Determination and Analysis of Soil Receptivity to *Fusarium solani* f. sp. *pisi* Causing Dry Root Rot of Peas

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ABSTRACT

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A procedure was developed to differentiate field soils according to their receptivity, ranging from suppressive to conducive, to *Fusarium solani* f. sp. *pisi*, one of the most important soilborne fungi causing dry root rot of pea. Experiments were carried out with samples of natural soil collected from commercial fields that had had a low inoculum potential for root rot in peas in previous years. In bioassays with computer-controlled soil water potential, light intensity, air temperature, and relative humidity, dry root rot severity responses to a range of inoculum levels were determined. Disease severity in different soil samples at the same infestation level showed that soil as a substrate strongly affects the inoculum potential of *F. s. pisi*. In samples that were selected because they produced only dry root rot, the amount of native *Fusarium* in pea rhizosphere soil was uncorrelated with root rot severity. Univariate and multivariate models were examined for their adequacy to describe and compare disease response data. Principal component analysis carried out on a table of samples by Weibull fitted disease responses or on a table of samples by average disease responses produced a similar receptivity order ($P \leq 0.01$) of the samples, but fitted values increased the quality of ordinations. Use of cluster analysis followed by a canonical variate analysis classified the tested soil into groups that differed significantly ($P \leq 0.05$ on the basis of χ^2) in soil receptivity to *F. s. pisi*. The value of this technique for further ecological research is discussed.

Previous field research on dry root rot of peas in the Netherlands showed that cropping frequency of peas or legumes significantly ($P \leq 0.05$) but weakly correlated with the root rot intensity (30). Whether such a weak association with cropping frequency could possibly be explained by differences among field soils in their degrees of suppressiveness to soilborne pathogens of peas has been studied (5,18). The recognition that soil factors affect the intensity of disease caused by soilborne pathogens stimulated research on this subject. Alabouvette et al (3) proposed the term "soil receptivity" (SR) to describe the effect of soils on inoculum potential, ranging from disease suppressive to conducive. Alabouvette (1,2) stated that every natural soil has some potential to reduce disease. Therefore, SR is part of inoculum potential, as defined by Garret (15), when "the energy available for infection of a host at the surface of the infection-court" is affected by the biotic and abiotic environment.

Much of the research on SR dealt with the wilt pathogen *Fusarium oxysporum* (3,9,20,35,43,53) and other host-pathogen systems (19,37,45,51,54). However, no information was available concerning SR to the *Fusarium* root rot pathogen of pea. Little attention was given to the quantification of SR or to developing criteria for comparing SR between soils and investigating factors responsible for differences in SR (10,12,13).

The objective of this study was to develop procedures, including bioassays, to differentiate between field soils for SR to *Fusarium solani* (Mart.) Sacc. f. sp. *pisi* (F. R. Jones) W. C. Snyder & H. N. Hansen, one of the most important soilborne pathogens causing dry root rot of peas. We describe SR and compare methods to analyze receptivity data. We also rank tested soils according to their degree of SR and classify them into groups differing significantly in SR.

MATERIALS AND METHODS

Selection of fields and soil sampling. Fifty fields, most of which had commercial crops, were selected. Root rot had not developed in these fields, or its occurrence had been slight (maximum root disease at flowering = 1.8 on a scale of 0–5) in previous investigations during 1986 and 1987 (27). Each field was 2–3 ha in size. Five of the fields were part of the same experimental site at the Research Station for Arable Farming and Field Production of Vegetables, Lelystad, Netherlands, but differed in the crop species grown in monoculture during the last 10 yr. During late autumn 1990 and winter 1991, all soil samples were collected after the fields were plowed. Soil samples were collected by taking 100 subsamples, 250 mm deep, with an auger. A W path through each field was followed, and 10-m-wide borders were excluded. The subsamples from each field were bulked to yield one soil composite sample (hereinafter referred to as "soil") of about 100 kg (27). Soils were stored in plastic bags at 5 C until further processed. Wet samples were gently dried by exposure to ambient air (2–12 C). When adequate moisture content was reached, samples were crumbled and passed through a sieve of 5 mm. If frozen, samples were crumbled and sieved prior to drying.

Natural infestation level of *Fusarium* in the soil samples. The presence of *F. solani* and other fusaria in the soils was determined in the rhizosphere soil of the pea cultivar Allround, which was grown for 21 days in 27 of the soils by dilution plate methods. The selective Fusarium agar (SFA) (6) and peptone-pentachloronitrobenzene agar (PPA) (26) were used to count the number of viable propagules of *Fusarium* spp. in soil or root macerate suspensions. Plates were incubated at 24 C in the dark (SFA) or under near-ultraviolet light ($\lambda = 365$ nm) (PPA). After 1 wk of growth, counts were made with a hemacytometer. Doubtful colonies were transferred to Czapek-Dox agar and potato-dextrose agar for further identification. No attempts were made to differentiate pathogenicity between the *Fusarium* isolates found.

Reference soil. To allow for comparisons between separate experiments, the same heat-sterilized soil was tested in all experiments as a reference for experimental conditions along with the arable soils. The reference soil was a light clay obtained from a field with good agronomic properties. It was originally highly contaminated with pea root pathogens. The soil was partially sterilized by heat treatment at 104 C for at least 5 h to eliminate pea root rot pathogens and other microflora (44).

SR test. To assay the effect of the SR of each soil sample, the severity of root rot was determined in a susceptible pea cultivar over a range of inoculum densities of the pathogen under standardized conditions (35,36).

Test pathogens. The inoculum of *F. s. pisi* consisted of a mixture of conidia of three highly virulent isolates, Fs48, Fs04, and Fs14 (29). Monospore cultures of these three isolates had been conserved on carnation leaf agar (14). To obtain conidia, cultures on Czapek-Dox agar were placed under near-ultraviolet light for 12 h at 24 C. After 21 days, the macro- and microconidia were washed from the agar surface in 10 ml of sterile demineralized water per plate. The mixture of conidia from the different isolates was filtered through a double layer of cheesecloth, and conidial density was determined.

Treatments. From each soil sample, subsamples were infested with 10, 100, 1,000, 10,000, or 50,000 conidia per gram of dry soil, resulting in treatments subsequently referred to as D1, D2, D3, D4, and D5, respectively. As a control, a noninoculated subsample (D0) was treated with sterile demineralized water only. The inoculum suspensions were atomized into the soil by using an air pressure of about 0.03 MPa and continuously rotating the soil in a plastic bag. Infested soil samples were placed in the dark at 5 C for 48 h to obtain equal distribution of water through the soil.

