these specialized holdings, on which cucumbers on their own roots are also

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produced on a large scale. In general the growers order the cucumber plants which they need from these firms. Although this specialization is generally advantageous, it may have consequences regarding diseases (BRAVENBOER, 1964).

In 1958, on one of the holdings specialized in grafting, a disease occurred which had previously been unknown in the Netherlands. A preliminary examination suggested a *Fusarium* species to be the pathogen (Proefstation voor de Groenten- en Fruitteelt onder glas te Naaldwijk, Jaarverslag 1958).

The disease was not observed in the three succeeding years and no further research was carried out. In 1962 and 1963, however, dying off of cucumbers occurred again and this time the outbreak was more severe and the disease spread over more holdings than in 1958. There proved to be a correlation between the occurrence of the disease and the origin of the grafted plants (BRAVENBOER & THEUNE, 1964), it being mainly on such plants that the disease occurred. On most holdings the first symptoms were observed some weeks after the cucumbers had been planted out, and the dying off of the plants continued until the end of the growing season. The proportion of plants dying from the disease varied from a few to practically one hundred percent within three weeks.

THE SYMPTOMS AND THE PATHOGEN

The first symptoms of the disease appeared at the commencement of cropping at the base of the rootstock of the plants, where light green watersoaked spots developed which quickly changed into a light or dark brown rot. The lower leaves of the scion yellowed and a reversible wilting occurred in the daytime when temperature was high. After a few days the wilted plants ceased to recover and the tips of the plants became dark green. When the plants died, slits in the stem base of the rootstock as well as in the scion, became covered with mycelium and spores up to 10 or 15 cm above the soil. The fungus invaded the cortical tissue at the base of the stem, which softened and decayed. Mycelium was also found in the xylem vessels. The roots did not seem to be attacked.

The fungus was easily obtained from macroconidia developing on stem pieces of *Cucurbita ficifolia* kept under moist conditions. By this means several isolates were obtained in pure culture from diseased plants grown in glasshouses in different localities in the Netherlands.

Spore measurements were in accordance with those of WOLLENWEBER & REINKING (1935) for *Fusarium javanicum* Koord. var. *ensiforme* (Wr. & Reinking) Wr. The large size of the conidia was striking: the one-celled conidia measuring on the average 8.4 × 3.8 μ, the 7-septate ones 74.5 × 5.6 μ (Fig. 1).

In South Africa a foot rot of cucurbits caused by *Fusarium javanicum* Koord. var. *theobromae* (Appel & Strk.) Wr. has been described by DOIDGE & KRESFELDER (1932) and by DOIDGE (1938). The spore measurements given by DOIDGE agree with those of the Dutch strains. CONROY (1953a,b, 1955, 1959, 1961) described a similar footrot occurring in New South Wales caused by *Fusarium solani* (Mart.) Appel & Wr. f. *cucurbitae* Snyd. & Hans. According to this author the disease seems to have been present in Australia since 1923 at least. In the field, pumpkin and squash appeared to be highly susceptible and cucumbers were attacked to a lesser degree. SNYDER (1938, 1940) observed a destructive foot rot on *Cucurbita pepo*, *C. moschata* and *C. maxima* in the coastal counties of

