

## Pathogenic fungi involved in root rot of peas in the Netherlands and their physiological specialization

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### Abstract

Research on root rot pathogens of peas in the Netherlands has confirmed the prevalence of *Fusarium solani*, *F. oxysporum*, *Pythium* spp., *Mycosphaerella pinodes* and *Phoma medicaginis* var. *pinodella*. *Aphanomyces euteiches* and *Thielaviopsis basicola* were identified for the first time as pea pathogens in the Netherlands. Other pathogens such as *Rhizoctonia solani* and *Cylindrocarpon destructans* were also found on diseased parts of roots.

*F. solani* existed in different degrees of pathogenicity, and was sometimes highly specific to pea, dwarf bean or field bean, depending on the cropping history of the field. *A. euteiches* was specific to peas, whereas *T. basicola* showed some degree of physiological specialization.

*Additional keywords:* *Pisum sativum*, *Vicia faba*, *Phaseolus vulgaris*, foot rot, *Aphanomyces euteiches*, *Fusarium solani*, *Mycosphaerella pinodes*, *Phoma medicaginis* var. *pinodella*, *Thielaviopsis basicola*

### Introduction

In the first half of the 1980s pea growing gained in importance in the EC countries due to a combination of a high demand for protein for feed and EC subsidies. This stimulated renewed interest in the effect of the frequency of pea crops in rotation on the occurrence of root rot. (In this paper root rot will be used to indicate lesions on and rotting of both roots and epicotyls.) Peas are traditionally known not to sustain frequent cropping, and a maximum of one pea crop in a 6-year rotation is considered appropriate. However, even with this low frequency, incidents in which crops suffer badly from root rot do occur. In the past, this has led to several efforts to identify damaging pathogens in the Netherlands. In 1927, Buisman studied the role of *Phycomycetes* in pea root rot. She found *Pythium irregulare* and *P. debaryanum* as causal organisms. Went (1934) reported on the role of *Fusarium solani*. Kerling (1949) studied *Mycosphaerella pinodes*, whereas Boerema et al. (1964) described the importance of *Phoma medicaginis* var. *pinodella* on pea and other legumes. These detailed studies, however, did not clarify the situation. In 1954 Labruyère and Riepma distinguished between root rot symptoms in Zeeland and Groningen, i.e. in the Southwest and Northeast of the Netherlands. The root rot in Zeeland, which was first attributed to *F. solani*, proved to be caused by bean (pea) leaf roll virus (Hubbeling, 1954); that in Groningen was primarily considered to be caused by bad soil structure, which would stress the roots and make them susceptible to pathogens.

In 1961, a project was started to elucidate the cause of the difference in pea yields

between the North and the South of the Netherlands. Results were published in a poorly accessible form (Anonymous, 1966; Riepma, 1967). Root rot was not always associated with bad soils, and was sometimes encountered on excellent soils. *F. solani*, the most frequent pathogenic species in diseased roots, was still considered to be a weak pathogen. No new species were reported.

In 1985, with so many factors still unclear, another project was started to elucidate the nature of the root rot pathogens and to estimate the current incidence of root rot on peas in the Netherlands. Particular attention was paid to the relations of cropping frequency of peas and other legumes and root rot incidence. Literature on pea root rot pathogens is available from all major pea growing areas (e.g. Zogg, 1964; Burke and Hagedorn, 1968; Burke and Kraft, 1974; Shipton, 1977). The most frequent pathogens include *F. solani*, *Fusarium oxysporum*, *Aphanomyces euteiches*, *P. medicaginis* var. *pinodella*, *M. pinodes*, *Thielaviopsis basicola* and *Pythium* spp. This wide array of pathogens may result in complicated interactions. Each pathogen has its own specific biology, some of them showing physiological specialization at species or even cultivar level (Sundheim, 1972; Grau et al., 1991). Additional variables are the interactions of these pathogens with other elements of the soil microflora, climate and soil type (Lloyd and Lockwood, 1963; Alconero and Hagedorn, 1967; Hagedorn, 1986).

