

## The Distribution and Frequency of Virulence Genes in Geographically Separated Populations of *Leptosphaeria nodorum*

A. L. Scharen, Z. Eyal, M. D. Huffman, and J. M. Prescott

First author: Agricultural Research Service, U.S. Department of Agriculture, Department of Plant Pathology, Montana State University, Bozeman 59717, USA. Second author: Department of Botany, The George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv 69978, Israel. Third author: Department of Mathematical Sciences, Montana State University, Bozeman 59717, USA. Fourth author: Wheat Program, The International Maize and Wheat Improvement Center (CIMMYT), El Batan, Mexico.

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### ABSTRACT

Scharen, A. L., Eyal, Z., Huffman, M. D., and Prescott, J. M., 1985. The distribution and frequency of virulence genes in geographically separated populations of *Leptosphaeria nodorum*. *Phytopathology* 75:1463-1468.

Virulence frequency of 33 isolates of *Leptosphaeria nodorum* from eight countries were evaluated on 38 wheat and triticale cultivars. Isolate  $\times$  cultivar interactions indicate that resistance and virulence have some specific effects. A computer program that estimates the number of genes, assuming a gene-for-gene relationship, was used to analyze the interacting matrix. The analysis hypothesized 21 different interacting genes in the 33-isolate  $\times$  38-cultivar matrix. The winter bread wheat, Red Chief, was assigned 19 hypothetical genes for resistance; cultivars Yamhill, 81UWWMN 2095, and MT 71-8-10 also were assigned large numbers of hypothetical genes. Isolates of *L. nodorum* from South America (Brazil, Chile, and Ecuador) expressed high relative virulence with those from Canadian and United States populations following. Among the United

States isolates of *L. nodorum*, those from Louisiana and Florida exhibited the highest relative virulence. Some wheat and triticale accessions exhibited a low percent necrosis in response to populations of both *L. nodorum* and *Mycosphaerella graminicola* that have wide virulence spectra. The cultivars most resistant to populations of the two pathogens were the winter hexaploid wheat cultivars JCR-979 (CI 16906), Red Chief (CI 12109), 81UWWMN 2095 (Maris Huntsman/VPM/Moisson), and triticale accession DU-75. A Bobwhite "S" CIMMYT line expressed the highest level of resistance to both pathogens among the spring hexaploid wheats. The implications of these findings on the deployment of germplasm and the accumulation of resistance to both pathogens is discussed.

*Additional key words:* glume blotch, *Septoria nodorum*, *Septoria tritici*, speckled leaf blotch.

*Leptosphaeria nodorum* E. Müller (anamorph, *Septoria nodorum* (Berk.) Berk.) the causal agent of Septoria nodorum blotch of wheat, has been studied considerably in recent years because of the damage it causes to wheat in several parts of the world (1,7,11,16,17). Mixtures of isolates of *L. nodorum* have been used in genetic studies and evaluation of germplasm response (8,11,13,16). Some authors (1,12,13,15) have referred to the presence or absence of physiological races or differential host-pathogen interactions among the obviously different populations of *L. nodorum*. The utilization of quantitative inoculation techniques enabled a more accurate evaluation of host symptoms in light of an obvious lack of qualitative host response (2,14,18). Allingham and Jackson (1) tested host  $\times$  pathogen relationships of 282 isolates of *L. nodorum* originating from northern Florida. Despite the recorded differential interactions, the 253 resistance patterns were not categorized into a conventional race classification. Rufty et al (12) tested nine isolates of *L. nodorum*, (eight from North Carolina and one from Montana) on seedlings of four winter wheat cultivars and found significant cultivar  $\times$  isolate interactions that were indicative of specific resistance, but the degree of specificity was not high. Scharen and Eyal (15) tested 14 different cultures of *L. nodorum* on 10 winter and spring wheats that differed in level of resistance. Pathogenic interactions were classified as intermediate or susceptible; still, the magnitudes of the interactions within the intermediate class were relatively low.

