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Yield reduction in wheat in relation to leaf necrosis caused by Septoria tritici

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Abstract

In 1980, field inoculations with *Septoria tritici* were performed on winter wheat cv. Okapi. Leaf necrosis progress curves were established; they were sigmoid and could be transformed into logit lines. There was a great difference in the slope of the logit lines between inoculated plots and non-inoculated controls. The mid-time values varied according to inoculum dosage and post-inoculation humidity treatment. Yields (kg ha^{-1}) and average grain weights (mg $grain^{-1}$) differed significantly between inoculated and non-inoculated plots, but seldom among inoculation treatments. Decrease of average grain weight completely explained yield loss, which was 878 kg ha^{-1} or 12% of control (7045 kg ha^{-1}). This crop loss is considerable for a cultivar which is not particularly susceptible. A good correlation was found between the amount of necrosis at development stages DC = 75 and 77 and yield depression. The integral of necrosis over time gave a high correlation with loss of kernel weight.

Additional keywords : Wheat, *Septoria,* epidemiology, crop loss.

Introduction

Leaf spot caused by *Septoria tritici* Rob. ex Desm. (perfect state: *Mycosphaerella graminicola* (Fuckel) Sanderson) arouses more and more interest as an important disease of wheat (Shipton et al., 1971). The disease seems to have increased in importance (Saari and Wilcoxson, 1974), possibly because of changes in cultivation methods. In some areas, it seems that improved genetic control of wheat rusts has enabled researchers to recognize the importance of *S. tritici;* alternatively, the rust-resistant germplasm may have a relatively high susceptibility to *S. tritici.* In Switzerland and Bavaria, areas notorious for heavy attacks of glume blotch caused by *Septoria nodorum* (Berk.; perf. state: *Leptosphaeria nodorum* Mueller), *S. tritici* is ever present (Zogg et al., 1950). In the Netherlands, *S. tritici* is always present in various amounts. It occurs in two waves, a late winter wave and an early summer wave, separated by the period of shooting. The present study is of an introductory nature and deals with the latter wave, viz. its artificial induction, its course and its effect on yield.

Materials and methods

The fungus. Lyophilized *S. tritici* isolates were obtained from E. Ubels (Research Institute for Plant Protection (IPO), Wageningen). Eight isolates were grown in petri dishes at 18 to 20 °C in darkness for 8 to 12 days. The medium contained per litre water 10 g Oxoid malt extract, 4 g yeast extract, 4 g glucose, 10 mg aureomycin and 15 g agar. The whole surface of the agar in the petri dishes was inoculated. The fungus forms a thick, slimy layer with spores not unlike macroconidia. No longer than 2 h before inoculation, the conidial mass was collected by means of a spatula, transferred to water (without emulsifier) and diluted to the desired spore density. In field experiments, about 1.3 petri dishes per m^2 of wheat crop were used for inoculation.

Field plots. The field experiment was performed at the experimental farm De Bouwing near Wageningen. The soil is a deep somewhat irrigular river clay soil. The plots were laid out in a field of winter wheat cv. Okapi, which is not particularly susceptible to *S. tritici.* Further data are given in Table 1. The experiment was a split plot experiment with five blocks (replications) and four randomized treatments per block. Treatments consisted of inoculations with different conidial densities O, A, B and C (Table 2). The gross area per plot was $3 \times 11 = 33$ m^2; the total experimental area was $20 \times 33 = 660$ m^2. The inoculations were made just after appearance of the flag leaf (DC = 39; Zadoks et al., 1974) and at flowering (DC = 65). The 3-m-wide plots were treated by means of a knapsack sprayer and a spray beam of 1.5 m length, going once up and down the plot, applying 3 l conidial suspension per plot. The treatments were performed in the evening, between 20.00 and 22.00 h. Depending on the weather, additional water was sprayed over the plots to obtain a satisfactory leaf wetness period. In addition, at flowering five bunches of plants in

Table 1. Cultural data of a field experiment with *S. tritici* on wheat.

