Virulence Patterns of Geographically Differing Isolates of *Pyrenophora tritici-repentis* and Sources of Resistance in Wheat

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ABSTRACT

Sah, D. N., and Fehrmann, H. 1992. Virulence patterns of geographically differing isolates of *Pyrenophora tritici-repentis* and sources of resistance in wheat. Plant Dis. 76:712-716.

Nineteen single-conidiospore isolates of *Pyrenophora tritici-repentis* were isolated from leaf samples of wheat collected from Brazil, Germany, India, and Nepal, and one ascospore isolate was obtained from the United States for a virulence analysis study. Eight wheat cultivars were inoculated with a conidial suspension from each isolate, and percent necrotic leaf area was measured 5–6 days later using video image analysis. A highly significant interaction was found between cultivars of wheat and isolates of *P. tritici-repentis*. Cluster analysis of the data indicated only a moderate variation in virulence among the isolates of *P. tritici-repentis* tested. In a host resistance study, a significant interaction between 21 wheat lines and four geographically differing isolates also was detected. In a greenhouse study, 61 spring and 34 winter genotypes were evaluated for resistance to *P. tritici-repentis*. When 21 genotypes were reevaluated in a growth chamber with four isolates, 12 winter and six spring wheat cultivars and lines were resistant to moderately resistant.

Additional keywords: *Drechslera tritici-repentis*, physiologic race, stable resistance

Tan spot, caused by *Pyrenophora tritici-repentis* (Died.) Drechs. (anamorph: *Drechslera tritici-repentis* (Died.) Shoemaker), is an economically important disease of wheat (*Triticum aestivum* L.) in many regions of the world (5,28). The disease has been found to cause substantial losses in yield under severe epidemic conditions (1,6,8, 19–21,23–25). The use of resistant cultivars offers an economically effective means of keeping losses to a minimum. However, resistance varies with wheat genotypes, leaf position, wet period, and fungal isolate (7). Resistance to *P. tritici-repentis* has been reported to be polygenic (18) or monogenic (13,14,16).

Isolates of *P. tritici-repentis* have been found to differ in virulence. On the basis of lesion size and percent necrotic leaf area, da Luz and Hosford (3) identified 12 virulence patterns among 40 isolates from the Central Plains of North America. Variation in virulence has been found among isolates from *Bromus inermis* Leyss. in the United States (9) and in a test with three isolates in India (17). A significant isolate × cultivar interaction was detected in a recent growth chamber study with isolates from New York and adjoining areas (22) but not in an earlier greenhouse study with isolates from Great Plains of North America (4). A clear understanding of the extent of variation in virulence would be helpful in developing wheat cultivars with stable resistance. Therefore, this investigation was undertaken to examine

Accepted for publication 2 January 1992.

the pathogenic variability among the isolates of *P. tritici-repentis* originating from different regions of the world. Our second objective was to determine the level of resistance in winter wheat cultivars from Germany and spring wheat lines and cultivars from countries with tan spot problems.

MATERIALS AND METHODS

Test cultivars. On the basis of disease reaction of 23 wheat cultivars and lines inoculated with two isolates of *P. tritici-repentis*, 12 genotypes were selected for final evaluation with four isolates. Based on disease reaction patterns, seven spring cultivars (Ning7840, BH1146, Fink"s", BR8, Chil"s", Vee"s", and Glenlea) and one winter cultivar (Urban) were selected as differentials for the virulence analysis study. The spring wheat cultivars BH1146, BR8, and Glenlea have been used in earlier virulence analysis studies (3,12,22).

Eight seeds of each cultivar were planted in 7 × 7 cm plastic pots containing vermiculite in a greenhouse with 24/15 C (day/night) temperature and 16 hr of light. Seedlings were thinned after emergence to six plants per pot and then transferred to a controlled-environment chamber at a constant temperature of 20 ± 2 C and 15 hr of light (325 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density per day). Plants were irrigated uniformly with Hewitt solution (KNO_3, $Ca(NO_3)_2 \times 4H_2O$, $NaH_2PO_4 \cdot H_2O$, $MgSO_4 \cdot 7H_2O$, H_3BO_3, $Na_2MoO_4 \cdot H_2O$, $Cu(II)SO_4 \cdot 5H_2O$, NaCl, $ZnSO_4 \cdot 7H_2O$, $Mn(II)SO_4 \cdot H_2O$, and Sequestren 138 Fe at the rate of 202, 475, 184, 184, 18.6, 1.21, 1.25, 58.5, 2.9, 16.9, and 1.0 g per liter of H_2O, respectively) on alternate days until completion of the experiments.