No isolate  $\times$  cultivar interactions were found with the uniformly resistant cultivars Anderson, Coker 68-8, and Red Chief or with the uniformly susceptible cultivars, Fortuna and Polk (15). Distinct

and significant isolate  $\times$  cultivar interactions were reported for *Mycosphaerella graminicola* on wheat, when the interaction was analyzed by using a genetic matrix analysis computer program (assuming a gene-for-gene relationship) to estimate the number of interacting genes (5,6).

The purpose of the present study was to investigate virulence patterns in populations of *L. nodorum* obtained from some countries where losses caused by the pathogen are economically important.

### MATERIALS AND METHODS

**The pathogen.** Isolates of *L. nodorum* were secured from single pycnidia. The number of isolates within a location varied depending on the size and availability of leaf samples. Thirty-three isolates of *L. nodorum*, which originated from eight countries distributed among four geographical regions, were included in the study. Twenty isolates of *L. nodorum* originated from North America: from the United States 17 (Alabama 3, Florida 1, Georgia 1, Louisiana 1, and Montana 11) and three from Canada (Saskatchewan). Eight isolates originated from South America: Brazil 5, Chile 2, and Ecuador 1. Four isolates originated from Europe: The Netherlands 3, and Portugal 1. One isolate of *L. nodorum* was secured from Tanzania in East Africa. Isolate MTN 82-37 of *L. nodorum* which was obtained from winter wheat at Sidney, MT, served as a constant check isolate in all trials.

**The host.** The same differential cultivar set was used in this study as that identified in our work with *M. graminicola* (3); it included accessions of spring and winter hexaploid wheats (*Triticum aestivum* L.), tetraploid durum wheats (*Triticum durum* L. var. *durum*), and triticales ( $\times$  Tritico-secale Wittmack). The choice of cultivars depended upon host response to both *L. nodorum* and *M. graminicola*. The susceptible hexaploid wheat cultivars, Fortuna (CI 13596) and Siete Cerros (also called 7C [CI 14493]), served as checks in all trials.

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Seeding, growing, and inoculation methods for seedlings were as previously described (2,3,14). The mean spore concentration per isolate per trial was adjusted within the range of  $4.0\text{--}5.0 \times 10^7$  pycnidiospores per milliliter. The percentage of necrotic seedling tissue was assessed for each leaf 15 days after inoculation. From 16 to 25 leaves of each cultivar were inoculated with each isolate of *L. nodorum*.

**Analysis of the data.** In the present study, the sequence of analysis was: testing for repeatability of methods, time effects

TABLE 1. Analysis of variance of mean necrotic leaf area of 33 isolates of *Leptosphaeria nodorum* and 38 wheat and triticale accessions

| Source               | Degrees of freedom | Mean square | P      |
|----------------------|--------------------|-------------|--------|
| Cultivars            | 37                 | 174,024.9   | <0.001 |
| Isolates             | 32                 | 47,716.2    | <0.001 |
| Cultivars × Isolates | 1,184              | 1,697.2     | 0.126  |
| Residual             | 627                | 1,565.2     |        |

TABLE 2. Cultivar response to 33 isolates of *Leptosphaeria nodorum* secured from eight countries<sup>a</sup>