Cultivar	:	Okapi			
Preceding crop	:	sugar beet			
Seeding date	:	79.10.22			
Row distance	:	20 cm			
Seed density	:	132 kg ha^{-1}			
Fertilizers	:	date	N	P_2O_5	K
		80.01.15	–	57	300
		80.03.21	107	57	–
		80.05.23	60	57	–
			167	171	300
Growth substances:		80.04.28	CCC 0.5 l ha^{-1}		
		80.05.16	CCC 1.0 l ha^{-1}		
Pesticides	:	80.05.20	triadimefon 0.25 kg ha^{-1}		

Tabel 1. Teeltgegevens van een veldproef met S. tritici op tarwe.

Tabel 2. Inoculum densities at indicated developmental stages of wheat (DC).

Treatments	Density of conidial suspension (10^6 conidia ml^{-1})	
	DC = 37/39	DC = 65
O and O*[1]	0.0	0.0
A and A*	0.5	2.0
B and B*	2.0	10.0
C and C*	2.0	20.0

[1] Treatments marked by asterisks were covered by polythene during 96 h after inoculation.

Tabel 2. Inoculatiedichtheden bij de aangegeven ontwikkelingsstadia (DC).

each plot with some 40 plants per bunch were covered by polythene bags during 96 h after inoculation (treatments O*, A*, B* and C*).

Disease assessment. The symptomatology of *S. tritici* is well known (Shipton et al., 1971), but at least in the early stages of disease development recognition of symptoms is not so easy (Shearer and Wilcoxson, 1980). James (1974) emphasized that crop losses should be related to the total amount of affected leaf area, including typical lesions and necrotic and chlorotic flecks. Therefore, the necrotic leaf area (NLA) was assessed as a percentage of total leaf area. The difference in NLA between inoculated (A, B, C) and non-inoculated (O) plots was considered to be due to *S. tritici.* Assessments were made in the laboratory at 10 dates (Table 3) using samples of 10 or 20 shoots or stems per plot. Different leaf layers were assessed separately.

Table 3. Assessment dates, stages of development (DC), numbers of shoots or stems used per plot, and leaf layers sampled (flag leaf is 1).

Date	Julian day	Number of shoot/stems per plot		DC	Leaf layers sampled
		OABC	O*A*B*C*		
80.06.06	157	10	–	47	4,5
12	163	10	–	59	4,5
20	171	10	–	69	4,5
24	175	20	–	69	1,2,3,4
30	181	20	–	71	1,2,3,4
90.07.07	188	20	10	73	1,2,3,4
15	196	20	10	75	1,2,3,4
20	201	20	10	77	1,2,3,4
28	209	20	10	83	1,2,3,4
80.08.04	216	20	10	87	1,2,3,4

Tabel 3. Waarnemingsdata, ontwikkelingsstadia (DC), bemonsterd aantal scheuten of halmen per object, en de bemonsterde bladlagen (vlagblad is blad 1).

Yield assessment. On 80.08.13, just before harvest, random samples of wheat ears were taken, four samples per plot with 20 ears per sample for treatments O, A, B and C (80 samples in total). For treatments O*, A*, B* and C* five samples per plot were taken with 10 ears each (100 samples in total). Samples were air-dried to about 15.5% humidity, threshed and weighed. Grain weight was determined using 200 kernels per sample. On 80.08.15 the plots were combine-harvested (swath width 2.2 m) and yields were determined.

Statistical analysis. Individual leaf records were averaged per leaf layer and per sample. The smallest statistical units used were plot averages. The data were subjected to standard ANOVA programs (SPSS package on DEC-10 computer; Nie et al., 1975) for transversal analysis (Zadoks, 1978). For longitudinal analysis necrosis records (%) were transformed into logit values (Zadoks and Schein, 1979) and the linear regression of logit NLA on time was determined. The resulting regression line, called logit line, is completely determined by its slope (Vanderplank's r) and an intercept (here $t_{0.50}$, the time at wich NLA attains the 50% value). The values r and $t_{0.50}$ can be subjected to ANOVA.

Results

Conditions for infection. Weather conditions during the 48 h following inoculation are crucial for the outcome of the experiment. Different combinations of inoculation days and treatments were given infection codes I1 to I5. Some data are given in Table 4. For infection of susceptible cultivars a minimum leaf wetness duration of 15 h is required; 35 h of leaf wetness, followed by 48 h with high humidity, is considered to be optimal (Renfro and Young, 1956). Field inoculations are to be followed by a high

Tabel 4. Some environmental data from the period of 48 h following inoculation.

