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Pythium uncinulatum sp. nov. and P. tracheiphilum pathogenic to lettuce

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Abstract
From mature lettuce heads with bottom rot symptoms several *Pythium* species were isolated, two of which were studied further. Pathogenicity tests with both fungi have been carried out only with seedlings.

P. uncinulatum sp. nov. was isolated frequently. Its relation to other *Pythium* spp. with spiny oogonia is discussed. It proved to be very pathogenic to seedlings of lettuce and somewhat less to those of cucumber and tomato.

P. tracheiphilum, which was isolated far less frequently, proved to be highly pathogenic to seedlings of lettuce, cucumber and cauliflower, and somewhat less to tomato and pea.

Introduction

One of the problems in lettuce *(Lactuca sativa)*, grown in greenhouses, is bottom rot (in Dutch: 'smet' = smudge), which is mainly serious on mature heads. Symptoms of bottom rot are not well-defined, but most characteristic is rotting away of the lowest leaves and blackening of the bases of these leaves. The injury can be caused by various soilinhabiting fungi, such as *Rhizoctonia* species, *Botrytis cinerea* and *Sclerotinia* spp. *Rhizoctonia* species was thought to be main pathogen, but recent investigations (Tichelaar, 1976) have shown that *Botrytis cinerea* is more often isolated from rotting lettuce leaves than any other organism. Among the isolates were several *Pythium* spp. In the affected tissue often ornamented oogonia could be seen, possibly belonging to the genus *Pythium*.

The most frequently isolated *Pythium* species were *P. sylvaticum* Hendrix & Campbell, a common species in Dutch soils (Van der Plaats-Niterink, 1975), and a species with spiny oognia. Some isolates were identified as *P. tracheiphilum* Matta, known to be pathogenic to lettuce (Matta, 1965, 1969; Zinkernagel and Kröber, 1977). The fungus with the spiny oogonia and *P. tracheiphilum* were investigated further and are described below, and were tested for pathogenicity.

Description of the species

Pythium uncinulatum Van der Plaats-Niterink & Blok sp. nov. (Fig. 1, Fig. 3 a, b)

Hyphae primariae hyalinae, ad 7 μm latae. Sporangia globosa, saepe intramatricalia, terminalia sed etiam nonnumquam intercalaria, 20–40 μm, plerumque 30–40 (in medio 34.5) μm diam. Tubi evacuationis ad 200 μm longi, in summo vesiculam zoosporarum formantes; zoosporae encystatae

15–16 µm diam. Oogonia terminalia in ramulis lateralibus, globosa, spinosa, 24–39 µm, plerumque 31–38 (in medio 34.2) µm diam. (spinis exclusis). Stipites oogoniorum flexuosi, 6 µm lati, nonnumquam sub oogonio dilatati. Paries oogoniorum protuberantiis spinulosis uncinulatis obtectus, quorum circa 30 visibiles in sectione optica; protuberantiae acutae, modice curvatae, plerumque 7–10 µm longae et prope basin 4–5 µm latae, spinarum rosarum similes, nonnumquam biapiculatae. Antheridia diclina, irregularia, saepe oogonio prope stipitem late adfixa, 1–8 cellulas antheridiales ferentia. Oosporae globosae, apleroticae, 21–35 µm, plerumque 27–33 (in medio 30.5) µm diam.; paries levis et 3–4 µm crassus. Coloniae in agaro solani tuberosi et dauci carotae vel ferina maydis confecto submersae neque differentiatae. Temperaturae cardinales: minimum 5 °C, optimum 24–25 °C, maximum 30 °C. Incrementum diurnum 15 mm 25 °C in agaro solani tuberosi et dauci carotae confecto.

Typus CBS 518.77, isolatus e *Lactuca sativa*, De Meern in Neerlandia, ab J. W. Veenbaas-Rijks, 1975.

Pythium uncinulatum Van der Plaats-Niterink & Blok sp. nov. (Fig. 1, Fig. 3 a,b)

Hyphae hyaline up to 7 µm wide. Sporangia globose, often produced intramatrically, terminal, sometimes intercalary, 20–40 µm, mostly 30–40 µm, average diameter 34.5 µm. Discharge tubes up to 200 µm long; zoospores, 15–16 µm diameter when encysted, produced in vesicles at the end of the discharge tubes. Oogonia spiny, terminal on short side branches, spherical, diameter (without spines) 24–39 µm, mostly 31–38 µm, average 34.2 µm. Oogonial stalks bent, 6 µm wide, occasionally widening under the oogonium. Oogonium wall with many spiny protuberances of which about 30 are often visible in one optical section. Protuberances acute, slightly bent, mostly 7–10 µm long and 4–5 µm thick at the basis, often resembling rose-thorns, occasionally with two tips. Antheridia diclinous, irregular, often broadly applied to the oogonium in the neighbourhood of the oogonial stalk, bearing 1–8 antheridial cells. Oospores spherical, aplerotic, 21–35 µm, mostly 27–33 µm, on average 30.5 µm in diameter; oospore wall smooth and 3–4 µm thick. Colonies on potato-carrot and cornmeal agars submerged, without a special pattern. Cardinal temperatures: minimum 5°C, optimum 24–25°C, maximum 30°C. Daily growth rate: 15 mm at 25 °C on potato-carrot agar.