Test plants. High-quality seed (7.0–7.5 mm in diameter) of *Pisum sativum* L. 'Allround' was surface disinfested in 5% NaClO for 10 min and then rinsed thoroughly in sterile demineralized water.

Experimental conditions. Black plastic minipots, 4 × 4 × 12 cm (width × length × height), were filled with test soil, and four pea seeds were sown in each pot at a depth of 2 cm. Water was gradually added to the pots up to approximately field capacity (10 kPa, pF = 2.0) (Table 1). During germination, temperature was kept at 20 C, and pots were covered to avoid water losses. One day after emergence, the minipots were placed on top of a block of florist foam (Smithers-Oasis, Agrimedia, Germany) in 4- × 24- × 32-cm test tanks. Each test tank contained six minipots representing the six treatments of one soil sample. The test tanks were part of a computerized system in a phytotron (Fig. 1), which automatically regulated soil water potential (28). Light intensity (400 μmol $m^{-2} \cdot s^{-1}$ for 12 h per day), relative humidity (80%), and temperature (22 C day and 18 C night) were adjusted automatically. During the first, second, and third weeks after germination, soil water potential was adjusted to pF 1.0, 1.5, and 2.0, respectively. Soil water potential was monitored by electronic minitensiometers in the treatments that had not been artificially infested.

Experimental design. Seeded pots were placed in a block with soil samples as the main plot (tanks) and inoculum densities of *F. s. pisi* (minipot) as subplots and replicated four times. The

TABLE 1. Characteristics of the soil samples tested for soil receptivity to *Fusarium* f. sp. *pisi* and population densities of *F. solani*, *F. oxysporum*, and *Fusarium* spp. in pea rhizosphere soil

Soil code	Soil type[a]	Humus class[b]	H_2O[c] (%)	Soil density[d]	DI[e]	*F. solani*[f]	*F. oxysporum*	*Fusarium* spp.
as	lcl	lh	29.0	1.1	0.5	0.88	0.01	0.01
ag	lcl	lh	28.1	1.1	0.8	0.01	0.01	0.01
bl	lcl	lh	23.9	1.1	1.0	0.01	0.84	4.30
bk	lcl	lh	32.0	0.9	0.8	1.71	0.01	0.60
gv	lcl	lh	24.6	1.2	0.6	nd[g]	nd	nd
ha	lcl	mh	32.2	1.0	0.8	2.16	0.73	0.01
jg	hcl	mh	45.0	0.9	0.9	nd	nd	nd
jn	hcl	lh	38.0	1.0	0.9	2.88	0.01	43.00
ja	hcl	lh	31.1	1.1	0.7	0.01	0.01	3.80
kh	vllo	lh	24.3	1.2	1.3	1.76	2.33	0.01
lf	sa/pt	sh	39.0	1.0	0.4	0.01	0.66	0.70
ls	hlo	lh	25.2	1.1	0.5	0.17	0.01	0.70
lu	hlo	lh	23.6	1.0	1.1	4.00	0.01	8.50
mu	lcl	lh	33.6	1.0	0.6	0.01	0.61	0.70
rc	hlo	lh	29.7	1.1	0.9	1.00	0.01	0.01
rg	hcl	lh	36.0	1.0	0.9	0.01	0.63	0.01
jr	hcl	lh	33.3	1.0	1.0	nd	nd	nd
rh	lcl	lh	30.0	1.1	0.5	nd	nd	nd
ro	hlo	lh	28.9	1.0	1.3	6.50	4.98	8.30
dm	vllo	lh	23.4	1.1	1.2	nd	nd	nd
tr	llo	lh	22.0	1.3	0.6	14.83	3.55	2.20
to	llo	lh	22.0	1.3	nd	2.18	0.01	0.90
ve	hlo	lh	23.7	1.1	1.2	1.88	3.13	0.70
wa	llo	lh	25.8	1.1	0.9	0.01	2.10	6.40
wi	llo	lh	22.5	1.1	0.6	0.01	0.84	3.00
zu	hcl	lh	43.2	0.9	0.8	0.01	0.70	1.80
cv	hlo	lh	26.0	1.2	–	7.17	0.01	1.10
cb	hlo	lh	26.0	1.2	–	0.70	0.01	0.10
cf	hlo	lh	26.0	1.2	–	7.38	2.50	0.01
cm	hlo	lh	26.0	1.2	–	0.01	0.01	0.01
co	hlo	lh	26.0	1.2	–	0.10	0.01	0.10
R	hlo	lh	26.0	1.2	4.0	8.40	1.21	3.30

[a] sa = sand; vllo = very light loam; llo = light loam, hlo = heavy loam; lcl = light clay; hcl = heavy clay; and pt = peat.
[b] lh = lightly humic; mh = moderately humic; and sh = strongly humic.
[c] Gravimetric water content of the soil sample at pF = 2 (10 kPa).
[d] Soil density used in the bioassay ($g \times cm^{-3}$).
[e] Root rot severity at flowering in the last pea crop: 0 = no necrosis; 5 = 100% necrotic roots; and – = no peas grown on these fields.
[f] Populations of *F. solani*, *F. oxysporum*, and *Fusarium* spp. (10^4 cfu $\times g^{-1}$ of dry soil) in pea rhizosphere soil.
[g] Not determined.

experiments were in a split-plot design. A maximum of 10 soils could be examined at each bioassay.

Disease assessment. After 3 wk of growth, plants were carefully uprooted. Roots were washed with tap water, and disease severity was assessed. The root rot disease index (DI; 0 = healthy, and 5 = 100% necrotic root or dead plant) was calculated as the weighted average of scores of the affected cotyledon, epicotyl, roots, and xylem (27).

Inoculum potential of natural soil. The value of the root rot severity in control pots (D0), the result of infection by indigenous pathogenic fungi, was considered to be an estimate of the standard inoculum potential (IPS) of the soil (25).

Statistical differentiation of SR. To assess the degree of SR, the data on disease expression from the SR tests of the field soil samples and the sterilized reference soil were analyzed statistically.

Comparing disease responses. Differences between soil samples in root rot severity over the range of infestation doses were examined by analysis of variance in a conventional split-plot analysis, and effects were separated by the LSD at $P = 0.05$. Analysis of this type of data, where each sample originates from one single field without replicates, is valid on the sample level (32). Parallel curve analysis (11) was used to investigate differences in the disease responses of five soil samples originating from different continuous croppings.