The root rot pathogens of legumes in the temperate zone, peas (*Pisum sativum* L.), dwarf beans (*Phaseolus vulgaris* L.) and broad beans (*Vicia faba* L.), are largely the same at species level. *M. pinodes*, however, is more or less limited to peas. Most researchers (Burke and Kraft, 1974; Kraft and Burke, 1974; Davis and Shehata, 1985; Kraft, 1986) agree that the important root pathogens show physiological specialization. Thus, the notorious root rot pathogen *F. solani* is recognized as f.sp. *pisi* for peas, f.sp. *phaseoli* for phaseolus beans and f.sp. *fabae* for faba beans. Clarson (1978), however, concluded from inoculation trials that the distinction in formae speciales is questionable. Peas, beans and other legumes were equally susceptible to these 'formae'. Comparable results were reported by Yang and Hagedorn (1968) and Messiaen and Cassini (1968).

Physiological specialization is important in relation to the effect of different legumes in the rotation. It is also important in screening of cultivars for resistance. The provision of accurate data on the pathogens involved in root rot, including their physiological specialization, contributes to a better management of pea production as it depends on safe rotations, if possible supported by the use of less susceptible cultivars.

The present paper deals with pathogenic fungi causing root rot of peas in the Netherlands and their physiological specialization. In an other paper we will discuss the relation of crop rotations to root rot of peas.

## Materials and methods

*Sampling soil for screening of pathogens.* From 1985 to 1987 soil samples were obtained from fields in the traditional pea production areas in the North and South of the Netherlands.

Most soils were clay loams or loams. All investigated fields had been cropped with a legume at least once in the past decade. Cropping history and crop data were recorded. One hectare of the most homogeneous part of each field was identified and sampled. Fifty soil cores of 20–25 cm depth were taken in a W-pattern. Soil cores were mixed together,

reduced to an aggregate size of maximum 0.8 cm and stored in the dark at 4 °C.

The typical pathogenic microflora of peas, dwarf beans and broad beans was studied in soil samples originating from experimental plots where these legumes had been grown continuously for 10 years (since 1979). Soil on which peas had been grown continuously since 1979 is indicated as CCP. The corresponding code for dwarf beans is CCB, and for field bean CCF.

Whether other legumes stimulate the increase in root rot pathogens of peas was investigated by isolating fungi from roots of peas grown in soil which had been cropped every second year since 1983 with garden pea, dwarf french bean or broad bean in the rotation: sugar beet – legume – potato – legume – spring wheat – legume. For each plot the legume crop remained the same in all years.

*The cropping history of fields.* In the field, the pea crop may consist of vining pea for the canning industry or dry pea for seed production or animal feed. No field with a history of field bean cropping was involved in the survey. Cropping effects of field bean on pathogenic fungi were studied in soils of experimental plots. Dwarf bean was traditionally grown in the South of the Netherlands. A cropping plan in the South consists for almost 3/4 of sugar beet, potato and wheat and in the North primarily of wheat and sugar beet.

*Isolation of pathogens.* Pathogens were isolated from diseased field plants, or from plants growing in pots filled with soil samples originating from the sources indicated above. In the latter case, plants were uprooted when they had reached the green flower bud stage, and the roots washed free of adhering soil. A subsample of five plants with root rot symptoms was selected for isolation purposes. Isolates were taken from dark brown to black lesions or from rotten roots (soft rot) only. Pieces of plant tissue were superficially sterilized in 1% NaOCl for 1 min., rinsed with sterile water and plated on media such as water agar, cherry agar, Czapek-Dox agar or PDA. After 5 days of incubation at 20 °C cultures were transferred for further identification. The presence or absence of each species was recorded per soil sample, with 100 samples screened, and expressed as percentage occurrence. Microscopical observation of diseased tissue, immediately or after incubation in sterile water, was used to complement the plating methods.

In 1988, soil samples inducing soft rot were specifically screened for the presence of *A. euteiches*. Details are described elsewhere (Oyarzun and van Loon, 1989).

*Pathogenicity and physiological specialization.* *F. solani*. Because of the dominant presence and the unclear role of *F. solani* in root rot of peas, pathogenicity tests were restricted to this pathogen.

Seventy-five isolates originating from different fields, as described above, were screened. To perform pathogenicity tests, monosporous isolates of *F. solani* were produced. Peas were grown in 2 × 4 × 12 cm plastic tubes with sand, to which a spore suspension of *F. solani* was added to generate 50 000 spores per g of soil. The tubes were incubated at 25 °C with 12 h per day of 30 000 lux (90 W m<sup>-2</sup>). Three weeks after inoculation a root disease index was scored on a 0–5 scale (0 = healthy, white roots and epicotyl; 5 = roots fully discoloured over a length of at least 5 cm).