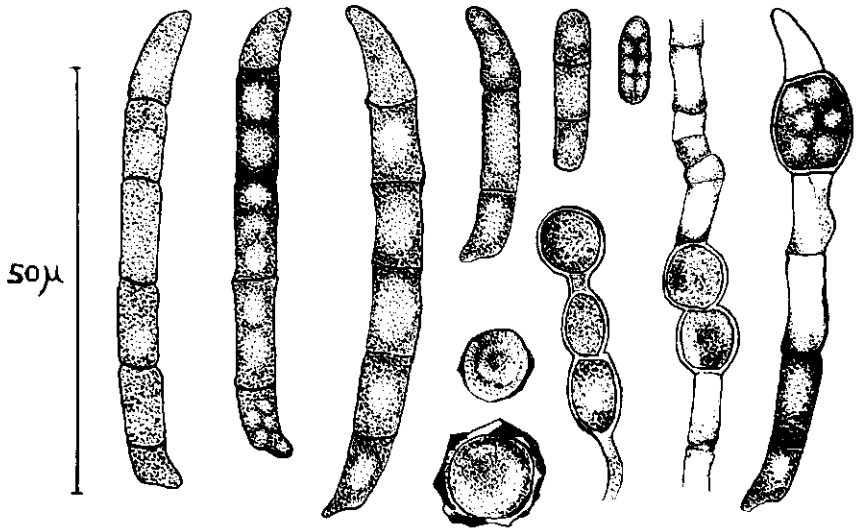

FIG. 1. Conidia and chlamydospores of *Fusarium solani* f. *cucurbitae*.
Conidiën en chlamydosporen van Fusarium solani *f.* cucurbitae.

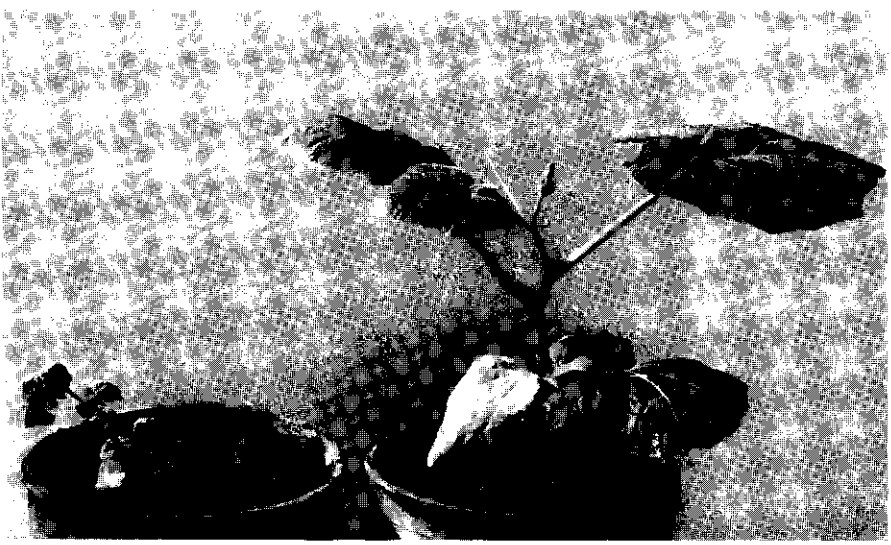

FIG. 2. *Cucurbita ficifolia*. Left: plant grown in soil infested with *Fusarium solani* f. *cucurbitae*, died off when about two weeks old. Right: plant grown in steamed soil, about three weeks old.

Cucurbita ficifolia. *Links: plant opgekweekt in grond besmet met* Fusarium solani *f.* cucurbitae, *afgestorven op de leeftijd van ongeveer twee weken. Rechts: controleplant, opgekweekt in gestoomde grond.*

FIG. 3. Fruit of *Cucurbita ficifolia,* about three weeks after the injection with 0.5 ml of a suspension of *Fusarium solani* f. *cucurbitae.*

Vrucht van Cucurbita ficifolia, *ongeveer drie weken na het toedienen van een injectie met een sporensuspensie van* Fusarium solani *f.* cucurbitae.

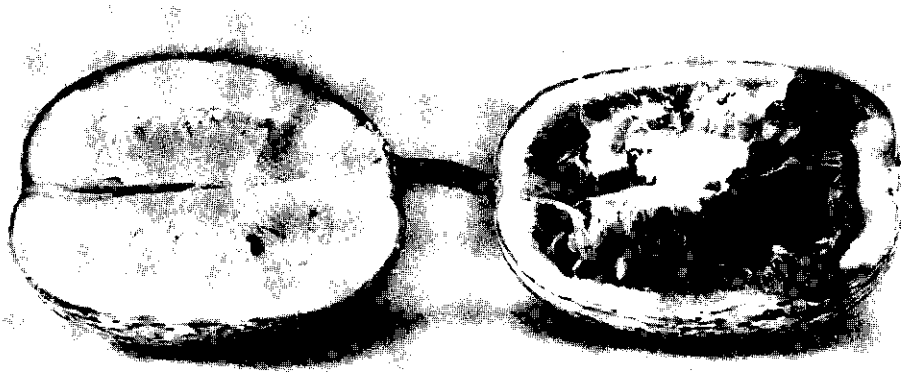

FIG. 4. Right: fruit shown in Fig. 3, cut open about eight weeks after treatment with the spore suspension. The flesh had partly decayed. Left: control, injected with sterile water.