Cultures examined:

CBS 518.77, type culture, isolated from diseased lettuce in De Meern by J. W. Veenbaas-Rijks, 1975.

CBS 517.77, CBS 516.77, CBS 515.77, all isolated by J. W. Veenbaas-Rijks from diseased lettuce plants grown near Breda, the Netherlands, 1975, 1976 and 1977.

This species has been isolated over 100 times from diseased lettuce, originating from different fields. The sporangia developed in a water culture on sterilized lettuce seedlings at about 13 °C after repeated changes of the water. Most sporangia were formed within the tissue of the seedling. The discharge tubes protruded out of the tissue with a variable length depending on the location of the sporangia in the tissue. Deep-seated sporangia often produced long discharge tubes to the surface of the seedling, where the large zoospores were formed in a vesicle. The antheridium is already initiated in an early stage as a terminal swelling of a hypha which contacts the swollen tip of a side branch of another hypha (Fig. 1 a, b, e). The latter grows faster and forms an oogonium which is still smooth in this young stage. The ornamentation on the oogonium wall soon develops. In this stage the antheridium forms a knot of more or less swollen branches and diverticles surrounding the oogonium especially in the neighbourhood of the oogonial stalk which is rather thick and often strongly curved

Fig. 1. *Pythium uncinulatum*: a–g, developing stages of sex organs; h, mature oogonium and oospore; i, young sporangium; j, empty sporangium; k, encysted zoospores; l, swollen hypha.

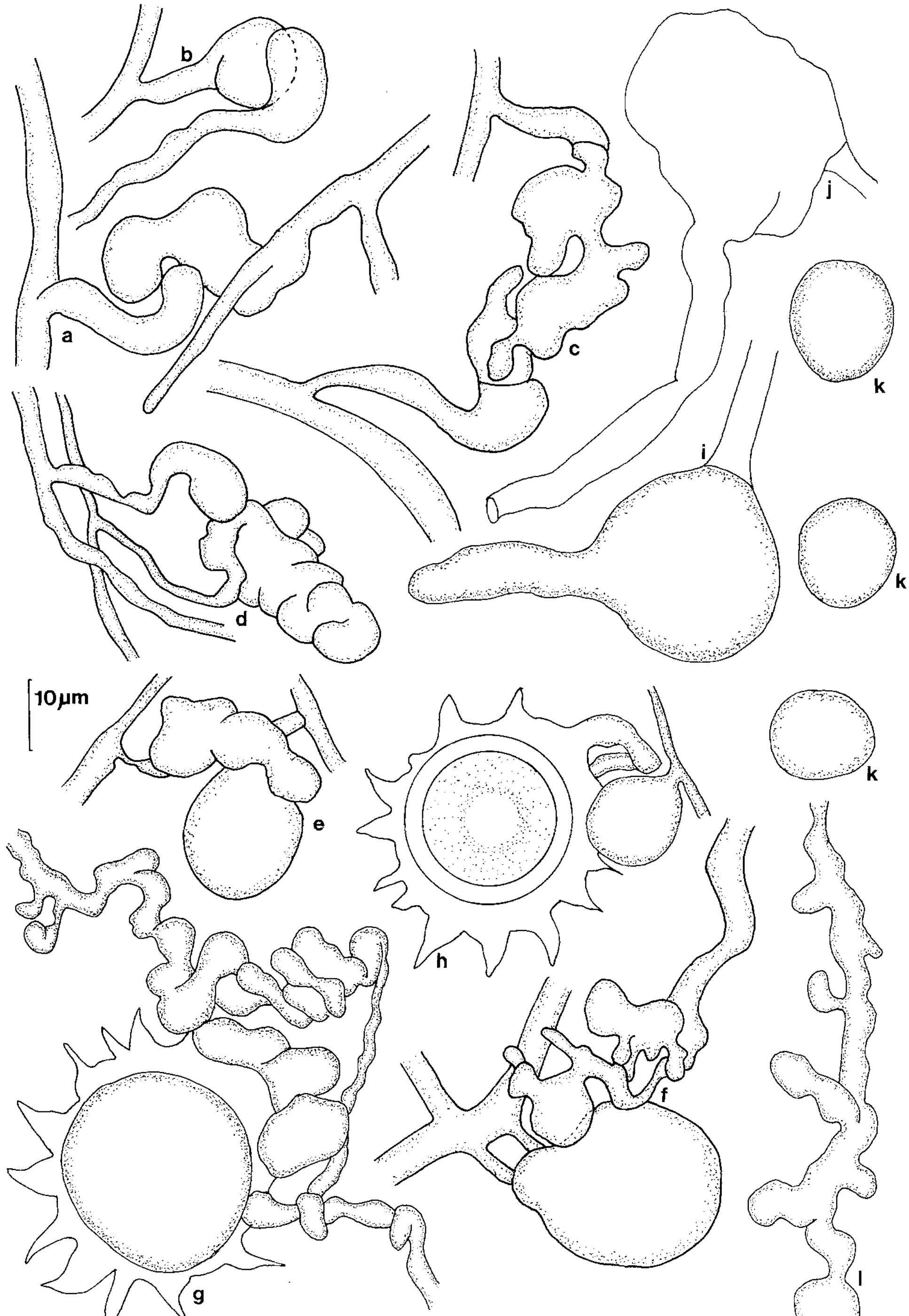

Fig. 1. Pythium uncinulatum; a–g, ontwikkelingsstadia van de sexuele voortplantingsorganen; h, rijp oögonium met oöspore; i, jong sporangium; j, leeg sporangium; k, geëncysteerde zoöspore; l, gezwollen hyfe.