Date	Julian day	DC	Infection code	Treatment	Leaf wetness period		Minimum temperature (°C)	
					without interruption	total during 48 h	0-24 h	24-48 h
80.05.23	143	37	I1	A C	15	22	8[1]	4[1]
25	145	39	I2	A C	13	13	4[1]	5[1]
27	147	39	I3	A B C	11	34	5[1]	5[1]
80.06.16	167	65	I4	A C	40	40	9	11
				A* C*	96		9	11
17	168	65	I5	B	18	31	11	7
				B*	96		11	7

[1] Averages of 0.10 and 0.15 m measurements at Wageningen meteorological station; other values from field measurements at 0.50 m height.

Tabel 4. Enkele milieugegevens over de periode van 48 uur volgend op de inoculatie.

humidity period of 96 h, obtained by means of plastic covers (Cooke and Jones, 1970). This method, applicable to small bunches of plants only, enhances the susceptibility of the crop (Shipton et al., 1971). The results indicate that the inoculation methods as applied in this study were adequate.

Disease progress. The increase of NLA is shown in Figs 1a en b. The curves for treatments O and O* show the progress of leaf necrosis withhout inoculation. The differences between the inoculated treatments and the non-inoculated controls must be attributed to artificial infection. The curves in Fig. 1b differ from those in 1a only after Julian day 181 (30 June). Both up to and after days 181 the effect of inoculation is evident. The early increase in NLA is due to infections I1, I2 (?) and I3 at development stages DC = 37 to 39; these inoculations affected leaf layers 4 and 3 (Fig. 1 c). The later disease increase is due to inoculations I4 and I5 at DC = 65; they refer to leaf layers 2 and 1 (Figs 1d – g). Whatever the leaf layers affected, treatment C with the highest inoculum density was the first to show significant differences with the control (leaf layer 3 on day 172, leaf layer 2 on day 189; $\geqslant$ 25 and $\geqslant$ 21 days after inoculation, respectively. Whereas on day 189 the treatments A, B and C of the flag leaf did not show a NLA significantly ($p \geqslant 0.05$) higher than the control, the treatments A*, B* and C* did. The differences must be attributed to the prolonged moist period under the polythene covers.

Logit transformation of NLA curves. Figs 1a-g show sigmoid NLA progress curves. Apparently, inoculation increased the rate of progress of leaf necrosis. The slope of the logit line in units per unit per day corresponds to Vanderplank's (1963) apparent infection rate r. Fig. 2 shows that the r values of inoculated treatments are much greater than those of controls. Whereas the variation in r between inoculation treatments is negligible, the $t_{0.50}$ values differ considerably. The ranking orders C*B*A* and C-B-A correspond with the order of decreasing inoculum dosages. The ranking order of the groups C*B*A* and CBA corresponds with the order of decreasing duration of exposure to high humidity after inoculation. Statistical data are given in Table 5. The relations of r and $t_{0.50}$ to inoculum density are obvious. With flag leaves, the difference between inoculated and non-inoculated was always significant at $p \leqslant 0.05$. In addition, the difference between lowest and highest inoculum dosage was significant in three out of four cases.

Yield data. Data on yield obtained by combine harvester are given in Table 6. Table 7 contains data from ear samples. Again, inoculation treatments differed significantly from controls, both for yield and grain weight. The maximum yield of 7045 kg ha^{-1} at a grain weight of 44.2 mg was reduced by infection to 6167 kg ha^{-1} at a grain weight of 39.0 mg. Reduction in yield and grain weight both were about 12%.

The data from Table 7 corroborate the results. Interestingly, yields of polythene-covered bunches were much lower than those of uncovered bunches, and this was true both for inoculation treatments and for the control. Possibly, 96 h of plastic coverage caused damage independent of disease.