Fungal isolates and inoculum production. Nineteen single-conidiospore isolates of *P. tritici-repentis* were isolated from diseased leaf samples collected from Brazil, Germany, India, and Nepal, and one single-ascospore isolate was obtained from the United States. The isolates used for inoculation in this study and their countries of origin included BD1–BD8 from Germany, PyD_7 from the United States, NL1–NL5 from Nepal, and IA1–IA5 from India. All isolates were stored at 4 C as cultures grown on V8 potato-dextrose agar (PDA) medium (150 ml of V8 juice, 10 g of Difco PDA, 3 g of $CaCO_3$, 10 g of Bacto agar, and 850 ml of distilled water) (11).

Inoculum was produced by the method used by Lamari and Bernier (11) with slight modification. Small plugs of cultures (0.5 cm in diameter) were transferred onto V8 PDA in petri plates and incubated in the dark at 20 C for 6 days. The mycelium then was scraped with a bent metal rod and incubated in fluorescent light (approximately 78 $\mu E \cdot m^{-2} \cdot s^{-2}$) at 22 C for 24 hr, followed by 20–22 hr in the dark at 15 C. Conidial suspensions were prepared by flooding the plates with sterile distilled water and scraping the outer edge of the colony with a glass slide. A drop of Tween 20 was added per 100 ml of suspension, and the concentration was determined with a Fuchs Rosenthal cell counter (Assistent Sontheim, Rhön, Germany) and adjusted by adding water before inoculation.

Virulence analysis study. The experiments were conducted in a randomized complete block design with a split-plot treatment arrangement. Isolates were used as main-plot treatments and cultivars as subplot treatments. There were three replications with six plants per replication. Seedlings at the two-leaf stage (17–18 days after planting) were sprayed with a suspension of 5,000 conidia per milliliter of water. Approximately 0.7 ml of inoculum was sprayed per plant with a glass tube sprayer. Plants were air-dried before transferring to a mist chamber. A fine mist of deionized water was sprayed with an automatic device for continuous 100 sec/hr. After 30 hr, plants were allowed to dry and then returned to the growth chamber at 20 ± 2 C and 65–95% relative humidity. After 5–6 days, percent necrotic leaf area was estimated on the second leaf (fully expanded at the time of inoculation) using video image analysis.

The video image analysis system consisted of one Philips CCD video camera (256 × 256 pixels), an A/D modem, a Sony color video monitor, and image processing software built in a microcomputer. Pictures taken by the camera automatically passed through an A/D modem and were processed by self-made image processing software. The system was standardized by measuring a 10 × 10 cm black paper before measurements of leaves. A blue filter (Kodak Wratten 47B) and a red-yellow filter (Kodak Wratten 15 and 25) were mounted on the video camera to measure the total and leaf area without necrosis, respectively. Differences in the two readings were used for calculating percent necrotic leaf area. Only 13 isolates could be used in one experiment because of the limited space in the growth chamber. A second experiment was done in exactly the same manner as the first one except that seven new isolates along with six isolates already tested previously were used for evaluation (Table 1).

Data were analyzed using the Cluster and GLM procedures of SAS (SAS Institute Inc., Cary, NC). Analysis of variance, least significant difference values, and Duncan's multiple range test were computed with SAS statements.