(Fig. 1 a, b). The spines of the oogonium wall which often have the shape of rose-thorns and sometimes have two tips (Fig. 1 g, h, and 3 a, b) are most characteristic of this species.

A number of other spinulose *Pythium* species also produce comparably large zoospores: *P. polymastum* Drechsler (1930), *P. dimorphum* F. F. Hendrix & W. A. Campbell (1971), *P. prolatum* W. A. Campbell & F. F. Hendrix (in F. F. Hendrix & W. A. Campbell, 1969), *P. anandrum* Drechsler (1930), and *P. mastophorum* Drechsler (1930). *P. unicinulatum* however, has smaller oogonia, smaller oospores, a thicker oospore wall and spines with a different shape to that of *P. polymastum*. *P. dimorphum* has ellipsoidal sporangia which sometimes proliferate, large chlamydospores, mammiform and hypogynous antheridia and in these respects it differs from *P. uncinulatum*. *P. prolatum* is also different from *P. uncinulatum*, in having longer sporangia, smaller oogonia and less complicated antheridia. *P. anandrum* has also smaller oogonia and oospores and lacks antheridia. *P. uncinulatum* can be separated from the most closely related species *P. mastophorum* by the shape of its spines, the size of the oogonia and oospores, the much thicker oospore wall and, according to Drechsler (1930), the slower growth at 24°C. *P. uncinulatum* is different from *P. megalacanthum* de Bary (1881) in not having proliferating sporangia.

Pythium tracheiphilum Matta (1965) (Fig. 2, 3c)

Hyphae hyaline, up to 6 μm wide. Sporangia terminal and intercalary, either spherical, 22–34 μm (av. 24.1 μm) in diameter or subspherical or elongated, 20–45 μm long and 16–29 μm broad. Discharge tube up to 15 μm long and 6 μm wide. Zoospores 8–10 μm in diameter when encysted. Chlamydospores often present in host tissue and sometimes in old cultures, terminal and intercalary, of variable shape and size, thick-walled, smooth. Oogonia smooth, spherical, terminal and intercalary, 13–18 μm, mostly 14–17 μm (av. 15.6 μm) in diameter. Antheridia 1–2, monoclinous, originating at rather short distances below the oogonium, occasionally diclinous. Oospores spherical, plerotic, smooth, wall 1.5–3.0 μm thick. Cultures on cornmeal and on potato-carrot agars submerged, without a special pattern. Cardinal temperatures: minimum below 4°C, optimum 25°C, maximum 37°C. Daily growth rate 24 mm at 25°C on potato-carrot agar.

P. tracheiphilum was originally isolated from *Lactuca sativa* L. in Italy by Matta (1965) and has already been recorded from lettuce in the Netherlands by van der Plaats-Niterink (1975).

Cultures examined:

CBS 323.65, type culture, isolated from diseased lettuce in Italy by A. Matta, 1965.

CBS 870.72, isolated from diseased lettuce in Wageningen, the Netherlands, by G. H. Boerema, 1972.

CBS 520.77 and CBS 519.77, isolated from diseased lettuce, Breda, by J. W. Veenbaas-Rijks, 1976 and 1977.

Pathogenicity tests

Although *P. uncinulatum* was isolated from lettuce frequently, its relation with bottom rot was uncertain. To investigate its pathogenicity, rapid tests were carried out on seedlings. In addition to lettuce some other crops were also tested.

Fig. 2. *Pythium tracheiphilum:* a–k, young sex organs; m–q, mature oogonia and oospores; r–v, sporangia; w and x, chlamydospores.