Generating parameters to express SR. In search of parameters representing differences in disease response curves and SR between soils, a number of biologically meaningful models were tentatively fitted by numerical methods. Among others, Gompertz, logistic, exponential, and Weibull models (17) were tested. In fitting the Weibull model (equation 1), the disease index was first converted into a "health index" (HI = 5 − DI), and initial parameter values were obtained by logistic regression.

$$\mathrm{HI} = A \times e^{-(\log(\textit{inoculum density}) \times B^{-1})^{C}} \qquad (1)$$

where A = HI without artificial infestation; B = scale parameter: Log(*inoculum density*) needed to reduce A to (e^{-1}) of its value; and C = value determining the shape of the response curve. In this form of the Weibull model (34), the higher the values of the parameters, the lower the IPS and the disease response to soil infestation. If $C = 1$, the Weibull model becomes the exponential model. Models enable the calculation of fitted values of disease responses and parameter values, which can be tested for their adequacy to characterize SR.

Characterization of SR by ordination. In search of the best procedure to assess SR, disease data were analyzed by indirect gradient analysis techniques such as polar ordination, principal component analysis (PCA), and correspondence analysis (CA) (22). For ordination, disease responses were represented by either 1) the abundance of plants in the five disease classes (the plant abundance per disease class was obtained by sorting individual root rot scores into five classes, 0–1, . . ., 4–5), 2) the average disease response per inoculum dose, or 3) the fitted values of disease responses obtained with the Weibull model. Plant abundance was compared by polar ordination using percentage dissimilarity (22) and by CA.

The average disease responses per soil × inoculum density combination and the Weibull fitted disease responses were examined by PCA. In PCA, severity per inoculum density was considered as an individual variable. Therefore, six variables were considered: D0 = IPS = disease response on noninoculated samples; and D1–D5 = disease responses of the five inoculum densities. First, as required for PCA, the linear relationship between variables was confirmed. Then, PCA was carried out on a matrix of the sums of squares and products or of variance-covariance. Results of ordinations were compared with parameter values obtained after data were fitted with the Weibull and exponential models.

Clustering the soil samples in SR groups. Clustering among samples was examined on a matrix of similarities with fitted values of disease responses by means of the average linkage method. The coefficient of similarity, S_{ij}, of the ith and jth samples was calculated according to Digby et al (11)

$$S_{ij} = \frac{1}{p}\sum_{k=1}^{p} S_{ij,k}$$

with (2)

$$S_{ij,k} = 1 - \left(\frac{x_{ik} - x_{jk}}{r_k}\right)^2$$

where x_{ik} = disease response with inoculum density; k = D0, . . ., D5; and r_k = range of k. The consistency of the clusters was examined by canonical variate analysis (CVA) on a matrix of groups by fitted disease responses.

The multivariate analyses were carried out by procedures in CANOCO (49), *Statistical Ecology* (22), GENSTAT 5 (11), and Statistix (4). Biplots were constructed by using procedures of CanoDraw 3.00 (42).

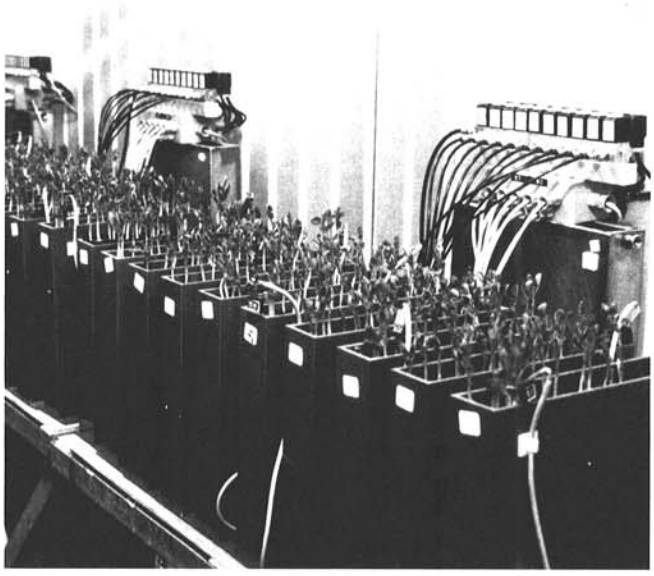

Fig. 1. Equipment used to test soil receptivity to *Fusarium solani* f. sp. *pisi*, which causes dry root rot of pea, under standardized conditions.

RESULTS

Selection of fields. Forty-six field soils were tested for their SR to *F. s. pisi*. Fifteen of these soils were discarded from further analysis because of severe natural infestation with root rot pathogens. The remaining 36 data sets used in further analysis consisted of 31 field soils and the reference soil, tested in each of the five experiments (Table 1).

Comparing disease responses. In five successive experiments, the disease responses in six different soils were compared with those in the reference soil. In each test, the root rot severity of plants in the reference soil always quickly reached high values at D1 and D2, whereas the soils from arable fields generated a great diversity of root rot responses to the increasing infestation levels D1–D5, as illustrated in Figure 2.

For each of the five experiments, the disease severity per infestation level significantly (analysis of variance, $P \leq 0.01$) depended on the inoculated soil sample. Since inoculum density is a quantitative factor, its total sum of squares could be partitioned into linear and higher components. The sum of squares for interaction between soil sample and inoculum density was partitioned accordingly. Significant interaction components were found between soil

sample and linear, quadratic, and higher order terms of inoculum density.

Some field soils were as conducive as the sterilized reference soil, whereas others strongly suppressed disease, even at the highest inoculum level. In some samples, even at D5 (50,000 conidia g^{-1} of soil added), root rot severity remained significantly lower than the disease severity in the reference soil at D1 (10 conidia g^{-1} of soil added). Absolutely suppressive soils, as defined by Baker and Cook (5), were not found.

Significant differences ($P \leq 0.05$) in the disease response curves, slope of disease progress, and disease maximum were found between the five soil samples originating from the same experimental parcel but differing in the crop species grown in monoculture during the last 10 yr (Fig. 2B). Soil cv, from continuous cultivation of *Vicia faba* L., was the most conducive, whereas soil cf, from continuous cultivation of *Linum usitatissimum* L., suppressed most disease.

Generating parameters to characterize SR. Curves of disease response to soil infestation varied in initial and maximum levels, shape, and rate. Curve parameters had to be determined to quantify differences in responses. To this end, several models were examined. Methods producing dimensionality reductions were also used to compare and interpret responses.