Host resistance study. The first experiment involved evaluation of 95 wheat lines and cultivars (34 winter and 61 spring wheats), which originated from Brazil, Canada, China, Germany, Israel, Mexico, Nepal, Paraguay, Thailand, and the United States, with a virulent isolate (PyD_7) under greenhouse conditions. The temperature in the greenhouse

Table 1. Percent necrotic leaf area on eight differential wheat cultivars produced by 20 isolates of *Pyrenophora tritici-repentis*

	Wheat cultivar							
Isolate	**Urban**	**Vee"s"**	**Chil"s"**	**BH1146**	**BR8**	**Fink"s"**	**Ning7840**	**Glenlea**
Experiment 1[y]								
BD1	64.2	36.1	59.6	63.4	54.7	33.3	79.8	70.2
BD2	42.5	35.4	41.1	49.4	46.5	33.3	47.8	50.0
BD3	42.7	35.3	44.5	53.2	45.4	21.5	53.7	61.6
PyD_7	45.8	22.5	44.9	60.3	49.6	28.6	57.1	86.3
BL1	55.3	38.9	51.5	85.9	50.3	37.4	67.2	81.8
IA1	38.4	24.5	54.0	54.2	37.9	36.3	27.2	83.8
BD4	35.4	13.3	11.8	26.0	19.6	18.6	38.9	50.8
BD6	36.4	13.1	49.3	38.7	45.1	14.9	51.6	50.4
IA2	9.8	13.0	25.1	14.9	8.3	24.5	13.0	71.5
NL1	25.4	16.6	16.3	39.8	22.0	24.8	36.0	81.8
NL2	9.4	16.7	19.8	19.3	11.8	7.5	18.0	21.9
NL3	49.1	57.0	66.9	77.9	67.5	49.6	87.2	85.9
BD5	36.4	19.0	22.9	18.6	37.3	22.0	18.9	75.4
Experiment 2[z]								
BD1	54.7	43.2	51.9	52.6	53.0	38.3	67.8	73.3
BD2	44.2	32.3	33.2	46.6	42.0	14.0	80.8	55.5
BD3	49.6	17.8	36.5	49.8	38.1	7.1	68.9	80.1
PyD_7	56.8	37.2	34.6	68.2	39.1	14.3	77.6	85.4
BL1	33.2	23.8	39.8	69.3	50.3	13.7	73.6	90.1
IA1	33.8	37.9	31.9	60.7	27.7	9.5	69.5	79.8
BD8	59.7	57.9	60.7	67.0	56.9	43.7	80.1	87.0
BD7	58.8	51.9	61.5	70.8	68.1	55.7	81.6	82.5
IA3	18.2	26.5	21.9	52.7	15.0	18.2	78.5	87.8
IA5	43.5	58.1	52.6	69.2	67.5	35.5	70.8	83.3
IA4	55.1	54.5	60.3	74.9	25.5	21.2	66.1	85.1
NL4	31.1	36.4	36.8	74.9	26.8	21.0	59.1	78.6
NL5	42.2	26.4	28.6	81.3	42.1	10.5	58.2	83.9

[y] $LSD_{0.05} = 19.7$.
[z] $LSD_{0.05} = 20.9$.

ranged from 15 to 24 C with 16 hr of light. The experiment was conducted in a completely randomized block design with three replications, with six plants per replication. Host resistance was evaluated based on mean lesion length. The largest well-separated lesion on the second fully expanded leaf of each plant was measured with a ruler.

In another experiment, 21 lines and cultivars (12 German winter wheats and nine spring wheats from abroad) with moderate to high resistance in the greenhouse test with 95 genotypes were further evaluated in a controlled-environment chamber (20 ± 2 C) with four isolates, BD1, NL4, IA5, and PyD_7 from Germany, Nepal, India, and the United States, respectively. Inoculum concentration was adjusted to 2,000 conidia per milliliter of water, and 0.5 ml of inoculum was sprayed per plant. Plants were incubated in the mist chamber for 24 hr. Percent necrotic area and lesion length were measured by the methods discussed earlier. All other experimental procedures, including design and number of replications, were the same as discussed for the virulence analysis study. The stability of resistance in the lines and cultivars was estimated by regressing the variance in virulence among the four isolates against the mean percent necrotic leaf area of each of the 21 cultivars following the method proposed by Carson (2).