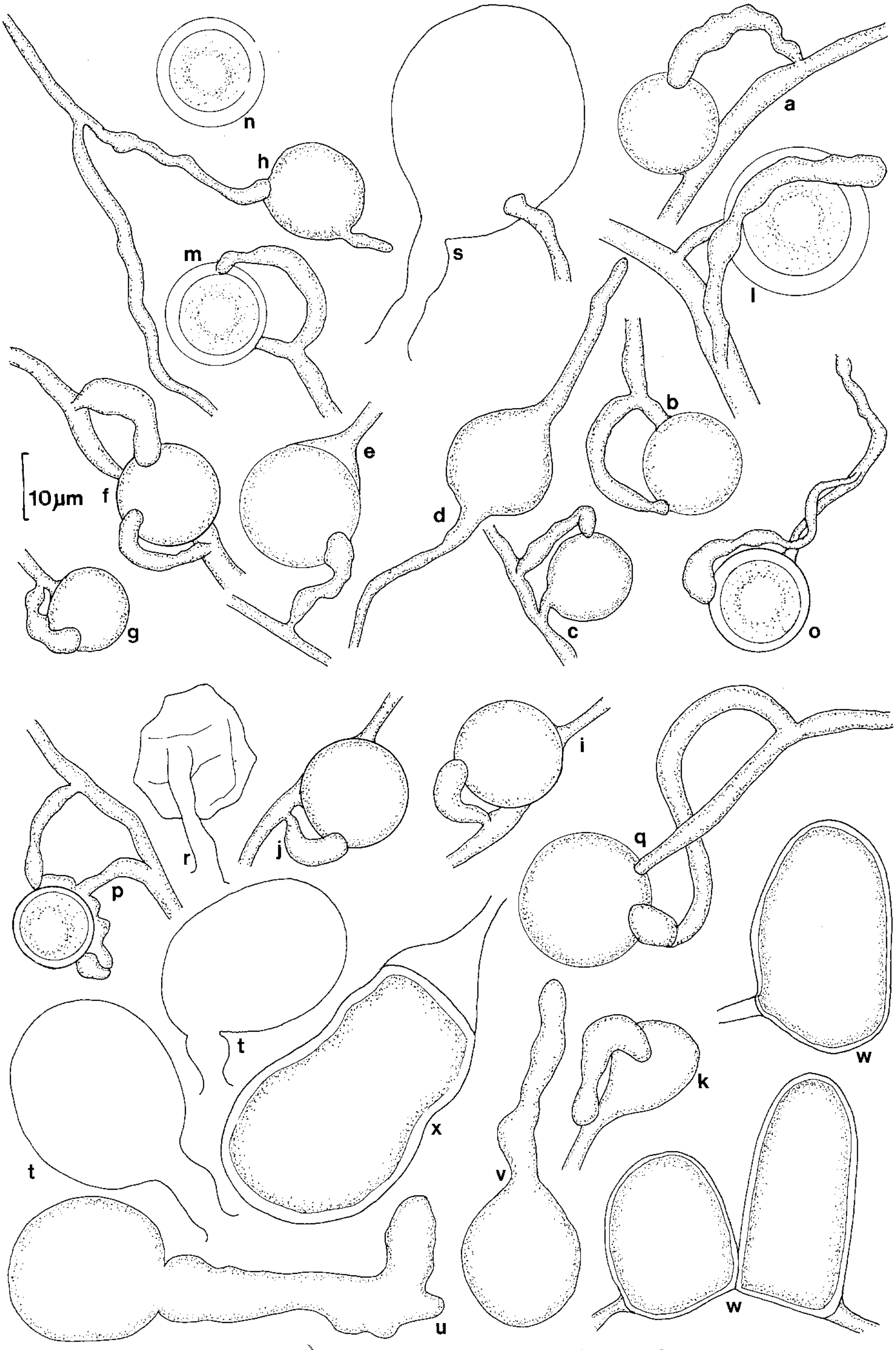

Fig. 2. Pythium tracheiphilum: a–k, jonge stadia van de sexuele voortplantingsorganen; m–q, rijpe oögoniën en oösporen; r–v, sporangiën; w en x, chlamydosporen.

Fig. 3. a. *Pythium uncinulatum:* Scanning Electron Microscope photograph of an oogonium. b. *Pythium uncinulatum:* oogonia and oospores. c. *Pythium tracheiphilum:* chlamydospores.