The correlations between rate of increase of NLA and yield or grain weight were statistically significant at $p \leqslant 0.001$ (Table 8). With respect to these correlations, there is no difference between flag leaf layer and top three leaf layers, nor is there a dif-

Fig. 1. Necrosis progress curves showing necrotic leaf area (NLA) as a proportion (x) of total leaf area against time in Julian days (d) and development stage in Decimal Code (DC). For treatments see Table 2.

a – Standard inoculation. Leaves 1-4 averaged.
b – Inoculation with prolonged humidity period. Leaves 1-4 averaged.
c – Standard inoculation. Leaf layers 3 and 4.
d – Standard inoculation. Leaf layer 2.
e – Inoculation with prolonged humidity period. Leaf layer 2.
f – Standard inoculation. Flag leaf layer.
g – Inoculation with prolonged humidity period. Flag leaf layer.

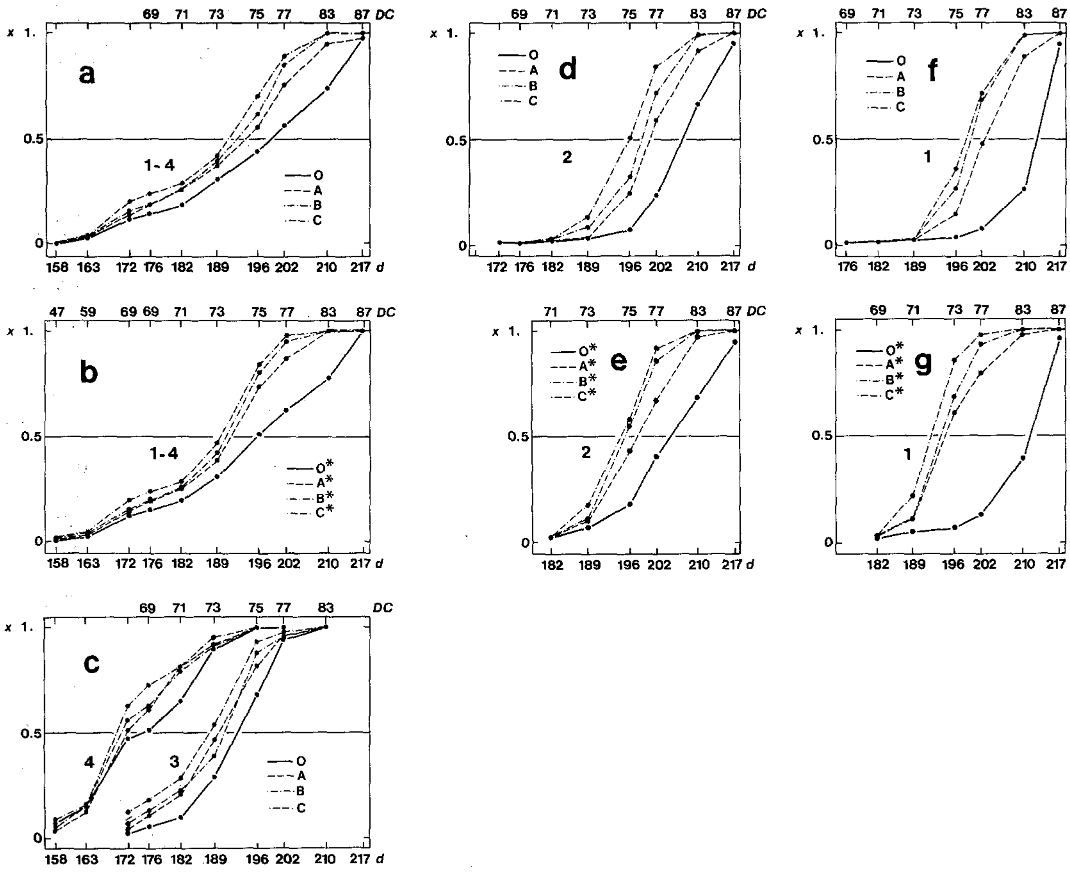

Fig. 1. Necrose-voortschrijdingscurven tonen het necrotisch bladoppervlak (NLA) als fractie (x) van het totaal bladoppervlak, afgezet tegen de tijd in Juliaanse dagen (d) en het ontwikkelingsstadium in Decimale Code (DC). Voor behandelingen zie Tabel 2.

a – Bladlagen 1-4 gemiddeld. Standaard-inoculatie.
b – Bladlagen 1-4 gemiddeld. Inoculatie met verlengde vochtperiode.
c – Bladlagen 3 en 4. Standaard-inoculatie.
d – Bladlaag 2. Standaard-inoculatie.
e – Bladlaag 2. Inoculatie met verlengde vochtperiode.
f – Bladlaag 1 (vlagblad). Standaard-inoculatie.
g – Bladlaag 1 (vlagblad). Inoculatie met verlengde vochtperiode.