RESULTS AND DISCUSSION

Disease symptoms started to appear within 42 hr of inoculation on all of the test cultivars. Disease progressed very rapidly in the controlled-environment chamber with high relative humidity (65–95%). None of the cultivars was found to be immune to any of the isolates tested. Isolates used in this study differed in the amount of disease incited on test wheat cultivars as measured by video image analysis (Table 1). The analysis of variance (ANOVA) for percent necrotic leaf area in both virulence analysis experiments showed highly significant effects of cultivar, isolate, and the cultivar × isolate interaction (Table 2). Original data were used for analysis as it did not warrant transformation.

The ANOVA has been advocated as a means of detecting specificity in the host-pathogen relationship, when all the isolates of the pathogen can cause disease on all the test cultivars of the host (26,27). However, it might not be a sensitive test as environment may cause significant interaction between host cultivars and pathogen isolates (10). A false significant cultivar × isolate interaction may be detected due to inaccurate measurement of disease severity (29). Only a slight variation in disease production on differential cultivars was observed between the first and second experiments, when isolates BD1, BD2, BD3, PyD_7, BL1, and IA1 were reinoculated for comparison (Table 1). In spite of the differences in the country of origin, virulence of the isolates as measured by the percent necrotic leaf area varied moderately. Similar variation in virulence has been reported by Schilder and Bergstrom (22) among the isolates of *P. tritici-repentis* from New York and adjoining areas.

Cluster analysis has been used previously to determine the similarity in virulence of pathogen isolates (15,22). Centroid, Ward's minimum variance, and Mcquitty's similarity analysis methods were compared as methods of cluster analysis in determining the similarity of the isolates tested. Very slight differences in cluster compositions were observed for repeated data when two experiments were analyzed separately. Methods of cluster analysis also slightly affected the clustering. Therefore, the results of the centroid method of cluster analysis, which is considered more robust to outliers and less biased than most other hierarchical methods, are presented (Table 1). No strong association was observed between the virulence pattern and the isolate's location of origin (Fig. 1).

Each of the three large clusters contained isolates originating from different countries. Group one contained isolates from Nepal, India, the United States, and Germany. The second group was formed by five German, two Indian, and two Nepalese isolates, whereas a third group contained one isolate each from Brazil, India, Nepal, and two from Germany. The virulence patterns of NL3 and IA1 were quite different from all of the other isolates. However, the isolates did not differ greatly in the amount of necrotic lesions produced on test cultivars and were not classifiable into distinct physiologic races. The results of

Table 2. Analysis of variance of percent necrotic leaf area on eight wheat cultivars produced by 20 isolates of *Pyrenophora tritici-repentis*

Source of variation	df	Mean square	
		Experiment 1	Experiment 2
Block	2	4,940.8	82.2
Isolate	12	5,518.8**[z]	1,720.7**
Main plot error	24	324.6	416.1
Cultivar	7	6,478.1**	14,560.9**
Cultivar × isolate	84	334.0**	302.4**
Subplot error	182	149.6	169.4
Total	311	...	...

[z] F test highly significant at $P < 0.01$.