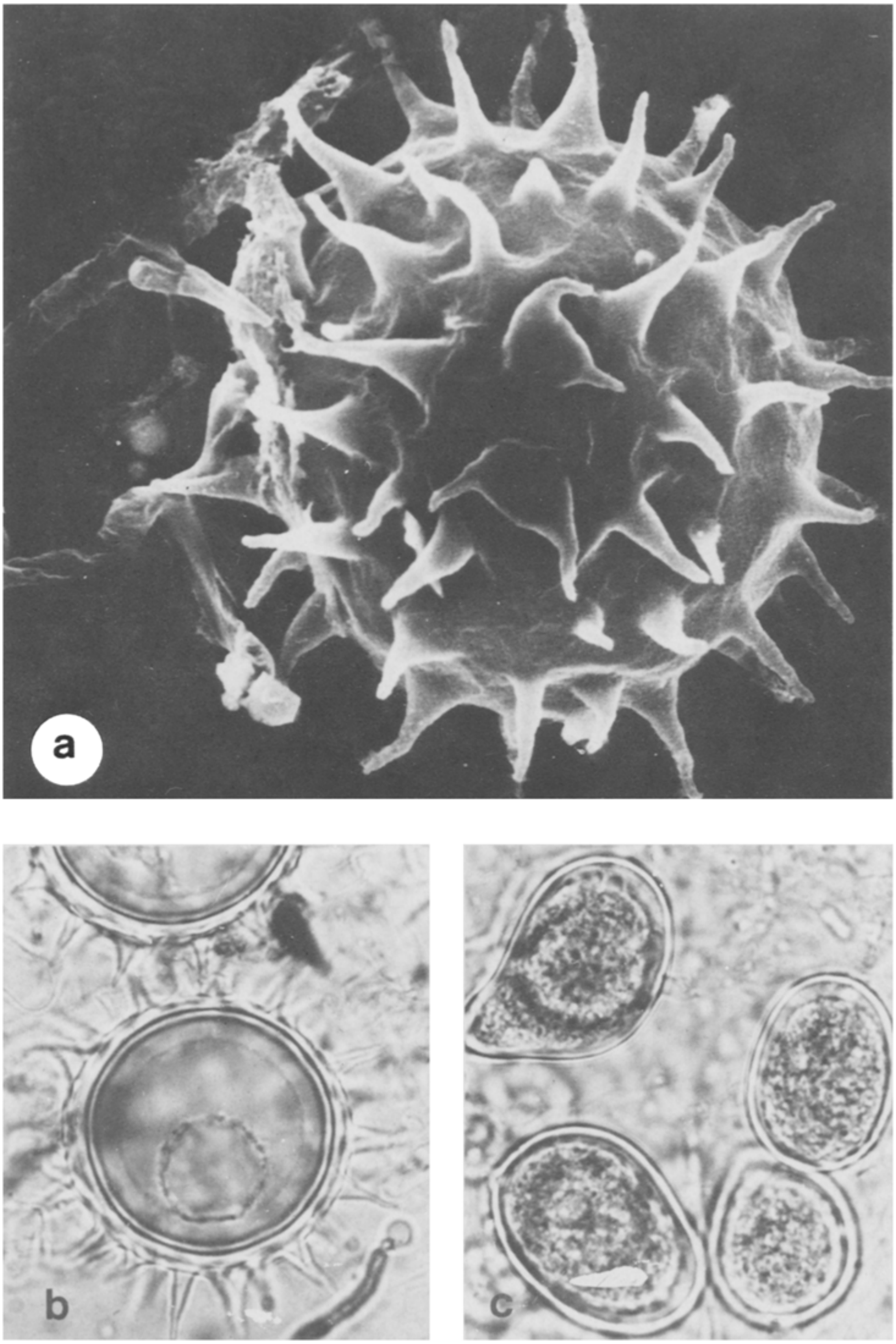

Fig. 3. a. Pythium uncinulatum: Rasterelektronenmicroscopische foto van een oögonium. b. Pythium uncinulatum: oögoniën en oösporen. c. Pythium tracheiphilum: chlamydosporen.

Although *P. tracheiphilum* was isolated infrequently, this fungus was included in all the tests, because it is known to be pathogenic to lettuce and some other crops (Matta, 1969).

Materials and methods

The isolates of *P. tracheiphilum*, as well as most isolates of *P. uncinulatum*, were isolated from lettuce at the Research Institute for Plant Protection. One isolate of *P. uncinulatum* was isolated from lettuce at the Plant Protection Service. In one experiment some additional *Pythium* species were used: *P. mastophorum*, obtained from the CBS, *P. polymastum*, isolated from lettuce at the Research Institute for Plant Protection some years ago, and *P. sylvaticum*, recently isolated from lettuce at the same institute. All *Pythium* spp. were grown on cornmeal agar.

For experiments with very young seedlings the seeds were disinfected with sodium hypochlorite 1.5% for about 1 minute, rinsed with sterile water and allowed to germinate in a petri dish with wet filter paper at room temperature. When the rootlets were 0.5–1.5 cm (i.e. after two or three days for lettuce) ten seedlings were placed in a petri dish (9 cm diam.) with sterile filter paper and 3 ml of sterile water. Two punches (0.5 cm diam.) of a two- or three-day-old culture of the fungus on cornmeal agar were deposited between the seedlings. For the control agar punches without fungus were used. The dishes were kept at room temperature.

For slightly older seedlings Matta's method (1969) was used, seeds being sown in steam-sterilized soil, which was kept open for several days. After two weeks the seedlings were lifted, most of the soil was rinsed off and the roots were dipped for 1–3 min. in a mycelial suspension of the test fungus. The suspension was made by mixing two plates of a three-day-old culture with 100 ml tap water in a blendor. For the control agar plates without fungus were used. The seedlings were then planted in a pot with steam-sterilized soil and kept at 15–20°C.

In two tests the soil was inoculated. In the first test two-week-old lettuce seedlings were planted in steam-sterilized potting soil which had been mixed with one agar plate per pot (10 cm diam., 8.5 cm high) three days earlier or just before planting. In the second test two-week-old seedlings in pressed peat blocks were planted in boxes of 45 × 30 × 20 cm, the upper 10 cm of which was inoculated by chopping three plates of a six-day-old culture of the test fungus into the soil. In both tests the plants were kept at 15–17°C.

Test crops were lettuce *(Lactuca sativa)*, endive *(Cichorium endivia)*, carrot *(Daucus carota)*, cauliflower *(Brassica oleracea* var. *botrytis)*, radish *(Raphanus sativus)*, tomato *(Lycopersicon esculentum)*, cucumber *(Cucumis sativus)*, pea *(Pisum sativum)*, leek *(Allium porrum)*, flax *(Linum usitatissimum)* and wheat *(Triticum vulgare)*.

Results

Very young seedlings of susceptible crops may show root necrosis within 24 hours after inoculation with virulent isolates of the pathogens. Disease rating was done after about four days, using a scale from 0 (no symptoms) to 10 (all seedlings totally rotten). From various tests it appeared that the severity of the attack is dependent on

Table 1. Disease rating of very young lettuce seedlings on filter paper, inoculated with different *Pythium* spp. (0 = no symptoms; 10 = seedlings totally rotten).