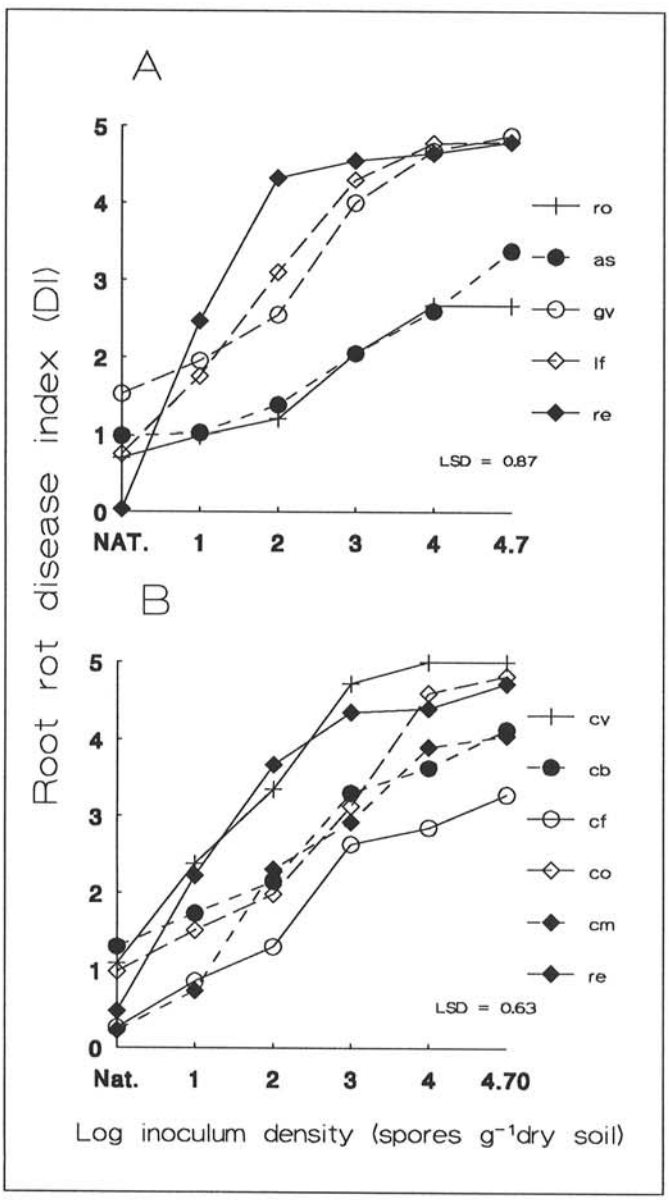

Fig. 2. Root rot disease responses of pea to a range of increasing inoculum densities of *Fusarium solani* f. sp. *pisi*. **A,** Effect on four different natural field soils. **B,** Effect on five soil samples that originated from one field but differed in cropping history: monocultures of field beans (cv), *Phaseolus* beans (cb), flax (cf), onions (co), and maize (cm). In both experiments, the same sterilized reference soil (re) was included.

Models with fixed shapes, such as logit and Gompertz, generally failed to fit the data. The Weibull and exponential models were more successful. With both models, the percentage of variance accounted for most often exceeded 70%. The exponential model has a slope parameter (RX), whereas the Weibull model has two parameters to describe scale (B) and shape (C). Parameter values from Weibull and exponential modeling are presented in Table 2. With both models, five soils had rather low fits, the variance accounted for being <65% (Table 2), mainly because of variability between replicates. The Weibull model failed to fit the data of three sterilized reference soils because root rot increased more than 63% ($B = 0$) at D1, i.e., when the percentage of healthy roots fell below 37% at D1. The exponential model fitted all data. However, as a result of its indeterminate upper limit, the change in shape from concave ($RX < 1$) to convex ($RX > 1$) alters the value of the asymptote (A) enormously, prohibiting its further interpretation.

Characterization of SR by ordination. PCA ordination carried out on a matrix of sums of squares and products or a variance-covariance matrix of average disease responses accounted for 80.6% of the variance by the first principal axis and 9.7% by the second ($n = 36$), for a total of 90.3%. With Weibull fitted disease responses, the percentage of variance associated with the first two axes was 81.5% for the first and 13.6% for the second, a total of 95.1%, an increase of nearly 5% ($n = 33$; Table 3). Variable loadings were transformed into correlations to visualize the relationships between variables and between variables and each axis (Table 3). Disease responses (D1–D5) are all highly correlated with the first principal axis, whereas D0 is the only variable highly correlated with the second axis. In addition, the second axis contrasted the responses associated to no-inoculum and low-inoculum doses (D0 and D1) with the high doses (D4 and D5), indicating differences in disease rate (24). Axis III, accounting for 3.4% of the variance, opposed the extreme responses (D0, D4, and D5) to the central ones (D1, D2, and D3), stressing curve shape differences between soils. Axes IV and higher did not provide any further information ($P \leq 0.05$, χ^2).

An ordination diagram of field soil samples was constructed on the basis of PCA on average disease responses without correction for IPS (D0) in a biplot (48) with Euclidian distances (Fig. 3). Fields are represented by asterisks and disease (variables D0–D5) by arrows. Arrows indicate the direction in which root rot severity increases. The horizontal axis (I-axis) represents the overall increase of disease by infestation, and the vertical axis in Figure 3 (II-axis) represents the location of the response curve on the y-axis in Figure 2. The variation in disease severity along the I-axis is the result of differences in the effect of the soil on disease. Therefore, the first PCA axis can be regarded as a gradient of SR to *F. s. pisi*. The value of the root rot severity on each soil can be assessed by perpendicular projection of the sample point onto the arrows representing the variable (48). The natural IPS, i.e., disease severity at D0, is almost perpendicular with respect to the first axis. Therefore the I-axis provides very little information on this parameter.

An SR order of the soils on the first principal axis in PCA of Weibull fitted values is presented (Fig. 4A). Soils with a high IPS (e.g., zu, bk, jg, and ag) were ordered in the same range as the more receptive ones (e.g., the reference soils). When the value of the root rot disease severity of the noninoculated treatment (D0) was subtracted from the disease severities at the increased infestation levels (D1–D5), the order of the soil samples was changed, especially the order of soils with a high IPS (Fig. 4B). Because of this correction, the percentage of variance accounted for by the first principal axis increased to 94.7%.