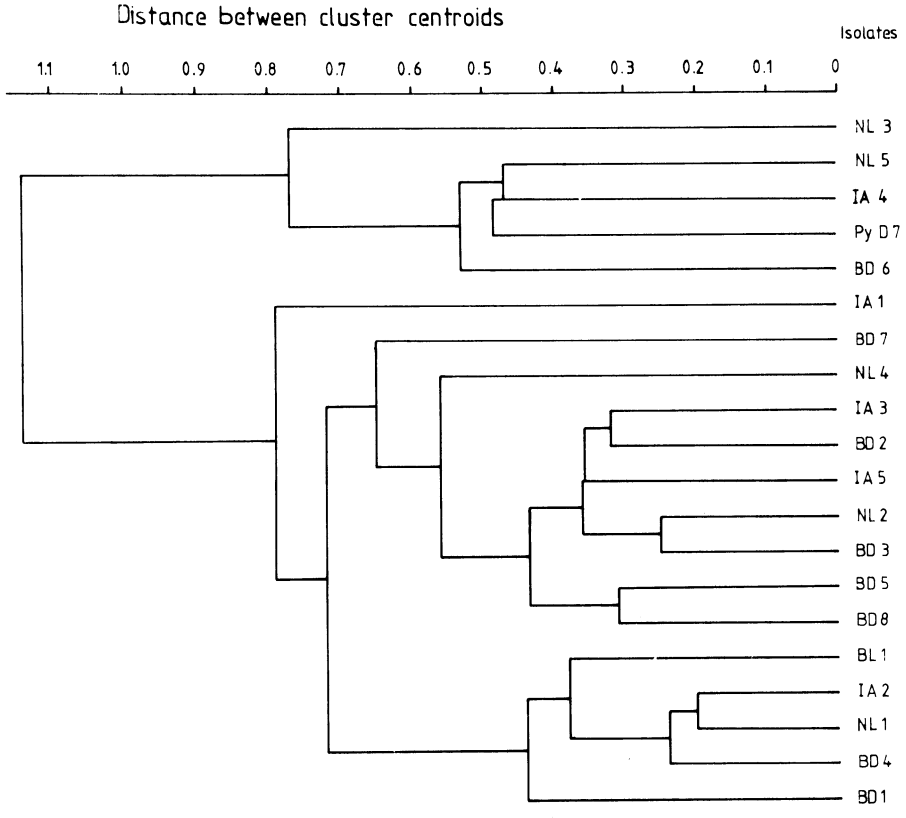

Fig. 1. Dendrogram showing differences in virulence of 20 isolates of *Pyrenophora tritici-repentis* based on their ability to incite percent necrosis on eight differential wheat cultivars.

this study support the findings reported earlier (22). The results imply that there is no distinctly different genetic pool of virulence and, therefore, high selection pressure on a cultivar with effective resistance is an unlikely phenomenon.

Highly significant differences in resistance were detected among eight test cultivars (Table 1). Cluster analysis of the data revealed that susceptible cultivars Ning7840 and Glenlea formed a cluster at the similarity level of 0.893 (Fig. 2). At the similarity level of 0.427, moderately resistant cultivars, Vee"s", BR8, Chil"s", and Urban, formed another cluster. Strong dissimilarity was apparent among moderately susceptible BH1146, resistant cultivar Fink"s", and other genotypes.

In the host resistance studies, significant differences in lesion length were observed when 95 wheat genotypes were evaluated against a virulent isolate, PyD_7, of *P. tritici-repentis* (Table 3). Twenty-one genotypes differing in resistance were reevaluated with four isolates originating from Germany, India, Nepal, and the United States. Highly significant differences in resistance among the genotypes and in virulence among the isolates were observed as measured by percent necrotic leaf area and lesion length (Table 3). Analysis of variance of lesion length and percent necrosis indicated significant isolate, cultivar, and isolate × cultivar interaction effects (Table 4). Therefore, comparison of resistance among wheat genotypes was possible only within a specific isolate.

In general, regardless of the isolate used, resistant genotypes (12 German winter wheats and six spring wheats from abroad) identified in the greenhouse test were resistant when compared with the susceptible cultivars Glenlea or SN29. Little tan spot has been observed in Germany on these winter cultivars grown in the field, and they could be used in breeding for spring wheat resistance. However, the ranking of the cultivar changed depending on the isolate or disease evaluation parameter used. For instance, cultivars Kraka, Vuka, and Club are considered moderately susceptible to isolate BD1 based on lesion length but not based on percent necrosis. Also, cultivar CHU245 showed a similar reaction to four isolates used based on lesion length but had a differential reaction based on percent necrosis. Therefore, the amounts of necrotic lesions should be assessed in evaluation of wheat genotypes to *P. tritici-repentis*. Generally, lesions produced on 21 lines under greenhouse conditions were smaller than under growth room conditions. This may be explained by a lower relative humidity (usually 40–60%) in the greenhouse than in the growth chamber (65–95%). Hence, the influence of relative humidity on tan spot disease development should be studied.