Inoculum	Disease rate
control	0
P. tracheiphilum	4–9
P. uncinulatum	4–10
P. mastophorum	1–2
P. polymastum	1–5
P. sylvaticum	1–2

Tabel 1. Ziekteïndexering van zeer jonge slazaailingen op filtreerpapier, geïnoculeerd met verschillende Pythium-soorten (0 = geen symptomen; 10 = zaailingen geheel verrot).

Table 2. Disease rating of very young seedlings of several plant species on filter paper, inoculated with *P. tracheiphilum* or *P. uncinulatum* (0 = no symptoms; 10 = seedlings totally rotten).

Plant species	Inoculum							
	control		*P. tracheiphilum*			*P. uncinulatum*		
	I	II	IA	IIA	IIB	IA	IIA	IIB
lettuce	0	0	4	6	6	7	4	6
endive	0	0	1	2	1	0	0	0
carrot	0	0	0	0	0	0	0	0
cauliflower	0	0	6	10	9	1	0	0
radish	0	0	2	1	2	0	0	0
tomato	0	0	2	5	6	1	3	3
cumcumber	0	0	7	10	10	6	1	4
pea	0	0	1	5	5	1	1	0
leek	0	0	0	1	0	0	0	0
flax	0	0	2	2	1	0	1	2
wheat	0	0	0	0	0	0	0	0

Tabel 2. Ziekteïndexering van zeer jonge zaailingen van diverse gewassen op filtreerpapier, geïnoculeerd met P. tracheiphilum en P. uncinulatum (0 = geen symptomen; 10 = zaailingen geheel verrot).

the age of the inoculum used and the time during which the fungus has been kept in culture after isolation. Ten isolates of *P. uncinulatum* were tested and three of *P. tracheiphilum*. There was no difference in pathogenicity between the different isolates of one pathogen. In Table 1 the summarized results are given from various tests with lettuce seedlings in petri dishes.

In Table 2 the results are shown of two tests (I and II) with very young seedlings of several crops. In test I one isolate (A) is used and in test II two isolates (A and B) of both *P. tracheiphilum* and *P. uncinulatum*.

From Table 2 it is clear that *P. uncinulatum* has a narrower host range than *P. tracheiphilum*. Cauliflower and cucumber are particularly susceptible to the latter (Fig. 4a). Dipping of roots of lettuce seedlings in a mycelial suspension of *P. tracheiphilum* resulted in considerably retarded growth after one week (Fig. 4b), but about two weeks after treatment the plants slowly started to recover. Seedlings inoculated in this way with *P. uncinulatum* did not show any symptoms at first, but after about

Fig. 4a Very young seedlings of cucumber (left) and lettuce (right), four days after inoculation with *P. tracheiphilum* (1), *P. uncinulatum* (2), and control agar (3).

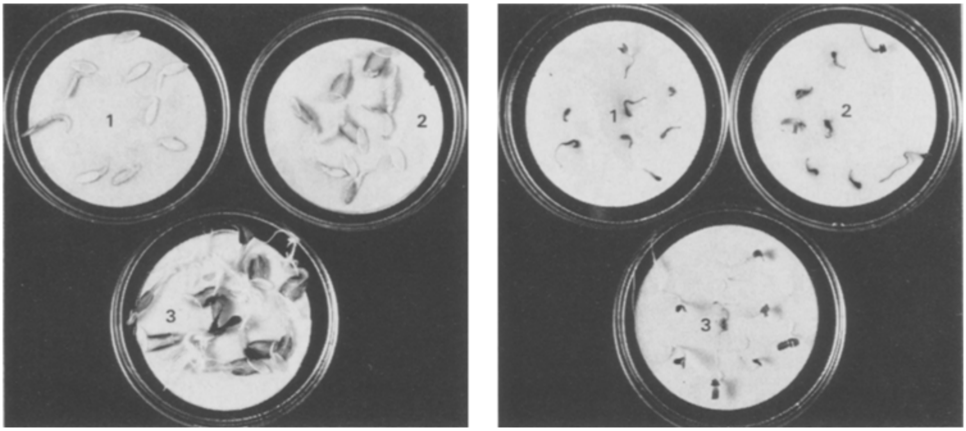

Fig. 4a Zeer jonge zaailingen van komkommer (links) en sla (rechts), vier dagen na inoculatie met P. tracheiphilum (1), P. uncinulatum (2) en blanke agar (3).

Fig. 4b One week after dipping roots of lettuce seedlings in a mycelial suspension of *P. tracheiphilum* the plants showed a considerable growth retardation. Left control plants.