Alternative ordinations. Analysis of soil samples according to plant abundance in disease classes by polar ordination with percentages of dissimilarity (22) produced an ordination strongly folded on the second axis. CA performed on the same data yielded

TABLE 2. Parameter values and percentages of variance accounted for by the Weibull and exponential models after fitting disease response to infestation of natural soil samples and sterilized reference samples with increasing doses of *Fusarium solani* f. sp. *pisi*[a]

Soil code	Weibull: $HI = A*e^{-(L*B-1)^C}$				Exponential: $DI = A + B*RX^L$			
	A	*B*	*C*	Variance (%)	*RX*	*B*	*A*	Variance (%)
as	4.03	4.99	2.46	92.0	1.50	0.43	0.48	91.9
ag	2.74	4.34	3.57	76.9	1.69	0.20	1.94	78.3
bl	3.01	6.79	2.13	39.9	1.40	0.30	1.65	40.9
bk	2.51	3.63	1.88	74.8	1.15	2.36	0.09	75.8
gv	3.39	2.87	2.71	94.0	1.04	20.60	−19.20	91.2
ha	3.66	5.08	5.83	82.5	3.15	0.01	1.31	81.9
jg	2.19	4.90	1.47	43.8	1.29	0.60	2.27	46.3
jn	3.59	6.19	1.41	79.0	1.12	2.70	−1.27	80.2
ja	3.33	3.86	1.75	74.1	1.09	5.50	−3.80	71.4
kh	3.23	5.86	1.53	69.1	1.16	1.69	0.08	69.9
lf	4.40	2.15	1.65	92.7	0.77	−6.26	6.88	91.0
ls	3.92	6.22	2.81	55.1	1.65	0.16	0.86	54.7
lu	3.63	5.65	2.10	58.3	1.33	0.67	0.62	59.0
mu	3.21	4.79	13.39	83.9	9.68	0.00	1.77	84.4
rc	3.89	4.93	11.08	77.4	8.75	0.00	1.10	77.5
rg	3.55	6.02	1.71	77.1	1.22	1.15	0.27	75.8
jr	3.13	6.94	1.75	80.0	1.30	0.53	1.33	80.1
rh	3.15	4.09	1.45	75.3	1.05	8.50	−6.60	75.4
ro	4.36	5.92	1.52	79.1	1.10	3.98	−3.37	78.0
dm	3.20	5.00	1.71	66.4	1.26	1.03	0.76	68.9
tr	3.71	4.15	2.04	88.6	1.20	2.10	−0.90	86.7
to	3.34	3.39	2.13	84.4	1.13	4.07	−2.55	86.2
ve	3.95	5.31	5.77	82.6	3.27	0.01	1.02	82.0
wa	3.85	4.92	10.34	73.2	7.02	0.00	1.14	73.4
wi	3.97	5.92	1.36	58.8	1.20	1.60	−0.50	61.3
zu	2.50	1.98	1.59	78.8	0.73	−3.21	5.76	77.3
cv	4.03	1.89	1.66	92.1	0.72	−5.38	6.38	91.7
cb	3.73	3.81	1.70	78.6	1.06	9.00	−7.80	77.9
cf	4.89	4.47	1.29	86.6	0.97	−21.00	21.10	86.0
cm	5.00	3.10	1.38	90.7	0.90	−10.70	10.70	89.4
co	3.79	3.25	3.22	92.8	1.20	3.10	−2.23	91.6
R1	...[b]	...	...	...	0.05	−4.53	4.95	96.8
R2	6.08	1.29	0.87	94.0	0.57	−4.62	5.05	93.9
R3	6.00	0.87	0.87	94.1	0.44	−4.97	4.94	93.7
R4	...	...	...	...	0.12	−4.96	4.96	99.3
R5	...	...	...	...	0.24	−4.44	4.60	94.6

[a]HI = health index; DI = disease index; *A* = HI without artificial infestation; *B* = scale parameter; *C* = shape parameter; *RX* = slope parameter; and L = Log(*inoculum density*).
[b]Because the result was not fitted by the model, the output does not yield values.

TABLE 3. Percentage of the variance (*P*) accounted for by the first four principal axes and the correlation coefficients of the disease variables (D0–D5)[a] with each axis after principal component analysis of Weibull fitted disease responses

Disease variable	Axis I (*P* = 81.5)	Axis II (*P* = 13.6)	Axis III (*P* = 3.4)	Axis IV (*P* = 1.2)
D0	−0.22	−0.94	−0.25	0.04
D1	−0.78	−0.57	0.25	−0.07
D2	−0.96	−0.10	0.25	−0.03
D3	−0.99	−0.09	0.04	0.05
D4	−0.97	0.14	−0.13	0.12
D5	−0.94	0.16	−0.21	0.22

[a]D0 = noninoculated soil sample treated with sterile demineralized water only; D1–D5 = samples treated with 10, 100, 1,000, 10,000, or 50,000 conidia of *Fusarium solani* f. sp. *pisi* per gram of dry soil, respectively.

a poor separation of the variables on the first axis ($\lambda = 0.40$) and a cumulative percentage of variance accounted for by the first axis of 62.4. Furthermore, samples showed some Arch effect. Detrended CA (DCA) by segments confirmed the small gradient represented by the first CA axis ($S_x = 1.0$). Therefore, ordination of soils by CA was considered less appropriate to order this set of data (22,50). In fact, a linear relation was found by pairwise plotting of disease responses, giving a good reason to use PCA.

Comparison of SR assessments by PCA ordination of nonfitted and Weibull fitted disease responses. Similar ($r = 0.94$) scores of the soil samples along the PCA first principal axis were obtained before and after Weibull fitting of the disease responses, GI and WI (Table 4). When fitted data were used instead of nonfitted data, the percentage of variance associated with the first two axes increased by 5%, whereas the meaning of the configuration did not change. Furthermore, the second axes, GII and WII, which represent differences in disease response caused by natural infestation, were almost perfectly correlated ($r = 0.99$). The value of the natural IPS did not correlate with the first axes, but it was highly correlated with the second principal axis ($r = 0.91$, $r = 0.90$). Weibull fitting of disease responses improved the ordination by PCA.

Comparison of PCA first axes, GI and WI, with Weibull parameter values. The SR order produced by the two (GI and WI) PCA first axes correlated well with the values of the Weibull scale parameter *B* ($r = 0.80$ and -0.75, $n = 33$). Multiple regression showed that by adding the location parameter *A* and shape parameter *C* the relation improved significantly (R^2 adjusted = 0.78 and 0.85; $P \leq 0.05$). The correlation between the first axes and the Weibull parameters was mainly caused by variation in parameter *B* (variance ratio = 134.8, compared with 0.2 and 37.9 for *A* and *C*, respectively), which represents differences between samples in the scale of the disease response by inoculum densities. The PCA first axis alone represents the same aspects of variation as the combination of the *B* and *C* Weibull parameters (scale and shape). PCA ordering is simple and satisfactory to differentiate SR.