Rechts: dezelfde vrucht als in fig. 3, opengesneden acht weken na het toedienen van de sporensuspensie. Het vruchtvlees was gedeeltelijk aangetast. Links: controle, geïnjiceerd met steriel water.

California caused by the same fungus. Though PRASAD (1949), who measured the conidia of the American isolates, presented only measurements taken from samples of septate and non-septate conidia together, there is no contradiction between the sizes of the conidia of the American and the Dutch isolates. Probably the *Fusarium* species described by DOIDGE, CONROY and SNYDER in different parts of the world are identical. SNYDER (1940) demonstrated the heterothallic character of the fungus by the use of single spore cultures. He obtained perithecia which he described as *Hypomyces solani* Rke & Berth. emend. Snyd. & Hans. var. *cucurbitae* Snyd. & Hans. DINGLEY (1961) recognised the perithecial form as *Nectria haematococca* Berk. & Br. var. *cucurbitae* (Snyd. & Hans.) n.comb. SCHIPPERS (1966) and SCHIPPERS & SNYDER (1967) who studied sex and compatibility of the Dutch strains proved that the Dutch isolates are interfertile with *F. solani* f. *cucurbitae* race 1 from the collection of W. C. SNYDER, Berkeley, California.

THE INFLUENCE OF THE TEMPERATURE ON GERMINATION AND MYCELIUM GROWTH

Germination did not occur at a temperature below 10°C. Temperatures between 25° and 30°C appeared to be optimal for mycelial growth. The maximum temperature for growth appeared to be over 35°C, which indicates that the fungus can thrive at high temperatures such as prevail in tropical and subtropical countries and in glasshouses where the growth of cucumbers is promoted by heating up to temperatures of 30°C and higher. On the other hand the fungus survived in soil kept in containers placed outdoors during the severe winter of 1962. It did not survive soil steaming.

THE PATHOGENICITY OF THE FUNGUS

Inoculum was prepared by growing the fungus in a mixture of sterilized sand and garden soil moistened with a liquid extract of oatmeal. The mycelium developed rapidly and the infested soil was then mixed with steamed soil in pots in which disinfected seeds of *Cucurbita ficifolia* were sown. Shake cultures were also successfully used for infestation of steamed soil. About a week after sowing, the seedlings emerged and within two weeks the first symptoms were visible. A light green watersoaked spot appeared at the stem of the base which quickly developed into a rot extending along the hypocotyl as longitudinal brown stripes. Two to three weeks after sowing most of the seedlings had succumbed, the rot having girdled the stems (Fig. 2). The fungus could be isolated from diseased plants. The different isolates appeared to be identical in pathogenicity. *C. ficifolia* seedlings were also successfully inoculated by injections of a spore suspension into the hypocotyl or immersion of the roots into such a suspension before planting. Symptoms developed in all cases, though only if the air humidity was sufficiently high.

How far the fungus could grow from the infected base of the stem through the stem of *C. ficifolia* in an upward direction was investigated by dipping the roots of a number of seedlings into a spore suspension containing 4×10^3 spores per ml before planting. At 50, 74 and 85 days after planting the stems of a few of those plants which survived were cut into pieces, parts of which were tested for the presence of the *Fusarium*. The fungus could be isolated only from sec-

tions which were cut up to 8, 10 and 7 cm from the base of the stem respectively, these being the only parts which showed disease symptoms. No systemic growth in the stems was detected, though in a more advanced stage of the disease the fungus filled crevices and slits which commonly occur at the base of old plants, without entering the stem. The mycelium mats remained superficially up to about 10 cm from the base of the stem. After the death of the plants, however, the fungus did invade higher parts. From a dead stem with a length of 200 cm it could be isolated up to 30 cm from the base, three weeks after the plant had died off. When grafts of cucumber on *Cucurbita ficifolia* rootstock were planted in infested soil, the fungus was able to pass from the stock into the scion.