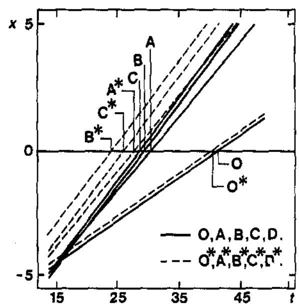

Fig. 2. Logit lines of the progress of necrosis on the flag leaf layer.
Time is given in Julian days, necrosis is recorded as logit NLA *(x)*. For treatments see Table 2. The half-times ($t_{0.50}$) are indicated.

Fig. 2. Logit-lijnen van de necrose-voortschrijding op het vlagblad.
Tijd in Juliaanse dagen, necrose in logit NLA (x). Voor de behandelingen zie Tabel 2. De halfwaardetijden ($t_{0.50}$) zijn aangegeven.

ference between yield and grain weight. The results for $t_{0.50}$ give higher values than for *r*, as can be expected from Fig. 3.

For an estimation of the disease-yield relationship, linear regressions of NLA on yield were calculated (Table 9). The regression coefficients are negative; the more disease, the higher NLA and the lower yield. The effect of a leaf layer depends on the date of NLA assessment, as may be expected. Multiple regression gives better results than single regression. Days 196 and 201 with DC = 75 and DC = 77, respectively, were promising for damage prediction based on the critical time method (Zadoks and Schein, 1979).

Another approach was to integrate the area under the NLA progress curve and to relate yield to the integrated value. The result (Fig. 3) for grain weight was even better than those of Table 9. The coefficients of determination for 40 data pairs (8 treatments in 5 replications) were 0.80 for the flag leaf and 0.81 for leaf 1 through 3, and for yield 0.72 and 0.71, respectively.

Discussion

The experiment was not flawless. The field was rather irregular. The experiment is a monocyclic or repeated monocyclic experiment, but secondary infection may have occurred. Triadimefon may have had a residual effect on the early development of *S. tritici.* Nevertheless, some useful data resulted.

The progress of natural leaf death toward the end of the season was adequately described by a logistic curve with an 'apparent rate of necrosis' *r* of 0.19 for total foliage (upper three leaves, treatment 0) and 0.18 for flag leaves. The correlations of logit lines and the progress of necrosis in time were highly significance of correlation coefficients at $p \leqslant 0.001$). As necrosis of the inoculated plots is due to the combined effect of natural death of leaves and pathogen-induced death, the new pathogen effect can be estimated as the differences between the *r* values for inoculated and control plots. Thus the apparent rate of infection *r* for the total foliage (upper three leaves) equals about 0.26 (A+B+C)/3−0.19 (O) = 0.07 and for the flag leaf 0.31 − 0.18 = 0.13 (Table 5).

These *r* values refer to *S. tritici* on a cultivar which is not particularly susceptible in a year not specially conducive to leaf spot and under conditions of artificial infection. The values found here were of the same order as *r* values known for yellow rust and brown rust *(Puccinia striiformis* and *P. recondita).* Whether such *r* values can be generalized and used for predictions remains to be seen.

Table 5. Statistical data on logit lines representing the progress of necrosis (NLA) on the flag leaf and the upper three leaves.