A significant positive correlation ($r = 0.98$, $P < 0.05$) was observed when mean host susceptibility was regressed on variation in variance among isolates (Fig. 3). This indicates that resistance in wheat would be stable and might not erode rapidly because of rapid shifts in pathogen genotype frequency. Results of this study also suggest that resistance identified with pathogen isolates from one geographic location might be effective against other. The results of this study supports the findings already reported earlier (2,22). However, the stability of resistance must be verified

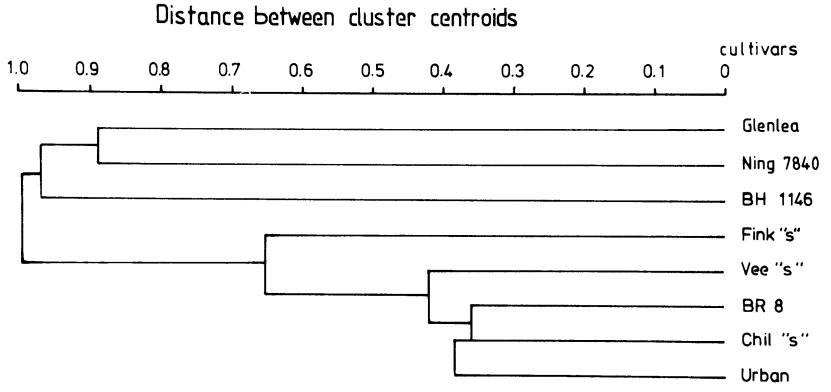

Fig. 2. Dendrogram showing similarity and successive clustering of eight wheat cultivars based on their susceptibility (percent necrosis) to 20 isolates of *Pyrenophora tritici-repentis*.

Table 3. Percent necrotic leaf area and lesion length incited by four geographically differing isolates of *Pyrenophora tritici-repentis* on 21 wheat cultivars and lines

Cultivar[x]	Disease severity (%)				Lesion length (mm)				
	BD1	NL4	IA5	PyD_7	BD1	NL4	IA5	PyD_7	PyD_7[y]
Arber	0.9 a[z]	2.8 a	1.1 a	1.4 a	1.17 a	0.61 ab	0.86 a	0.56 a	0.83
Kraka	2.3 ab	6.4 a	23.6 bc	8.2 ab	2.47 cd	1.33 a–e	2.3 fg	1.72 fg	0.42
Tristan	2.8 ab	2.7 a	12.8 a–c	3.3 ab	1.94 a–c	1.25 a–e	2.0 d–g	1.42 d–f	1.25
Vuka	3.6 ab	2.6 a	4.8 ab	1.1 a	2.5 cd	1.06 a–c	1.5 b–d	0.89 a–c	1.17
Knirps	5.1 ab	3.0 a	5.7 ab	3.6 ab	1.39 ab	0.72 ab	1.0 ab	1.17 b–e	0.47
3Bon/YR/3/F3570//KAL/BB	5.3 ab	3.4 a	5.0 ab	7.6 ab	1.72 a–c	1.11 a–d	1.56 b–e	0.97 a–d	1.0
Club	5.6 ab	0.7 a	1.3 a	15.8 ab	2.36 cd	1.14 a–d	1.22 a–c	0.81 ab	0.64
^{42}C S/A.curv.//Glenn81/3/ ALD"s"/PYN"s"	6.4 a–c	5.8 a	6.6 a–c	15.0 ab	1.86 a–c	1.06 a–c	1.53 b–d	0.97 a–d	1.22
Fink"s"	6.7 a–c	4.5 a	4.7 ab	7.7 ab	2.1 bc	0.58 a	1.22 a–c	1.19 b–e	0.86
Ares	6.8 a–c	2.6 a	8.1 a–c	7.1 ab	2.39 cd	1.20 a–e	1.61 c–e	1.66 f	0.92
Ambros	7.3 a–c	3.4 a	5.4 ab	9.6 ab	2.11 bc	1.11 a–d	1.84 d–f	1.11 b–e	1.08
Obelisk	7.7 a–c	3.6 a	15.3 a–c	10.1 ab	2.52 cd	1.20 a–e	2.36 fg	1.70 fg	1.11
Astron	8.2 a–c	3.0 a	25.5 bc	4.9 ab	2.3 cd	1.89 de	2.47 g	1.28 b–f	1.06
6CS/A.curv.//Glenn81/3/ ALD"s"/PYN"s"	8.9 a–c	15.0 a	18.7 a–c	17.1 ab	2.11 bc	1.36 a–e	2.0 d–g	1.45 d–f	1.67
CS/AC1	11.1 a–d	10.0 a	26.5 c	32.6 cd	2.0 bc	1.75 c–e	2.06 d–g	1.72 fg	1.86
Bon/YR/3/F3570//KAL/BB	12.7 b–d	5.1 a	19.0 a–c	35.6 de	1.81 a–c	1.41 b–e	2.14 e–g	2.14 g	1.42
Albrecht	12.8 b–d	3.9 a	11.4 a–c	5.9 ab	2.44 cd	1.17 a–d	1.61 c–e	1.14 b–e	0.67
Milan	16.3 c–e	3.7 a	19.1 a–c	18.9 bc	1.81 a–c	1.14 a–d	1.58 b–e	1.36 c–f	0.43
SN29	19.2 de	34.2 b	75.7 e	76.2 f	3.52 e	3.08 f	3.78 h	3.53 h	2.39
CHU245	22.7 e	5.0 a	45.4 d	49.7 e	2.97 de	1.97 e	2.39 fg	1.59 ef	2.25
Glenlea	24.3 e	48.2 c	75.3 e	70.6 f	3.45 e	3.22 f	3.53 h	3.39 h	2.44