Though it had become clear that seedlings of *C. ficifolia* could be severely attacked in heavily infested soil, experiments were made to determine whether escape might occur when seedlings were grown in only slightly infested soil, such as could be expected in glasshouses recently invaded by the fungus. Twenty five ml of successive ten-fold dilutions of a spore suspension containing 4×10^4 spores per ml was added to each pot containing steamed soil in which a ten days old seedling was planted. Five plants were treated with each dilution (Table 1). After four days the growth of the plants treated with the undiluted suspension was retarded. After ten days three of the five plants of this group showed symptoms and after about four weeks all plants had died off. The other plants showed symptoms at a later date or not at all. Plants treated with the highest dilutions, still symptomless 78 days after inoculation, were cut into pieces from which the fungus could not be isolated. The experiment was repeated with dilutions of a spore suspension containing 4×10^7 spores per ml with similar results. It was concluded that the heavier the inoculum potential in the soil, the more rapidly did death of the plants occur. A slight infestation may lead to late infection or even to escape of the plants. Whether escape is also

TABLE 1. Number of diseased and dead plants occurring in soil to which 25 ml of different dilutions of a spore suspension was added. Five plants per dilution.
Aantal zieke en dode planten opgekweekt in grond besmet met 25 ml van een sporensuspensie in verschillende verdunningen. Vijf planten per verdunning.

	Days after inoculation								
Dilutions	10	15	24	30	41	48	59	64	*Verdunningen*
Undiluted, 4×10^4 spores per ml	3	4(1)	1(4)	(5)	(5)	(5)	(5)	(5)	*Onverdund, 4×10^4 sporen per ml*
10^{-1}	2	5	(5)	(5)	(5)	(5)	(5)	(5)	10^{-1}
10^{-2}	–	–	4	4	4	4(1)	4(1)	(5)	10^{-2}
10^{-3}	–	–	–	–	–	2	5	3(2)	10^{-3}
10^{-4}	–	–	–	–	–	–	–	–	10^{-4}
Control	–	–	–	–	–	–	–	–	*Controle*
	Dagen na inoculatie								

In brackets: *the number of dead plants*
Tussen haakjes: het aantal afgestorven planten
–: No disease symptoms/–: *Geen ziektesymptomen*

possible when plants become contaminated at a late developmental stage, was studied by inoculating plants of different ages. Every week for six weeks five seedlings were planted in pots of steamed soil. A glass rod was placed in the soil next to each seedling. At the time of inoculation the rod was carefully removed and the hole was filled with a spore suspension. In addition the crown of the plant was gently rubbed with a dense suspension. Control plants were treated with sterile water in a similar way. The treatments were replicated five times. The first symptoms of disease appeared on all plants at the same time after inoculation. The younger plants having a soft stem, eventually collapsed somewhat earlier than the six weeks old ones which were kept upright by woody elements in the stem. No difference in degree of attack was thus apparent between the younger and the older plants, if the inoculum potential was adequate to establish infection. This is in accordance with the experience of the growers that full-grown plants can still become diseased.

RANGE OF HOST PLANTS

From the practical point of view it was considered important to know, whether crops such as Freesia, tomato, melon or beans would be attacked by the fungus when grown in infested soil and whether steaming of the soil would be necessary after a glasshouse had been cleared of a diseased cucumber crop. To obtain information on the host range of this *Fusarium*, five ten day old seedlings of the following plant species were planted in steamed soil infested with a shake culture of the fungus: cucumber cv. 'Improved Telegraph', melon cv. 'Oranje Ananas', gerkhin cv. 'Petit vert de Paris', tomato cv. 'Moneymaker' and tobacco, *Nicotiana tabacum* cv. 'Xanthi'. The latter were 35 days old. In addition bean seeds, *Phaseolus vulgaris*, were sown in infested soil and five bulbs of each of the Freesia varieties 'Snowqueen' and 'White Swan' were planted.