| Wheat type and cultivar          | Mean necrosis ± standard error <sup>b</sup> (%) | Hypothetical genes (no.) |
|----------------------------------|-------------------------------------------------|--------------------------|
| <b>Hexaploid spring wheats:</b>  |                                                 |                          |
| Frontana                         | 9.2 ± 0.6                                       | 7                        |
| Bobwhite "S"                     | 12.7 ± 2.8                                      | 5                        |
| ZN-157                           | 13.3 ± 3.1                                      | 5                        |
| DH-5                             | 14.5 ± 3.3                                      | 5                        |
| Kavkaz (KVZ)/7 C                 | 14.6 ± 3.2                                      | 3                        |
| Miriam                           | 15.5 ± 3.6                                      | 6                        |
| KVZ-K4500.L.A.4                  | 16.1 ± 3.4                                      | 5                        |
| Colotana                         | 16.1 ± 3.8                                      | 5                        |
| Olaf                             | 20.3 ± 4.3                                      | 4                        |
| Titan                            | 21.8 ± 5.2                                      | 3                        |
| Lakhish                          | 22.1 ± 4.6                                      | 3                        |
| H574-1-2-6                       | 26.3 ± 5.2                                      | 2                        |
| Anza                             | 30.0 ± 5.9                                      | 3                        |
| Siete Cerros (susceptible check) | 41.3 ± 7.6                                      | 1                        |
| Fortuna (susceptible check)      | 55.0 ± 10.0                                     | 0                        |
| <b>Hexaploid winter wheats:</b>  |                                                 |                          |
| JCR-979                          | 3.9 ± 0.8                                       |                          |
| 81UWWMN 2095                     | 6.0 ± 1.7                                       | 14                       |
| Red Chief                        | 7.1 ± 1.7                                       | 19                       |
| MTN 71-8-10                      | 7.4 ± 2.2                                       | 13                       |
| MTN 72-11-9                      | 9.0 ± 2.2                                       | 11                       |
| Yamhill                          | 9.2 ± 2.0                                       | 14                       |
| EA-7                             | 9.3 ± 2.4                                       | 7                        |
| 81UWWMN 2024                     | 9.3 ± 2.1                                       | 11                       |
| DQ-12                            | 9.7 ± 0.2                                       | 6                        |
| Weibull 7389                     | 12.7 ± 3.0                                      | 3                        |
| Aurora                           | 16.1 ± 4.3                                      | 2                        |
| W 101                            | 16.2 ± 3.5                                      | 2                        |
| KVZ                              | 24.6 ± 5.0                                      | 2                        |
| Bezostaya 1                      | 24.7 ± 4.8                                      | 3                        |
| Wampum (susceptible check)       | 41.3 ± 7.5                                      | 1                        |
| <b>Tetraploid wheats:</b>        |                                                 |                          |
| VOC 447                          | 12.2 ± 2.8                                      | 7                        |
| Nursit 163                       | 12.6 ± 3.7                                      | 3                        |
| Zenati Bouteille                 | 16.4 ± 4.8                                      | 3                        |
| Rolette                          | 17.8 ± 4.1                                      | 5                        |
| Ward                             | 18.0 ± 3.9                                      | 4                        |
| Etit 38                          | 26.0 ± 5.2                                      | 3                        |
| <b>Triticales:</b>               |                                                 |                          |
| DU-75                            | 4.7 ± 1.6                                       | 17                       |
| Beagle                           | 14.1 ± 3.1                                      | 6                        |
| Mapache                          | 16.5 ± 3.8                                      | 4                        |

<sup>a</sup> Cutpoint between resistant and susceptible responses was placed at 17.94% necrosis.

<sup>b</sup> Mean percent necrosis derived from 27 isolates of *L. nodorum*.

(environment) on host response, and isolate consistency; classifying the cultivars into two groups (resistant and susceptible); and establishing virulence frequencies (assuming a gene-for-gene relationship). Details concerning the techniques and computer programs are given elsewhere (3).

**Host response to *M. graminicola* and *L. nodorum*.** Relationship between the responses (percent necrosis) of 42 wheat and triticale accessions to 37 isolates of *M. graminicola* and 33 isolates of *L. nodorum* was assessed by using a linear regression analysis (3).

## RESULTS

**Host-parasite interactions.** The wheat and triticale accessions used in this study are shown in Table 1 of our previous paper (3). Analysis of variance of the isolates × cultivars matrix (33 isolates of *L. nodorum* × 38 wheat and triticale accessions) indicated significant isolate and cultivar effects, but a nonsignificant interaction between them (Table 1).

**Cultivar classification.** As described in (3), an initial cutpoint was calculated as the median of the set of values for the two intermediate response groups (moderately resistant and moderately susceptible) as obtained from a cluster analysis based on six groups. For the present data, the value was 26.0%. A standard error of 8.1%, obtained from the two-way analysis of variance, was associated with the initial cutpoint. The final cutpoint chosen was 26.0 – 8.1 or 17.9%.