[x]All cultivars except Arber, Tristan, Vuka, Knirps, Club, Ares, Ambros, Astron, Albrecht, Milan, and Obelisk are spring wheat.
[y]Trial conducted in a greenhouse with 95 genotypes, the LSD ($P \leq 0.05$) is 0.64. Only 21 genotypes are shown for comparison.
[z]Means within a column followed by the same letters are not significantly different according to Duncan's multiple range test ($P \leq 0.05$).

Table 4. Analysis of variance of percent necrotic leaf area and lesion length incited by four geographically differing isolates of *Pyrenophora tritici-repentis* on 21 wheat cultivars

Source of variation	df	Mean square	
		Disease severity (%)	Lesion length (mm)
Block	2	112.1	1.677
Isolate	3	2,392.2*[z]	9.395**
Main plot error	6	333.3	0.593
Cultivar	20	2,554.2**	5.024**
Cultivar × isolate	60	261.9**	0.22**
Subplot error	160	69.0	0.127
Total	251	...	...

[z]* and ** = F value significant at $P < 0.05$ and $P < 0.01$, respectively.

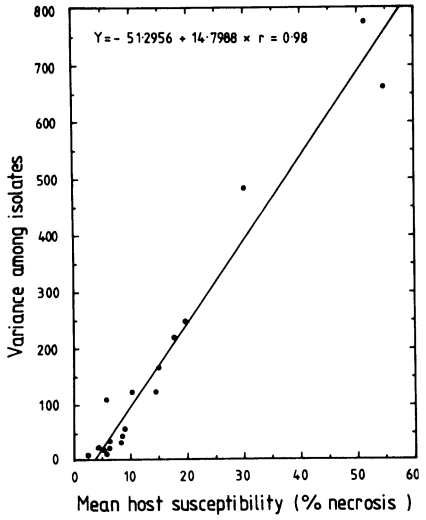

Fig. 3. Relationship between mean percent necrosis of 21 wheat lines/cultivars and the variance among four geographically differing isolates of *Pyrenophora tritici-repentis*.

under field conditions in an environment conducive to disease development.

ACKNOWLEDGMENTS

We thank Alexander von Humboldt-Stiftung, Bonn, Germany, for providing a research fellowship to the first author to carry out this research. We also thank A. Obst of Bayerische Landensanstalt für Bodenkultur und Pflanzenbau, München, and R. M. Hosford of North Dakota State University for providing the German and the United States isolates, respectively. We also thank A. von Tiedemann for growth chamber facilities and manuscript review; B. Altwicker and M. Bossmann for technical assistance; J. Hetzler for the wheat germ plasm and disease samples; and R. Feig for manuscript typing.

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