The cucumber plants showed symptoms of disease similar to those described for *Cucurbita ficifolia*. Secondary roots developed in great numbers, which kept the plants alive for a couple of weeks. Most plants died, however, after 15 to 20 days. The melon plants died in 21 and 12 days respectively in two experiments. The gerkhins showed symptoms after 12 days. The tomato and tobacco plants, the beans and the Freesia's did not show symptoms and the fungus could not be isolated from their roots. It was concluded that these crops were not susceptible to the fungus. If one of them is grown after a diseased crop of cucumbers, steaming of the glasshouse soil does not seem to be necessary though it may be advisable to avoid spreading the pathogen with infested soil to other glasshouses where cucumbers are grown.

In search of a substitute for the *C. ficifolia* rootstock, the susceptibility to the parasite of a number of other representatives of the Cucurbitaceae was tested. The following species were selected: *Cucurbita moschata*, *Cucurbita maxima*, *Cucumis melo* var. *cantalupensis*, *Cucurbita pepo* var. *ovifera*, *Cucurbita pepo* var. *ovifera* 'Pyriformis' and *Benincasa hispida*. Cucumber plants were used as control. A fortnight after planting in infested soil all species showed symptoms. There proved to be some differences in the time at which the different species had died off completely, but after one month all plants had succumbed, the cucumbers last of all. So far no suitable substitute for the *C. ficifolia* rootstock has been found.

TRANSMISSION OF THE FUNGUS BY SEED

The assumption of CONROY (1953a) and also of SNYDER (1938) that seed might serve as a carrier of the pathogen was confirmed by the experiments of GRIES (1946) and later by TOUSSOUN & SNYDER (1961). GRIES, who stated that the disease was already present in Connecticut in 1939, injected fruits with a spore suspension at approximately five day intervals. The percentage of contaminated seeds decreased with the age of the seeds and with the distance between the point of inoculation and the site where the seeds were borne. From contaminated non-viable seeds the fungus might establish itself in the soil.

TOUSSOUN & SNYDER placed fruits of ornamental gourd, *Lagenaria* sp., on sterilized soil mixed with a spore suspension. Zonate necrotic spots appeared and the pathogen gained entrance to the seed cavity. Seeds, even mature ones, could become invaded and spores might adhere to the outside of the seed coat. From these sources the fungus might parasitize the young plant. Dissemination of the pathogen into new regions is considered by TOUSSOUN & SNYDER to occur chiefly through infected seed.

The origin of the disease in the Netherlands is obscure; seed contamination might well have been the source of infection of thousands of grafted plants distributed all over the country. It was therefore of importance to study the effect of contamination of fruits and to investigate whether seed transmission could occur under the Dutch conditions for growing *Cucurbita ficifolia* rootstock. In the Netherlands the fruits of *C. ficifolia* are stored for some time after harvest to enable the seeds to ripen before they are removed from the fruits. During the storage period a number of fruits may decay, from many of which non-pathogenic *Fusarium* species could be isolated (VAN DER AA & PRUD'HOMME VAN REINE, 1964). In one case, however, *F. solani* f. *cucurbitae* was found (BRAVENBOER, 1964).

To study the possibility of seed contamination the experiment described by TOUSSOUN & SNYDER (1961) was repeated. Five ripened one year old fruits were placed on steamed soil mixed with a spore suspension of the pathogen. Each pot with infested soil bearing a fruit on top was wrapped in plastic and kept in the glasshouse. After one month the fruits showed a watersoaked spot where they had been in touch with the soil. The fruit flesh had changed into a orange-brown disintegrated soft mass or even into a stinking dark coloured fluid. In about 40% of the seeds the fungus was present under the seed coat. After sowing in steamed soil about 25% of the seeds germinated and from most of the seedlings the pathogen could be isolated. The fruits that had been placed on uninfested soil did not show any sign of attack. The results of TOUSSOUN & SNYDER were therefore fully confirmed.