**Virulence frequencies.** Virulence frequencies were estimated by using the DIFFER and GENEALOGY computer programs (3,5,6)

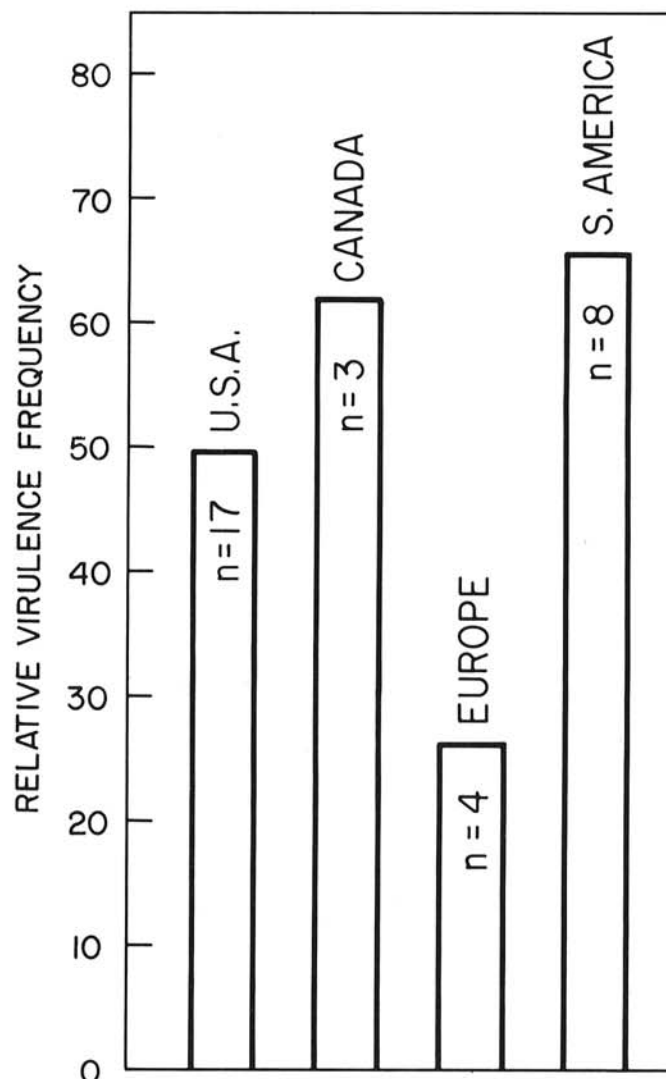


Fig. 1. Relative virulence frequency of *Leptosphaeria nodorum* in four geographic regions (n = number of isolates of *L. nodorum*).

which (assuming a gene-for-gene relationship) estimate the minimum number of genes. The gene-for-gene analysis hypothesized 21 different interacting genes in the matrix of 33 isolates of *L. nodorum* × 38 cultivars (Table 2). Hypothetical genes were assigned to the winter wheats, Red Chief (CI 12109), Yamhill (CI 14563), 81UWWMN 2095 (Maris Huntsman//VPM/Moisson), and MTN 71-8-10 (CI 12752/CI 13554). The triticale line DU-75 was estimated to possess 17 hypothetical genes affecting resistance to *L. nodorum*. The winter wheat accession JCR-979 (CI 16906) could not be assigned any genes since it was highly resistant to all isolates of *L. nodorum* tested in the study.

The tetraploid line VOC 447 (LD 393/2/Langdon/ND 58-322) and the spring wheat, Frontana (CI 12470) each were assigned seven hypothetical genes for resistance. The number of assigned genes for resistance to *L. nodorum* in winter hexaploid wheat accessions was markedly higher than the number of hypothetical genes assigned to spring hexaploid and tetraploid wheats and to the triticale (with the exception of DU-75) accessions used in the study.