The parameter *RX* of the exponential model had little correlation with the PCA first axis and was uncorrelated with parameter

B of Weibull. However, it gave an almost perfect correlation with the shape parameter *C* of the Weibull model (Table 4). Spearman rank correlation produced a considerable improvement of the association of *RX* with the PCA axes and Weibull's scale parameter *B* (Table 4). Since this ranked *RX* represents only a partial aspect of disease response variation, the ordering of soils for SR by PCA is preferred.

Clustering soils in SR groups. Cluster analysis was carried out by average linkage on a matrix of similarities between soils on the basis of Weibull fitted disease responses. At 95% similarity, five groups were formed (Fig. 5). One of the groups contained only three soil samples with high IPS. This group was added to the group that neighbored it in the PCA receptivity gradient. On the basis of the disease responses of the samples in each group, the soil groups were named strongly reducing (Str), moderately reducing (Mrd), slightly reducing (Srd), and conducive (C).

CVA, a variant of discriminant analysis carried out to investigate differences between groups, showed maximum separation on two dimensions ($P \leq 0.05$, on the basis of χ^2; $\lambda_1 = 11.6$ and $\lambda_2 = 1.35$, representing the ratio of between-group to within-group variation, respectively). When Figure 6 was constructed, Mahalanobis distances between the means of each group were adjusted for variation within groups and scaled in such a way that the canonical variate space within each group was the unity in all directions (11). A multivariate normal distribution of data, i.e., soil samples normally distributed in a six-dimensional space, was assumed. A 95% confidence area could be drawn for sample scores with a radius equal to the square root (SQR) of the χ^2 value at 95% with two degrees of freedom (axes), in this case 2.45. The circles drawn in Figure 6 include 95% of the soil samples in each group. This area is the confidence interval for the canonical mean, a point in the cluster representing minimal internal variance. The confidence interval for the means of the group equals $2.45/\mathrm{SQR}(n)$ (n = number of soil samples in the group). The groups C, Srd, and Str were well separated, but Mrd overlapped with Str. The canonical means differed significantly.

Relationship between IPS, SR, and indigenous *Fusarium* spp. in soils. The ranked values of these variables were compared by Spearman rank correlation. Analysis showed no significant association between the natural IPS of the soil samples, the degree of SR (expressed as rank on the first principal axis), and the number of propagules of *F. oxysporum* and *Fusarium* spp. present in roots or rhizosphere soil. The lack of correlation between IPS and SR had been revealed earlier by values in PCA. The amount of *F. solani* in pea roots, however, was positively correlated with suppressiveness and inversely correlated with IPS ($P = 0.05$; $n = 27$).

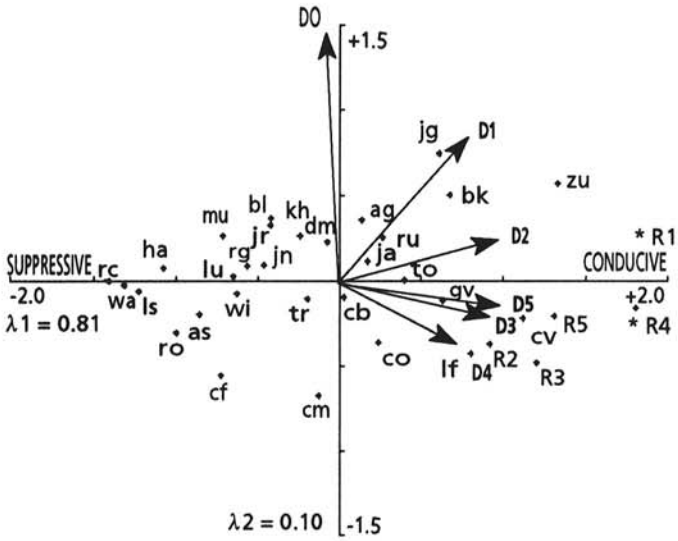

Fig. 3. Principal component analysis biplot of soil receptivity (SR) data. Ordination diagram of the SR data with disease response variables represented by arrows and soil samples by asterisks. The biplot is constructed with Euclidian distances for optimal separation of soil samples. The direction of the arrows represents the direction in which the value of the response of the corresponding variable increases most, and the length of the arrows equals the magnitude of the change in that direction. Soil subsamples were infested with 10, 100, 1,000, 10,000, or 50,000 conidia per gram of dry soil, resulting in treatments D1, D2, D3, D4, and D5, respectively. D0 = control, a noninoculated subsample treated with sterile demineralized water only. R1–R5 = sterilized reference samples.

Suppressive ----------> conducive [I-axis; 81.5% var.]

A

rc	ve	wa	ls	ha	ro	as	mu	cf	lu	wi
-3.0	-3.0	-2.9	-2.6	-2.2	-2.0	-1.6	-1.5	-1.4	-1.2	-1.2
rg	jn	bl	jr	kh	tr	cm	dm	cb	ag	ja
-1.0	-0.8	-0.7	-0.3	-0.2	-0.1	0.1	0.2	0.5	0.7	0.9
co	rh	to	jg	gv	bk	lf	r2	cv	r3	zu
1.0	1.0	1.3	1.8	2.0	2.0	2.3	2.4	2.9	3.1	3.5

Suppressive ----------> conducive [I-axis; 94.7% var.]

B

mu	rc	wa	ve	ha	bl	ls	jg	jr	ag	lu
-2.4	-2.4	-2.3	-2.2	-2.1	-2.1	-1.9	-1.5	-1.3	-1.3	-1.2
rg	kh	jn	dm	as	bk	wi	ro	ru	ja	tr
-1.1	-1.1	-0.9	-0.8	-0.7	-0.6	-0.5	-0.4	-0.2	0.1	0.2
cb	to	zu	cf	co	gv	cm	cv	lf	r2	r3
0.6	0.7	0.7	1.2	1.4	1.5	2.9	3.4	3.7	4.5	6.2

Fig. 4. Order of soil samples according to their scores on the first principal axis obtained by principal component analysis on Weibull fitted root rot responses of pea to soil infestation with *Fusarium solani* f. sp. *pisi* **A,** before and **B,** after correction for inoculum potential of the soil.