Column	*Explanation*
1	Treatment
2	Linear regression coefficient = Vanderplank's r
3	$t_{0.50}$ calculated in days from development stage DC = 65
4	Coefficient of determination (square of correlation coefficient)
5	Δr (treatment minus mean of controls)
6	$\Delta t_{0.50}$ (treatment minus mean of controls)

1	2	3	4	5	6
Leaf layer 1 (flag leaf)					
O	0.180 a[1]	41.1 a	0.73	–	–
O*	0.175 a	39.6 a	0.80	–	–
A	0.280 b	31.6 b	0.92	0.10	– 8.8
B	0.326 c	29.1 c	0.94	0.15	–11.3
C	0.325 c	28.4 cd	0.94	0.15	–12.0
A*	0.306 c	27.5 de	0.96	0.13	–12.9
B*	0.327 c	26.1 e	0.95	0.15	–14.3
C*	0.318 c	23.9 f	0.94	0.14	–16.5
Leaf layer 1 through 3					
O	0.189 a	32.7 a	0.87	–	–
O*	0.186 a	32.0 a	0.92	–	–
A	0.237 b	27.4 b	0.92	0.05	– 5.0
B	0.277 c	25.8 c	0.93	0.09	– 6.6
C	0.269 c	24.5 de	0.94	0.08	– 7.9
A*	0.269 c	25.3 cd	0.94	0.08	– 7.1
B*	0.277 c	23.8 e	0.96	0.09	– 8.6
C*	0.272 c	22.7 f	0.97	0.08	– 9.7

[1] Values followed by the same letter do not differ significantly at $p \leqslant 0.05$ according to Duncan's multiple range test.

Kolom	*Verklaring*
1	*Behandeling*
2	*Lineaire regressie coëfficiënt = Vanderplank's r*
3	*$t_{0.50}$ in dagen na DC = 65*
4	*Coëfficiënt van determinatie*
5	*Δr (behandeling – gemiddelde der controles)*
6	*$\Delta t_{0.50}$ (behandeling – gemiddelde der controles)*

Tabel 5. Statistische gegevens over logit-lijnen die de voortschrijding van de necrose op het vlagblad en de bovenste drie bladeren beschrijven.

Table 6. Yield data, based on harvested plots of 22 m².

Treatment	Yield		Grain weight	
	kg ha^{-1}	% of control	mg	% of control
O	7045 a[1]	100	44.2 a	100
A	6364 b	90	39.7 b	90
B	5955 b	85	38.0 b	86
C	6182 b	88	39.2 b	89
(A + B + C)/3	6167	88	39.0	88
Reduction	878	12	5.2	12

[1] Values followed by the same letter do not differ significantly at $p \leqslant 0.05$ according to Duncan's multiple range test.

Tabel 6. Opbrengstgegevens, gebaseerd op netto veldjes van 22 m².

Table 7. Yield data from ear samples.

Treatment	Yield		Grain weight	
	g per 10 ears	% of control	mg	% of control
O	15.6 a[1]	100	42.9 a	100
A	14.3 b	92	39.3 b	91
B	13.4 b	86	38.2 b	89
C	13.5 b	87	38.0 b	89
(A + B + C)/3	13.7	88	38.5	90
O*	13.4 a	100	43.5 a	100
A*	10.8 b	80	37.2 b	86
B*	11.0 b	82	34.7 c	80
C*	10.3 b	77	35.1 c	81
(A* + B* + C*)/3	10.7	80	35.7	82

[1] Values followed by the same letter do not differ significantly at $p \leqslant 0.05$ according to Duncan's multiple range test.

Tabel 7. Opbrengstgegevens van aarmonsters.

Table 8. Correlation of the slope of the logit line (Vanderplank's r value) or the $t_{0.50}$ to yield or grain weight.

Leaf layer	Yield (kg ha^{-1})				Grain weight (mg)			
	r		$t_{0.05}$		r		$t_{0.50}$	
	CC	CD	CC	CD	CC	CD	CC	CD
1	−0.77[1]	0.59	0.83	0.69	−0.78	0.60	0.87	0.76
1 through 3	−0.78	0.61	0.83	0.69	−0.77	0.59	0.89	0.77

[1] Entries are correlation coefficients CC and coefficients of determination CD based on 40 pairs each. For explanation see text.

Tabel 8. Een veldproef met S. tritici op tarwe. Correlaties van Vanderplank's r en $t_{0.50}$ met opbrengst (kg ha^{-1}) en zaadgewicht (mg korrel^{-1}).

Table 9. Linear regression between NLA at different stages and grain weight.