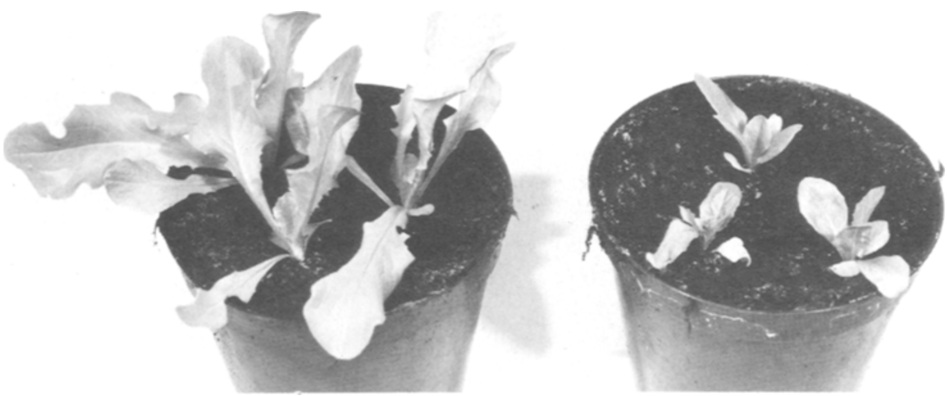

Fig. 4b Eén week nadat de worteltjes van slazaailingen gedoopt werden in een myceliumsuspensie van P. tracheiphilum vertonen de planten een duidelijke groeivertraging. Links controleplanten.

Fig. 4c The root system of lettuce plants which were dipped in a mycelial suspension of *P. tracheiphilum* (left) or *P. uncinulatum* (right) before planting.

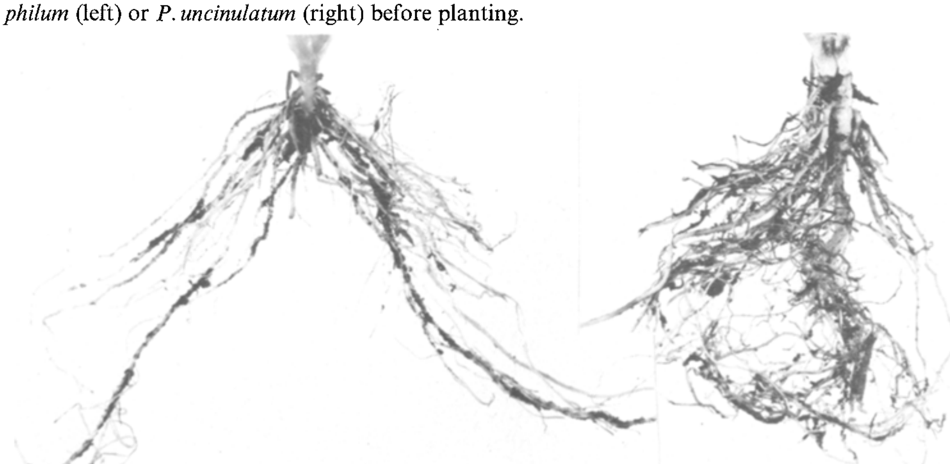

Fig. 4c. Het wortelstelsel van slaplanten die voor het uitplanten gedoopt werden in een myceliumsuspensie van P. tracheiphilum (links) of P. uncinulatum (rechts).

Table 3. Average weight in g per head of lettuce previously inoculated with *P. tracheiphilum* or *P. uncinulatum*.

Treatment	After 24 days	After 44 days
control	10.6	36.8
P. uncinulatum	9.7	25.6
P. tracheiphilum	3.0	31.5

Tabel 3. Gemiddeld gewicht in g per krop sla, tevoren geïnoculeerd met P. tracheiphilum of P. uncinulatum.

four weeks the plants showed some growth retardation. Some of the plants were judged 24 days after the treatment, the remainder after 44 days. The main roots of plants dipped in *P. tracheiphilum* suspension were severely damaged, whereas later developed side roots showed only a few necrotic spots. No discolouration of the tracheal tubes in the roots or the stem could be detected. The main roots of plants dipped in *P. uncinulatum* suspension were less damaged but most of the side roots also showed several necrotic spots (Fig. 4c). The average weight per head of lettuce is shown in Table 3.

In another test seedlings of lettuce, endive, radish, cucumber, pea and flax were dipped in mycelial suspensions of the two test fungi. Three days after treatment all cucumber seedlings dipped in *P. tracheiphilum* suspension had wilted and only two of the nine plants later recovered. The lettuce plants and some of the radish plants were also slightly wilted; they all recovered but remained a little retarded in their growth. Plants dipped in *P. uncinulatum* suspension showed no symptoms in the beginning. After about three weeks the lettuce plants showed some growth retardation. The plants were judged 39 days after treatment. Endive and pea were not influenced by any of the fungi. In the case of treatment with *P. tracheiphilum* the main roots of cucumber (the two remaining plants), lettuce and flax were necrotic, but side roots could freely develop and usually showed no more than a few necrotic spots. The tubers of radish were not visibly influenced, but their weight was about 60% of that of the control plants. Only in cucumber and lettuce the above-ground growth was significantly reduced. The treatment with *P. uncinulatum* affected the roots of the lettuce plants clearly, while cucumber and flax roots had some necrotic spots only. The above-ground growth of only the lettuce plants was slightly reduced.

The growth of lettuce plants grown in soil inoculated with *P. uncinulatum* was markedly retarded, but only slightly so in soil with *P. tracheiphilum*. When the soil was inoculated three days before planting, the symptoms were more pronounced. The root system in soil with *P. tracheiphilum* was almost as extensive as that of control plants, but the roots showed some necrotic spots. The root system in soil with *P. uncinulatum*, however, was significantly reduced: many roots were short, light brown, and had dead tips. From the necrotic spots in the roots both fungi could easily be re-isolated. In the bases of the lowest leaves contacting the soil with *P. tracheiphilum* and which had become brown, oogonia of the fungus could easily be found, and the fungus could be isolated. This was more difficult with leaves in touch with soil with *P. uncinulatum*.