DISCUSSION

Qualitative differences in SR. Root rot disease responses, induced by infestation with *F. s. pisi*, strongly differed between the soil samples. According to the definition of SR by Alabouvette

TABLE 4. Simple correlation coefficient matrix and Spearman rank correlation matrix of the first two principal component axes created by principal component analysis on average disease responses (GI and GII) and Weibull fitted disease severities (WI and WII), the parameters of the Weibull model (*A*, *B*, and *C*), the exponential model slope parameter *RX*, and the values of the disease severities on samples not artificially infested (IPS)[a]

	GI	GII	WI	WII	*A*	*B*	*C*	*RX*	IPS
Simple correlation coeffficient									
GI	...								
GII	−0.05	...							
WI	−0.94	−0.07	...						
WII	0.10	−0.99	−0.00	...					
A	−0.09	0.86	0.01	−0.87	...				
B	0.80	−0.37	−0.75	0.41	−0.41	...			
C	0.42	−0.10	−0.54	0.18	−0.11	0.17	...		
RX	0.45	−0.13	−0.55	0.19	−0.10	0.22	0.98	...	
IPS	−0.10	−0.91	0.21	0.90	−0.91	0.24	0.03	0.02	...
Spearman rank correlation									
GI	...								
GII	−0.04	...							
WI	−0.94	−0.02	...						
WII	0.05	−0.99	−0.01	...					
A	0.15	0.90	−0.19	−0.89	...				
B	0.75	−0.38	−0.73	0.37	−0.21	...			
C	0.35	−0.23	−0.48	0.27	−0.26	0.22	...		
RX	0.71	−0.41	−0.73	0.45	−0.30	0.66	0.78	...	
IPS	−0.18	−0.89	0.23	0.88	−0.94	0.15	0.24	0.24	...

[a] $n = 33$; $r = 0.325$; and $P \leq 0.05$.

et al (3), this variation in disease response means that differences in SR to *F. s. pisi* in pea exist.

Production of disease responses. To assess differences in SR, the methods used for collecting disease data are crucial. Standardization of the environmental conditions, artificial infestation, and careful experimental design are needed. SR for diseases caused by soilborne plant pathogens has been investigated in several ways, usually with limited standardization of climatic conditions. To compare levels of SR, bioassays were carried out in a phytotron with standardized light intensity, temperature, and humidity of both soil and air (28). Aqueous spore suspensions were used to avoid mixing substrates because mixing may affect SR.

Corman et al (10) explored disease progression with time starting with different infestation levels, and Perrin (33) did so with a single fixed initial inoculum level. Rouxel and Regnault (38), Rouxel and Briard (37), Lucas et al (21), and Sarniguet et al (39) investigated disease responses to a range of artificially increased infestation levels in soils determined at one time after planting. Our choice to test SR to *F. s. pisi* according to the latter procedure was based on the consideration that the assessment of root rot severity is a destructive procedure. Minipots were used to obtain a complete exploration of the soil by roots, maximizing encounter of infection courts and pathogen, and thus permitting maximum expression of an inoculum potential. Testing time was kept as short as possible to avoid unfavorable root environment caused by overrooting in the pots.

Differentiating SR. In characterizing SR, the problem is to distinguish between disease response curves in a variable soil environment. To this purpose, disease responses were linearized (54), or parameters obtained by fitting data (including areas under the disease response curve) were analyzed by PCA (7) or cluster analysis (8). Rarely, multivariate analysis has been used to characterize SR (13,19).

The assessment of the disease responses, either as incidence or as severity and with or without time dependency, determines the procedures to differentiate SR. Corman et al (10) investigated the incidence of Fusarium wilt in time, and calculated the survival probability as an indicator of SR. When disease incidence or disease severity was assessed as a function of inoculum, SR variation was illustrated as differences in response intensities between soils per infestation level (1,3,37,52). However, a quantitative discrimination of SR requires more than merely an illustration of differences per inoculum level. To assess SR, overall differences in disease response curves should be investigated. Since we consider the level, shape, and slope of the disease response curves to be essential characteristics of SR, we sought a procedure to deal with these aspects. Therefore, the first step consisted of fitting the disease response curves. Fitted values and parameters, characteristic of the disease response in each soil, were retained for further analysis.

Models. To fit disease responses, mathematical models may be employed that do not contain parameters with a biological meaning (23). However, we preferred to employ models yielding parameters with a biological meaning. Since variation in shape of response curves was found, models with predetermined shapes may not fit the data, as indeed was found for the Gompertz model. Flexible models, such as the Weibull model, fitted most of the data. However, the Weibull parameters for scale (B) and shape (C) did not always vary in the same direction (Table 2). Thus, each parameter separately remained inconclusive for ranking SR, nor did the combination of parameters B and C yield unequivocal ranking of SR.

The exponential model produced results similar to those of Weibull but also fitted extreme responses. In particular, the model fitted curves from sterilized soils. The exponential slope parameter RX behaved in a manner similar to that of the Weibull shape parameter C, and, since C was regarded as inadequate, so was RX.

Although the two models did not give a very high fit, the values obtained were satisfactory if diversity of responses and experimental variability is considered. The low percentage of variance explained by both models for some soil samples was ascribed to variation between replicates, but these were retained in the analysis because of their heuristic value.

Ordinations. If SR represents a gradient from suppressive to conducive effects of soils on soil inoculum potential, multivariate techniques offer an alternative to make such a gradient explicit (48). In PCA ordination, a new variable (the first axis) was created as a linear combination of the disease responses. The first axis