Julian day	DC	Value	Simple regression of leaf layer				Multiple regression of leaf layers	
			1	2	3	(1+2+3)/3	1+2	1+2+3
181	71	r[1]	−0.86[3]	−2.10	−0.70	−1.84	–	–
		CD[2]	ns[4]	ns	0.45	0.40	ns	0.50
188	73	r	−0.85	−1.06	−0.42	−0.89	–	–
		CD	0.43	0.38	0.47	0.59	0.49	0.64
196	75	r	−0.23	−0.36	−0.52	−0.34	–	–
		CD	0.70	0.69	0.48	0.78	0.75	0.79
201	77	r	−0.22	−0.29	−0.71	−0.37	–	–
		CD	0.75	0.67	ns	0.74	0.75	0.75
209	83	r	−0.22	−0.43	–	−0.45	–	–
		CD	−0.62	0.58	–	–	–	

[1] r is the regression coefficient.
[2] CD is the coefficiënt of determination.
[3] Entries are based on 40 data pairs.
[4] Means not significant at $p \leqslant 0.01$.

Tabel 9. Een veldproef met S. tritici op tarwe. Lineaire regressie van korrelgewicht op necrotisch bladoppervlak.

Fig. 3. Correlation between grain weight (mg) and area under the necrosis progress curve (%) for the flag leaf layer (1) and for the four upper leaf layers (1-4). For treatments see Table 2. CD = 0.795 at n = 40 (8 treatments at 5 replications). Time *t* is given in days after DC = 65 (Table 5).

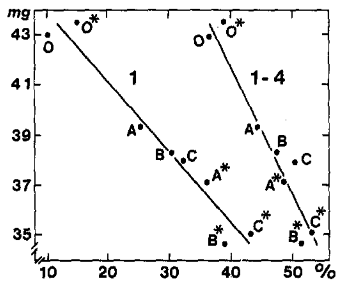

Fig. 3. Correlatie tussen korrelgewicht (mg) en oppervlak onder de necrosevoortschrijdingscurve (%) voor het vlagblad (1) en voor de vier bovenste bladeren (1-4). Voor behandelingen zie Tabel 2. De coëfficient van determinatie CD = 0,795 bij n = 40 (8 behandelingen met 5 herhalingen).

The rate of grain filling is in the order of 200 to 400 kg ha^{-1} d^{-1}, depending on temperature (Spiertz and Ellen, 1978). Table 5 indicates that $\Delta t_{0.50}$ of the flag leaf due to *S. tritici* infection is about −12 days. As the flag leaf produces about one quarter of the grain filling assimilates, yield depression due to *S. tritici* on the flag leaf is estimated as 1/4 × 12 × 300 = 900 kg ha^{-1}. This figure is in rough agreement with the calculated yield depression of 878 kg ha^{-1} from Table 6. As the injury due to *S. tritici* occurred rather late in the season and the grain had been set already, the damage was expressed only as a reduction of grain filling in consequence of a reduction of photosynthate-producing foliage. In the present case, apparently, total pathogen-induced necrosis fully explains the yield reduction observed. Whether such a straight-forward injury-damage relation can be generalized, again, remains to be seen.

Samenvatting

Opbrengstderving bij tarwe in relatie tot bladnecrose veroorzaakt door Septoria tritici

In 1980 werden inoculaties verricht met *Septoria tritici* in een veldproef met wintertarwe 'Okapi'. De bladnecrose-voortschrijdingscurves werden bepaald. De S-vormige curves konden getransformeerd worden tot logit-lijnen. De geïnoculeerde en niet geïnoculeerde objecten verschilden aanzienlijk in de hellingen van de logit-lijnen. De halfwaardetijden varieerden al naar inoculatiedosis en vochtbehandeling na inoculatie. De verschillen in opbrengst (kg ha^{-1}) waren significant voor geïnoculeerd tegenover niet-geïnoculeerd. De opbrengstderving van 878 kg ha^{-1} (gelijk aan 12% van de niet-geïnoculeerde controle 7045 kg ha^{-1})werd volledig verklaard door de vermindering van het korrelgewicht. De schade is aanzienlijk voor een cultivar die niet bijzonder vatbaar is. De opbrengstderving correleerde goed met de hoeveelheid necrose waargenomen bij de ontwikkelingsstadia DC = 75 en DC = 77. De necrose geïntegreerd over de tijd correleerde goed met de verlaging van het korrelgewicht.

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