Physiological specialization of *F. solani* was studied with highly virulent monosporous isolates obtained from CCP, CCB and CCF plots, and from commercial fields. For com-

parison isolate F48 was added which was kindly provided by J.M. Kraft (Washington State, USA). In two experiments, seedlings were inoculated by dipping their roots in suspensions of  $10^6$  macroconidia per ml, and subsequently incubated in a liquid nutrient medium. These experiments were performed with a 2-month interval. The inoculum for the second experiment originated from re-isolation of the pathogen from the corresponding first experiment.

To further examine whether there was physiological specialization this type of experiments was repeated with several isolates obtained from pea and with Kraft's F48. In these experiments, sterilized sandy loam was inoculated with conidial suspensions to reach 5000 cfu per g of soil. Nine monospore isolates, including the very virulent F48, were examined on two cultivars per crop: peas 'Colette' and 'Allround', phaseolus beans 'Salerna' and 'Narda' and faba beans 'Compacta' and 'Alfred', representing the horticultural and agricultural form of the crop, respectively. For technical reasons the experiment was performed in two runs with six and three isolates, respectively. The first was designed as a split-plot, in four replications, with cultivars in main plots and the isolate in the sub-plot. The second was designed as a split-split-plot, in four replications, with the cultivar form of the host species as subplot and the isolate as sub-sub-plot. Incubation was at 24 °C with 12 h of 30 000 lux ( $90 \text{ W m}^{-2}$ ).

*A. euteiches*. Three isolates of the pathogen were cultured in cornmeal/sand. Test plants were inoculated by mixing the inoculum with a sterilized sandy loam soil and adding zoospores to the seedlings, as described elsewhere (Oyarzun et al., 1990). Temperature was set at 24 °C; 12 h light per day of 30 000 lux ( $90 \text{ W m}^{-2}$ ) was supplied. Soft root rot was assessed 3 weeks after sowing. The experiment was designed as a split-plot, in four replications, with host species as plot and cultivar as the sub-plot.

*T. basicola*. Plants were grown in plastic tubes,  $3 \times 3 \times 20$  cm on a mixture of equal volumes of sterilized sand, potting soil and clay soil. Isolates of *T. basicola* were obtained from roots on a selective medium (Papavizas, 1964). A spore suspension consisting of a mixture of three isolates, maintained on malt agar,  $10^6$  endoconidia per ml, was added to seedlings near the cotyledons, to reach 4000 conidia per g of soil. Incubation was at 22 °C and 12 h per day of 30 000 lux ( $90 \text{ W m}^{-2}$ ). Roots were assessed two weeks after sowing. The experiments were designed as a split-plot as with *A. euteiches*, in eight replicates.

## Results

*Root rot pathogens from soil samples*. This study allowed the linking of certain disease symptoms to the presence of specific pathogens. From dry, brown, dark brown to blackish lesions on roots and epicotyls of peas grown on soil samples from farmers' fields from all over the country, *F. solani* and *F. oxysporum* were most frequently isolated, both on 62% of the fields (Fig. 1). *F. oxysporum*, best known as the causal organism of wilting, was often isolated from lesions as the sole organism. Other *Fusarium* spp., notably *F. culmorum*, *F. avenaceum* and *F. graminearum*, were found in 41% of the samples. In Fig. 1, 'Ascochyta', which is often used to indicate *P. medicaginis* var. *pinodella*, *M. pinodes*, and *Ascochyta pisi*, refers to the first two organisms only. They were found at a frequency of 18%. General pathogens such as *R. solani* and *C. destructans* were also recorded at