In another experiment five similar fruits were injected with a spore suspension containing 5×10^4 spores per ml. One fruit was treated with sterile water. The fruits were wrapped in plastic and kept in the glasshouse (Fig. 3). After two to eight weeks all fruits which had been treated with the spore suspension had rotted (Fig. 4). Some of the seeds appeared to be internally infected with the parasite. About 50% of the seeds germinated, and a number of the resultant seedlings were infected.

To investigate at which developmental stage of the fruits the danger of infection is greatest, *C. ficifolia* plants were grown in the laboratory garden. During

TABLE 2. Number of inoculated, abscissed and harvested fruits. Number of seeds infected with *Fusarium solani* f. *cucurbitae*.
Aantal geïnoculeerde, afgevallen en geoogste vruchten. Aantal zaden besmet met Fusarium solani *f.* cucurbitae.

Age of the fruits in days at the time of inoculation	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	*Leeftijd van de vruchten in dagen op de tijd van inoculatie*
Number of fruits inoculated	23	17	12	12	14	10	10	2	*Aantal geïnoculeerde vruchten*
Number of fruits abscissed	23	16	11	12	13	0	0	0	*Aantal afgevallen vruchten*
Number of fruits harvested; seeds viable and non-viable					1	2	4	1	*Aantal geoogste vruchten; zaden al en niet kiemkrachtig*
Number of seeds examined	0	0	0	320[1]	440	360	280	40	*Aantal onderzochte zaden*
Number of seeds internally infected				78	185	44	59	0	*Aantal zaden inwendig besmet*[2]
Variation in % of infected seeds per fruit				0–87.5	2.5–95	0–45	0–75		*Variatie in % besmette zaden per vrucht*

[1] From abscissed fruits
Uit afgevallen vruchten

[2] Most seeds non-viable
Meeste zaden niet kiemkrachtig

July and August female flowers were marked on the day the buds opened. Ovaries and subsequently fruitlets were injected at the base or at the apex each with 0.5 ml of a spore suspension containing 5×10^4 spores per ml. In due course an abundance of ripening fruits became available and eight groups could be distinguished, each with fruits of comparable age (Table 2). As controls, fruits were injected with sterile water. All the fruits were harvested in October as early frosts started to damage the plants. A difficulty encountered was the frequent abscission of fruits after a rainy day when pollination had been inadequate because of lack of insects and also after the fruits had been injected, even with water. The latter may have been caused by the entry of micro-organisms through the wounds made by the needle. The later the fruits were inoculated the later they fell off, sometimes even four to five weeks after treatment. The flesh of the inoculated fruits liquified into a colourless or blue-greenish stinking fluid up to 2 l per fruit, from which the fungus could be isolated.

All fruits inoculated before the 21st day after flowering fell off sooner or later and they contained only non-viable seeds. Fruits that were inoculated at a later stage contained, next to non-viable, also viable seeds in that part of the fruit in which still healthy looking flesh was present. Only eight fruits matured fully. Most of their seeds were viable. Some seeds were healthy but other ones were outwardly and also inwardly contaminated with the fungus. From fruits inoculated at the age of 36 to 40 days after flowering none of 40 seeds that were examined was contaminated with the pathogen. The fruits injected with water which did not fall off, contained only healthy seeds. It was concluded that infection of fruits three to five weeks after flowering might lead to development of viable but infected seeds.