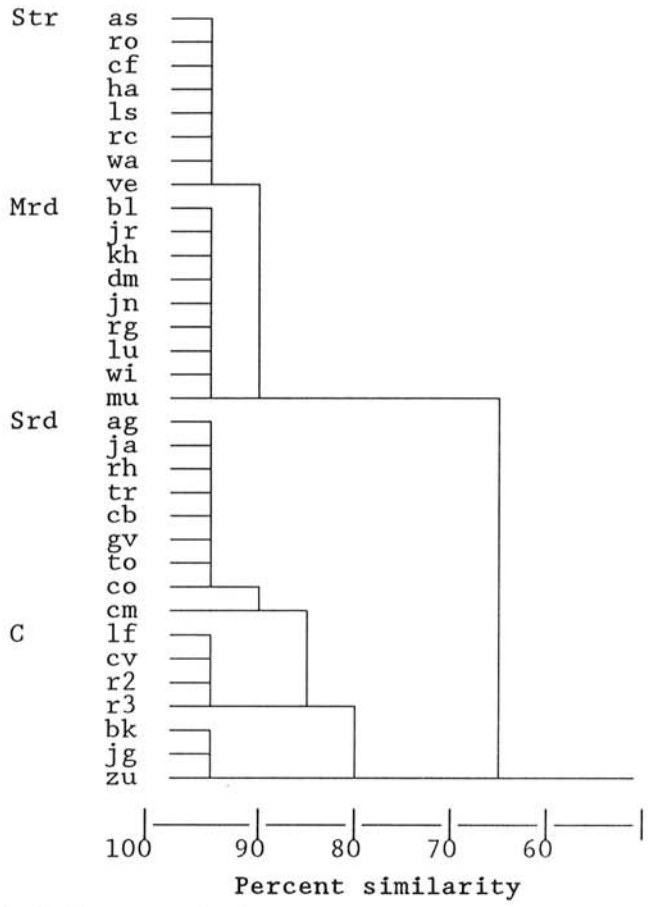

Fig. 5. Cluster analysis of soil receptivity data. The dendrogram was constructed from linkage cluster analysis on similarity coefficients of different soil samples (n = 33) obtained from Weibull fitted values of disease responses. Clusters: Str = strongly reducing; Mrd = moderately reducing; Srd = slightly reducing; and C = conducive.

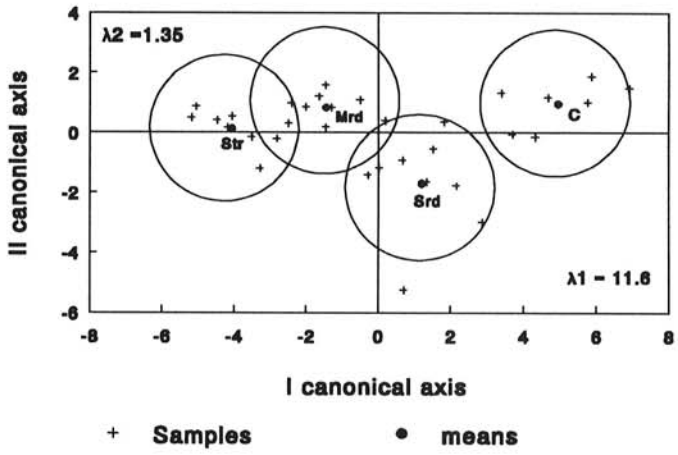

Fig. 6. Canonical variate analysis. Plots of the first two discriminant function axes and the canonical mean of four groups of soil receptivity to *Fusarium solani* f. sp. *pisi*. Axis units are expressed in units of standard deviation. Canonical means of groups: Str = strongly reducing; Mrd = moderately reducing; Srd = slightly reducing; and C = conducive (n = 33).

contains almost exclusively SR information (Fig. 3 and Table 3). The dispersion of the soils along this first axis (Fig. 3) is caused by properties of the soils counteracting the effect of increased inoculum densities of the pathogen on root rot. The second axis mainly represents the disease variability caused by natural infestation (D0 = IPS).

Doublet et al (13) presented SR ordinations to *Plasmodiophora brassicae* by CA. They obtained an ordination that was strongly folded on the second axis, the Guttman effect. Nevertheless, they projected samples on the first axis to represent ranks of SR. If more dimensions have to be used that are not orthogonal, then the data should be detrended, a procedure that was omitted by Doublet et al (13). Because CA was less adequate for our data, PCA was employed for further differentiation.

In the comparison of SR assessments, Weibull fitting of disease responses improved the ordination by PCA. Also, the first PCA axis was more adequate for ordering soils than Weibull's parameters. When information of natural IPS (D0) was removed from PCA, the first ordination axis represented shape and slope of the disease responses, and the percentage of variance accounted for by this axis increased to 95%. However, neglecting IPS does not give better biological distinction and leads to the anomaly that samples differing largely in soil inoculum potential, while yielding the same disease response to infestation, would be placed at the same SR level.

PCA-generated variables have been used to assess effects of environmental factors on disease incidence (8,16,24,41) and plant losses (46,47) or to characterize microbial populations (39), as reviewed by Hau and Kranz (17). According to our results, it is an elegant way to express SR to soilborne plant pathogens, being simple, reproducible, and available in several computer programs. PCA might be applied to develop an improved scale of SR that is standardized in its "zero point" and measuring unit and warrants further investigations.

Searching for factors causing differences in SR. PCA can be employed to explore which factors may be responsible for differences in SR between soils. Grouping of soil samples according to receptivity offers an extra facility for such exploration. Clustering of data (Fig. 5) was not intended to discriminate between variables responsible for group association. CVA was used to look for group coherence. Our analysis indicated three completely separated groups: conducive (C), slightly reducing (Srd), and strongly reducing (Str) soils. On the basis of CVA, most of the samples were intermediately receptive to *F. s. pisi* (Fig. 6). This is in agreement with PCA (Fig. 3). Theoretically, it could be expected that IPS somehow represents SR. IPS and SR were uncorrelated for *F. s. pisi*. This may imply that SR with regard to *F. s. pisi* in pea works through a more specific antagonism. Increasing suppressiveness was correlated positively with the number of *F. solani* colonies in pea roots, whereas the latter was negatively correlated with the natural IPS. In addition, the amount of *F. solani* in rhizosphere soil was uncorrelated with IPS. This indicates that a saprophytic *F. solani* could be active as an antagonist.

Soil samples from closely related fields differing in cropping history were classified in significantly different SR groups. This result stresses the importance of the biological factor to SR.

Under the experimental conditions used, common root rot, a disease caused by *Aphanomyces euteiches* and *Pythium* spp., developed in a considerable number of soil samples that were not artificially infested. High natural infestation by these fungi impeded the assessment of the effect of additional *F. s. pisi* inoculum. For this reason, such soil samples were excluded from statistical analysis, but all of these samples could be considered to be highly conducive to root rot.

In natural systems, diversity is considered to be an important obstacle to disease reaching an epidemic level. In agriculture, soil homogeneity and uniform crop properties are instrumental in obtaining high yield and quality. No stabilization in an ecological sense can be expected in agricultural soil because of the short growing periods and the continuous disruptions of the arable layer. However, even in such disturbed soils, an interrelated complex of factors does exist that greatly affects the activities of pathogens on host plants (31,40). The recognition of such properties of a soil is indispensable for the understanding and use of biological control and for breeding plants for resistance to soilborne pathogens. The combination of procedures presented permits research dealing with the identification of ecological characteristics correlated with differences in SR. Further research should elucidate possible causal mechanisms.

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