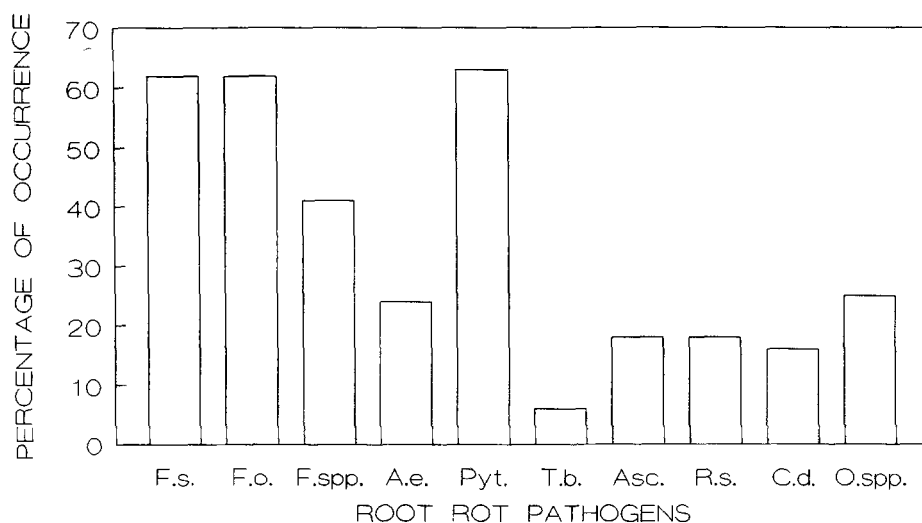


Fig. 1. Frequency of occurrence of fungal species in diseased roots and epicotyls of peas. The figures are the averaged results of isolations of fungi by several methods from samples of 100 different origins (F.s. = *Fusarium solani*; F.o. = *F. oxysporum*; F.spp. = other *Fusarium* spp.; A.e. = *Aphanomyces euteiches*; Pyt. = *Pythium* spp.; T.b. = *Thielaviopsis basicola*; Asc. = '*Ascochyta*'; R.s. = *Rhizoctonia solani*; C.d. = *Cylindrocarpon destructans*; O. spp. = other spp.)

18 and 16%, respectively. Other species/genera isolated added up to 25%.

From soft, light cream to golden brown root lesions, *A. euteiches* was identified for the first time in the Netherlands in 1988 (Oyarzun and Van Loon, 1989). The frequency was 24%. This pathogen was the most damaging of all, death of pea seedlings following extended soft rot. The frequency of *Pythium* spp. was about equal to that of the two dominant *Fusarium* spp., 63%.

A typically black root rot, not extending beyond the level of cotyledon attachment, was found in test plants growing on samples from several fields situated all over the country. The causal organism proved to be *T. basicola*. It was found on 6% of the samples.

In the 1:2 rotations of vegetable legumes with other field crops (Table 1), *M. pinodes* and *P. medicaginis* var. *pinodella* were only found in the rotations with peas. *Verticillium* spp. were found on pea roots in soils without a history of pea growing. *F. solani*, *Fusarium* spp. (among which *F. oxysporum*) and *R. solani* were found on pea roots independently of the history of legume cropping of the soil.

*F. solani* was frequently found in roots, cotyledons, epicotyls and vascular bundles of pea plants grown on CCP, CCB or CCF soil (Table 2). *F. oxysporum* was isolated from cotyledons especially. *R. solani* and *F. solani* were frequently isolated from dwarf beans on CCB soil. From broad beans on CCF soil *F. solani* was rarely isolated, but *C. destructans* was frequent. On CCP soil *P. medicaginis* var. *pinodella* was frequently isolated from underground parts of both peas and broad beans. Its presence on broad beans, but not on peas on CCF soil is remarkable. In this experiment, *T. basicola* was only found on field bean and dwarf bean on CCF and CCB soil respectively. Several tests were performed to investigate the presence of *A. euteiches* in CCF or CCB soils, without positive results. *A. euteiches* proved to be specific to the pea field. In general, *Pythium* spp. showed up in all

Table 1. Semi-quantitative representation of fungi isolated from diseased underground tissue of peas grown in soil samples taken after growing vegetable legumes. Each legume species had been cropped for the second time in a 1:2 alternated rotation with potato, sugar beet and spring wheat.

Fungal species	Preceding legume		
	Vining pea	Broad bean	Dwarf french bean
<i>Mycosphaerella pinodes</i>	++	—	—
<i>Phoma medicaginis</i>	++	—	—
<i>Fusarium solani</i>	++	++	++
<i>Fusarium</i> spp.	++	++	++
<i>Rhizoctonia solani</i>	++	++	+
<i>Cylindrocarpon destructans</i>	—	—	+
<i>Verticillium</i> spp.	— + +		

— = absent; + = present; ++ = common.

Table 2. Semi-quantitative representation of isolates of fungi frequently obtained from diseased underground tissue of peas, dwarf beans and field beans grown as test plants in soil originating from fields with a history of continuous cropping to peas (CCP), broad beans (CCF) and dwarf beans (CCB).