Discussion

Besides the species which play a role in damping-off (like *P. ultimum* and *P. irregulare*), other *Pythium* species are rarely isolated from lettuce plants. Three species with spiny oogonia are known from lettuce, viz. *P. spinosum*, *P. megalacanthum* and *P. polymastum*, of which the last one was originally described from lettuce (Drechsler, 1930). Jain (1951) found a leaf rot of lettuce in India caused by *P. aphanidermatum*. In the United States this species is also found to be pathogenic to lettuce (Endo, personal communication). Biraghi (1940) isolated an unidentified *Pythium* species from wilting lettuce plants in Italy. From the description it seems possible that it was *P. tracheiphilum*, which Matta (1965) later found to be a vascular pathogen of lettuce. The name *P. tracheophilum* without author is mentioned by Middleton (1943) 'proposed for a pathogen causing stunt of lettuce, treated in an unpublished thesis'.

Before 1976 *P. polymastum* and *P. tracheiphilum* were both once isolated from lettuce in the Netherlands (van der Plaats-Niterink, 1975). *P. tracheiphilum* has also recently been isolated from lettuce in Germany (Zinkernagel and Kröber, 1977). *P. tracheiphilum*, isolated in the Netherlands since 1976, was only obtained from lettuce with bottom rot symptoms.

In our tests *P. tracheiphilum* proved to be highly pathogenic to seedlings of lettuce, cucumber and cauliflower but somewhat less to tomato and pea, whereas endive, radish and flax were only slightly affected. Carrot, leek and wheat were not affected (Table 2). When the roots of two-week-old seedlings were dipped in a mycelial suspension of *P. tracheiphilum* before planting, cucumber plants were severely affected and lettuce plants somewhat less. When soil was inoculated with *P. tracheiphilum*, however, lettuce plants were only slightly affected. Vascular browning, as mentioned by Zinkernagel and Kröber (1977), was not seen.

P. uncinulatum proved to be pathogenic to lettuce seedlings, especially fresh isolates of the fungus. Cucumber and tomato seedlings were less susceptible and other plant species were hardly or not at all influenced. Whereas dipping of lettuce roots in a mycelial suspension of *P. uncinulatum* before planting had only a slight effect, planting of lettuce seedlings in inoculated soil gave a marked growth retardation.

P. polymastum was not very pathogenic in our test, perhaps because it had lost some of its pathogenicity after several years of culture on agar media.

Up to now experiments with *P. tracheiphilum* and *P. uncinulatum* have been carried out with seedlings only. From the results it may be concluded that *P. tracheiphilum* has a rather broad host range and may cause troubles with several crops, especially cucumber. *P. uncinulatum* seems to have a restricted host range with lettuce as the main host. Experiments with mature plants still have to be done to prove whether there is a relation between the presence of the forementioned *Pythium* spp. in the soil and the occurrence of bottom rot in lettuce. However, since the fungi can be isolated from lettuce leaves touching inoculated soil, it seems possible that *Pythium* spp. play a role in this disease.

Samenvatting

Pythium uncinulatum sp. nov. en P. tracheiphilum als pathogenen van sla

Van slaplanten met smetsymptomen werden behalve *Botrytis cinerea, Rhizoctonia* sp. en *Sclerotinia* spp. dikwijls *Pythium*-soorten geïsoleerd. Twee hiervan zijn nader onderzocht.

P. uncinulatum (Fig. 1, 3a, 3b), die dikwijls werd geïsoleerd, wordt beschreven als nieuwe soort en de relatie met andere *Pythium*-soorten met gestekelde oögoniën wordt besproken. In proeven bleek *P. uncinulatum* zeer pathogeen te zijn voor zaailingen van sla en iets minder voor zaailingen van komkommer en tomaat (Fig. 4a, Tabel 2). Het planten van slazaailingen in met *P. uncinulatum* geïnoculeerde grond had meer effect dan het dopen van de wortels in een myceliumsuspensie van de desbetreffende schimmel vóór het planten. Het effect uitte zich in groeivertraging van de plant en beschadiging (necrose) van het gehele wortelstelsel.

P. tracheiphilum (Fig. 2, 3c), die slechts een paar maal werd geïsoleerd, was zeer pathogeen voor zaailingen van sla, komkommer en bloemkool (Fig. 4a) en iets minder voor zaailingen van tomaat en erwt (Tabel 2). Groeiremming van de planten was sterker wanneer de wortels van de zaailingen vóór het planten in een myceliumsuspensie van *P. tracheiphilum* gedoopt werden (Fig. 4b), dan wanneer de zaailingen in geïnoculeerde grond geplant werden. De hoofdwortels van de zaailingen werden ernstig beschadigd, maar zich later vormende zijwortels werden weinig door de schimmel beïnvloed.

Tot nu toe zijn de pathogeniteitsproeven slechts met zaailingen uitgevoerd. Proeven met volwassen planten moeten volgen om te onderzoeken of er een verband kan bestaan tussen de aanwezigheid van de betreffende *Pythium*-soorten in de grond en het optreden van smet in sla.

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