DISCUSSION

The origin of a disease in cucumbers occurring in the Netherlands in 1962 could be traced back to holdings especially equipped for grafting cucumbers on *C. ficifolia* rootstocks. This specialization of vegetable propagation carries with it the danger of the subsequent wide distribution of the disease if it becomes established in the propagation nursery. Formerly the harvested *C. ficifolia* fruits were brought into the grafting nursery and stored under the benches on which the cucumber and rootstock seedlings are grown. Many fruits decayed during the ripening process. Until recently this decay did not result in disease and it was concluded that in this process no organisms were involved which were pathogenic to cucumbers or their rootstocks. In one case, however, *F. solani* f. *cucurbitae* was isolated from a decaying fruit. Once a fruit has become infected with this fungus, the consequences may be disastrous, as a number of its seeds may be infected as well. After these seeds are sown, the soil on the benches will become infested and as it is used several times as a seedbed, the disease will spread rapidly and soon a great number of plants will become infected. As thousands of seedlings and grafts are daily sent to a great number of holdings where the plants are grown, the sudden and simultaneous occurrence of the parasite can be explained. In each of the years 1958, 1962 and 1963, in which an outbreak occurred, the origin of the diseased plants could be traced back to one of the holdings from which the grafts originated.

Nowadays, growers are well aware of the possibility that seeds from decaying

C. ficifolia fruits may be contaminated outwardly as well as inwardly by the parasite. These seeds are probably the main source of infection and it is possible to prevent an attack by this *Fusarium* by using only seeds from undamaged fruits. Moreover the soil on the benches must be steam-sterilized regularly to avoid the effects of fungal contamination from other sources. If these measures are taken, growers can avoid attack by *F. solani* f. *cucurbitae*, as was proved in 1964 and 1965.

SAMENVATTING

In 1962 en 1963 kwam in Nederland een voetziekte voor bij kaskomkommers, geënt op *Cucurbita ficifolia*-onderstam. De ziekte werd veroorzaakt door *Nectria haematococca* Berk. & Br. var. *cucurbitae* (Snyd. & Hans.) Dingley (syn. met *Hypomyces solani* Rke & Berth. emend. Snyd. & Hans. var. *cucurbitae* Snyd. & Hans., *Fusarium javanicum* Koord. var. *ensiforme* (Wr. & Reinking) Wr. en *Fusarium solani* f. *cucurbitae* Snyd. & Hans.). De schimmel bleek identiek te zijn met isolaties uit Cucurbitaceae, afkomstig uit andere landen (fig. 1). Zaailingen van *C. ficifolia*, opgekweekt in besmette grond, vertoonden ongeveer twee weken na het zaaien een aantasting aan de voet van het hypocotyl, waarna de planten snel volledig afstierven (fig. 2). Ofschoon de schimmel via de entplaats in de komkommer-bovenstam kon doordringen, werd de levende stengel nooit systemisch doorgroeid. Als de grond slechts licht geïnfecteerd werd, bleken planten van *C. ficifolia* nog op latere leeftijd aangetast te kunnen worden (tabel 1). Dit is in overeenstemming met het verschijnsel van het afsterven van komkommers in kassen als de planten juist vrucht gaan dragen.

Alle Cucurbitaceae die in besmette grond werden opgekweekt, stierven af. Er werd geen vervanger voor de *C. ficifolia*-onderstam gevonden die resistent was tegen deze *Fusarium*. Andere planten die in de kassen gekweekt worden zoals freesia's, bleken resistent te zijn.

De schimmel bleek met zaad te kunnen overgaan, hetgeen o.a. aangetoond werd door een groot aantal vruchten van verschillende leeftijd te injiceren met een sporensuspensie (tabel 2). Alleen die welke drie tot vijf weken na de bloei geïnjiceerd waren, bevatten later kiemkrachtige zowel uitwendig als inwendig met de schimmel besmette zaden op die plaatsen, waar het vruchtvlees weinig of niet was aangetast (fig. 3 en 4). Het is mogelijk, dat de schimmel door het gebruik van zaad uit gekneusde en besmette vruchten binnengekomen is in de kassen van gespecialiseerde entbedrijven, vanwaaruit dagelijks duizenden enten en zaailingen door het gehele land worden verzonden. Op deze wijze kan de snelle verspreiding van het pathogeen verklaard worden. In latere jaren kon de ziekte vermeden worden door slechts zaden uit gave vruchten voor het opkweken van *C. ficifolia*-onderstammen te gebruiken en de grond in de tabletten geregeld te ontsmetten.

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