Fungal	CCP			CCF			CCB		
	Pea	Field bean	Dwarf bean	Pea	Field bean	Dwarf bean	Pea	Field bean	Dwarf bean
<i>Fusarium solani</i>	+++	+++	++	++	+	0	+++	+	+++
<i>Fusarium oxysporum</i>	+++	++	+	+++	++	+++	+	+	++
<i>Fusarium</i> spp.	0	+	0	+	0	0	++	+	0
<i>Phoma medicaginis</i>	++	++	0	0	++	0	0	0	0
<i>Pythium</i> spp.	++	+	0	+	+	++	+	0	+
<i>Rhizoctonia</i> spp.	++	0	0	0	0	++	0	0	+++
<i>Cylindrocarpon destructans</i>	0	++	0	0	+++	0	0	0	+
<i>Aphanomyces euteiches</i>	+++	—	—	—	0 <sup>a</sup>	—	—	—	0 <sup>a</sup>
<i>Thielaviopsis basicola</i>	0	—	—	—	+++	—	—	—	+++

+ = one isolate; ++ = two isolates; +++ = three to five isolates of five investigated plants; 0 = no isolate obtained; — = not tested.

<sup>a</sup> Bio-assay with pea for the presence of *A. euteiches* was also negative, whereas it was positive for CCP soil.

combinations. Overall, *Fusarium* was the most frequent fungus isolated. Several fungi were always isolated from any one plant.

*Pathogenicity of F. solani.* The results of the screening for pathogenicity of 75 isolates of *F. solani* on peas are presented in Fig. 2. All isolates were pathogenic to pea and more than 50% of the isolates proved to be moderately to highly virulent.

*Physiological specialization. F. solani.* Results of the first two experiments in hydro-culture with isolates obtained from crops grown continuously on the same field are sum-

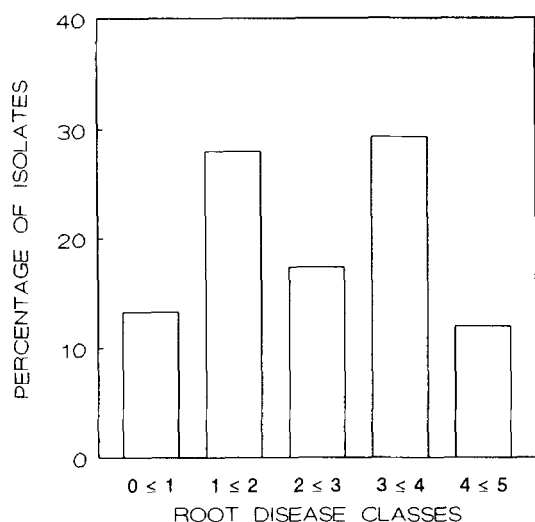


Fig. 2. Frequency distribution of 75 *Fusarium solani* isolates over different root disease index classes (0–1: not or hardly virulent; 4–5: highly virulent) tested on peas.

marized in Table 3. Variance analysis indicated a significant interaction between the *Fusarium* isolates and the crop species ( $P < 0.001$ ). In the first experiment, the *F. solani* isolate from pea was the most virulent one, especially on pea itself. This isolate caused slight to moderate root rot of field bean and dwarf bean respectively. The isolate from field bean on CCF soil only slightly attacked pea, but caused a remarkably heavy root rot of dwarf bean compared with the moderate root rot caused by the isolate on field bean itself. The infection of pea was restricted to the cotyledon attachment area.

The CCB isolate was unable to attack pea considerably. Its effect on field bean and dwarf bean was slight. Inoculation of dwarf bean both with CCP and CCF isolates gave a higher root rot index than with its 'own' CCB isolate.

The repetition of the experiment led to a comparable result, except for the much higher

Table 3. Experiment 1, mean root disease index (0–5) for three legume species following cross-inoculation with isolates of *Fusarium solani* obtained from these three crops grown continuously on the same field. Experiment 2 is a repetition in which inoculation was performed with strains re-isolated from the crop indicated in the first column. Both experiments performed in hydroculture.

Crop	<i>F. solani</i> isolated from					
	Pea on CCP		Field bean on CCF		Dwarf bean on CCB	
	Expt 1	Expt 2	Expt 1	Expt 2	Expt 1	Expt 2
Pea	3.28	3.07	0.90	3.50	0.15	0.59
Field bean	1.50	1.65	1.85	3.76	1.00	1.24
Dwarf bean	2.00	1.42	2.53	2.56	1.33	1.70

Interaction crop  $\times$  isolate:  $P < 0.001$ . For all comparisons in Expt 1: LSD = 0.40 ( $P < 0.05$ ). For all comparisons in Expt 2: LSD = 0.80 ( $P < 0.05$ ).

Table 4. Mean root disease index (0–5) on two cultivars of each of the host species pea, faba bean and phaseolus bean, inoculated with isolates of *Fusarium solani* obtained from pea roots.

Isolate	<i>Pisum sativum</i>			<i>Vicia faba</i>			<i>Phaseolus vulgaris</i>		
	Col.	All.	Mean	Com.	Alf.	Mean	Sal.	Nar.	Mean
F48	5.00	5.00	5.00	5.00	3.18	4.09	1.10	2.13	1.62
CT 2.1	0.38	1.63	1.01	1.13	0.85	0.99	0.15	0.03	0.09
–14	2.28	3.40	2.84	2.15	1.45	1.80	0.13	0.98	0.56
–07	2.95	3.83	3.39	1.38	1.30	1.34	0.23	0.33	0.28
–05	1.35	3.23	2.29	0.48	1.33	0.91	0.15	0.68	0.42
–02	3.55	3.73	3.64	1.05	0.13	0.59	0.13	1.23	0.68
–46	0.63	1.80	1.21	1.05	1.18	1.11	0.23	0.18	0.20
–19	1.13	1.93	1.53	2.28	1.20	1.74	0.28	0.65	0.46
–04	2.68	4.00	3.34	1.38	1.38	1.38	0.95	1.75	1.35

Cultivars: Col. = Colette; All. = Allround; Com. = Compacta; Alf. = Alfred; Sal. = Salerno; Nar. = Narda.

For the first six isolates, interaction cultivar 3 isolate:  $P < 0.001$ . For all comparisons of single assessments:  $LSD = 0.96$  ( $P = 0.05$ ), except when comparing values within columns,  $LSD = 0.98$ ; for the last three isolates, interaction host species 3 isolate:  $P < 0.001$ .  $LSD = 0.72$  ( $P = 0.05$ ), except when comparing means within columns:  $LSD = 0.53$ . (N.B. data obtained in separate experiments.)

Table 5. Mean root disease index (0–5) for different host species inoculated with *Thielaviopsis basicola* and *Aphanomyces euteiches* originating from pea.

Pathogen	<i>Pisum sativum</i>		<i>Vicia faba</i>		<i>Phaseolus vulgaris</i>	
	Mar/Col <sup>a</sup>	Finale	Compacta	Alfred	Salerna	Narda
<i>T. basicola</i>	3.5a	3.1b	1.0d	1.3d	2.9c	3.0bc
<i>A. euteiches</i>	3.7a	3.4b	0.0	0.0	0.0	0.0

<sup>a</sup> For each crop two cultivars were tested separately; for pea ‘Marzia’ was used in the experiment with *A. euteiches* and ‘Colette’ with *T. basicola*.

Figures in the same line followed by the same letters are not statistically different (Duncan’s test;  $P = 0.05$ ).

virulence of the CCF isolate (re-isolated from plants in the first experiment) on peas and field beans.

The results of the experiments with several isolates of *F. solani* of different origin, including F48, are summarized in Table 4. The isolates were tested on two cultivars per crop. Differences between crops were more important than between cultivars within crops. Most isolates scored highest on pea.

*T. basicola* and *A. euteiches*. The results of inoculation of peas, phaseolus beans and faba beans with *T. basicola* and *A. euteiches*, both originating from pea, are shown in Table 5. *T. basicola* had a high pathogenicity to pea and phaseolus bean, whereas *A. euteiches* was specific to pea.



## Discussion

The most frequently occurring pea pathogens, as determined in this study, are not different from those found in other pea growing countries. Two pathogens, *A. euteiches* (Oyarzun and Van Loon, 1989) and *T. basicola*, were new records on peas for the Netherlands.

In most instances the pathogens isolated from a specific crop, or from crops grown in soil on which only one and the same legume had been grown for many years, showed a high but not an absolute degree of specificity. This result can be interpreted as a form of physiological specialization. Such a physiological specialization of a quantitative nature has been well documented for many soil-borne pathogens. *F. solani* and *A. euteiches* are good examples. Messiaen and Cassini (1968) distinguished ff.sp. of *F. solani*, but stated that the separation of e.g. f.sp. *phaseoli* and f.sp. *pisi* was rather vague. In general they identified isolates from pea as f.sp. *pisi* and those from phaseolus bean as f.sp. *phaseoli*, based on the comparatively heavy attack of the original host. Some isolates were identified as *pisi* + *phaseoli*, attacking both hosts about equally. In our experiments *F. solani* could be isolated from pea, dwarf bean or field bean, grown in any rotation. Different degrees of physiological specialization were found. There was a strong tendency for the most severe attack to be on the original host in cross-inoculation trials, but host overlap was common (Table 3). Zadoks and Van Leur (1983), analyzing these situations, called them 'small interaction phenomenon'.

The high degree of pathogenicity of many isolates (Fig. 2) contradicts the traditional view of *F. solani* as a weak pathogen.

A mixture of three isolates of *A. euteiches* only attacked pea, and thus these isolates had a strict f. sp. *pisi* status. However, this is not typical for *A. euteiches* in general. Pfender and Hagedorn (1982) isolated *A. euteiches* f.sp. *phaseoli* from dwarf bean roots and distinguished it from *A. euteiches* f.sp. *pisi* by comparing their pathogenicity on peas and beans. *A. euteiches* f.sp. *pisi* attacked peas and beans, killing peas and provoking a slight root rot on dwarf beans, whereas *A. euteiches* f.sp. *phaseoli* caused moderate to severe root rot of beans, but did not harm peas. Holub et al. (1991) described how *A. euteiches* generally attacked lucerne, but showed quantitative differential reactions with pea. According to Grau et al. (1991) isolates from pea have always the broadest spectrum, but this is clearly not the case for our isolates. We failed to demonstrate the presence of *A. euteiches* in soils after 10 years with continuous cropping of dwarf beans or field beans. This result seems in line with the statement of Reinking (1942) that *A. euteiches* does not occur in soil never cropped with pea.

Table 2 shows *T. basicola* to occur massively on field bean in CCF and on dwarf bean in CCB soil, whereas pea on CCP soil remained free from this pathogen. Table 5, however, confirms that cross-pathogenicity does occur. We have no explanation for this discrepancy. The absence of *T. basicola* from CCP soil seems to be exceptional, since *T. basicola* is so highly virulent on both pea and bean, whereas it is hardly pathogenic on field bean. The pathogen is reported to show some form of specialization (Lloyd and Lockwood, 1963).

*P. medicaginis* var. *pinodella* was found predominantly on roots of field bean and pea in CCP soil and on field bean only in CCF soil. This might indicate a certain degree of physiological specialization, in which an assumed f.sp. *pisi* parasitizes both pea and field

bean, whereas a f.sp. *viciae* only attacks field bean. Dwarf bean remained free from attack. Results of studies on physiological specialization in soil-borne pathogens are often difficult to interpret. This may be caused by a modification of pathogenic conduct of the ff.sp. on other plant species by environmental factors, such as the attack of roots by incompatible ff.sp. of *F. solani* under anaerobic conditions (Burke and Kraft, 1974; Miller et al., 1980; Kendra and Hadwiger, 1987; Smucker and Erickson, 1987; Allmaras et al., 1988). The pathogenicity of some of the pathogens to one or two crops only, might mean that other legumes in a crop rotation with pea need not be considered as severely as pea itself. This will apply for *A. euteiches*, the most devastating of the pea pathogens dealt with in the present paper, and highly specific to peas. The less pathogenic fungi *P. medicaginis* var. *pinodella* and *M. pinodes* are also specific to pea. Tables 1 and 2 show differences in dominant pathogens as a function of narrow rotations with just a single legume species, but at the species level of the pathogens the differences are limited. The data suggest the presence of formae speciales corresponding to the crop. Fungi such as the versatile, omnipresent and damaging *F. solani* seem to adapt gradually to any legume host. This can be envisaged either as real adaptation or as selection of rare genotypes which are favoured by a specific host. In a subsequent publication we will elaborate on the consequences of the present results on pea rotations and root disease.

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