The 21 hypothetical genes for resistance (designated SN1 to SN21) to *L. nodorum* derived from analysis of the 33-isolate × 38-cultivar matrix were best estimated by 11 of the cultivars from Table 3 as follows: 4574-1-2-6 (SN3 + SN18), Olaf (SN1 + SN4 + SN11 + SN18), Colotana (SN1 + SN2 + SN5 + SN11 + SN18), Bezostaya 1 (SN1 + SN6 + SN18), Etit 38 (SN1 + SN10 + SN18), Lakhish (SN1 + SN12 + SN18), Rolette (SN1 + SN2 + SN6 + SN13 + SN18), PAT 19 (SN1 + SN2 + SN11 + SN14 + SN18), Beagle (SN1 + SN2 + SN11 + SN12 + SN15 + SN18), KVZ/7C (SN1 + SN16 + SN18), and TAM W101 (SN17 + SN18).

The susceptible wheat cultivars, Wampum and Siete Cerros, were assigned the single resistance genes SN1 and SN18, respectively.

The relative virulence per isolate of *L. nodorum* was calculated by dividing the total number of compatible (susceptible) host reactions per region, state, or country by the corresponding number of isolates of *L. nodorum*. The relative virulence of the South American isolates of *L. nodorum* was similar to that of the Canadian isolates and higher than that of the United States isolates (Fig. 1). The populations of *L. nodorum* from the three regions

(United States, Canada, and South America) were markedly more virulent than the European isolates that were tested.

Within the United States, the isolates of *L. nodorum* from Florida and Alabama were more virulent than the isolates secured from Montana and Georgia (Fig. 2). The isolates from Saskatchewan were highly virulent and were similar to the isolates secured from Tanzania. The isolates from Portugal and The Netherlands possessed relatively low virulence. The isolates of *L. nodorum* from Ecuador, Brazil, and Chile exhibited high virulence.

The frequency and distribution of hypothetical specific genes for virulence (designated VSN1 to VSN21) for each of the regions,

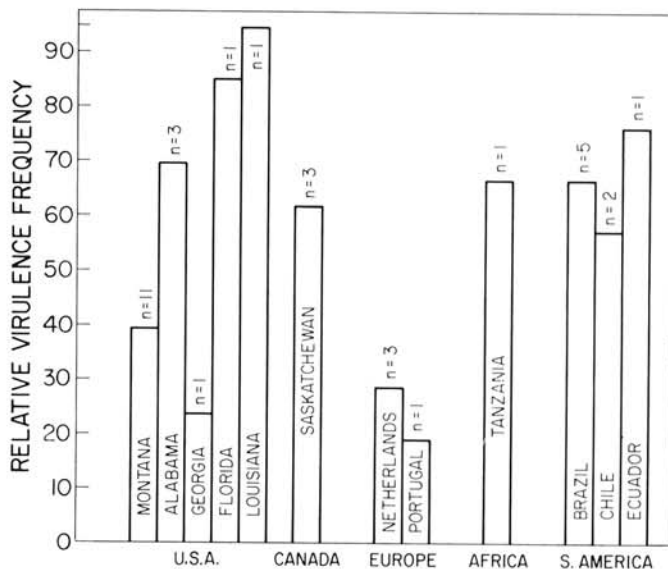


Fig. 2. Relative virulence frequency of 33 isolates of *Leptosphaeria nodorum* secured from states and countries in five geographic regions ( $n$  = number of isolates of *L. nodorum*).

TABLE 3. Hypothetical resistance genes derived from analysis of a reaction matrix between 33 isolates of *Leptosphaeria nodorum* and 25 isolates of hexaploid wheat, tetraploid wheat, and triticale

| Cultivars        | Hypothetical resistance genes, SN |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
|------------------|-----------------------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|
|                  | 1                                 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
| Wampum           | +                                 |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| MD55-114-3       |                                   | + |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| H574-1-2-6       |                                   |   | + |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| Olaf             | +                                 |   |   | + |   |   |   |   |   |    | +  |    |    |    |    |    |    |    |    |    |    |
| Colotana         | +                                 | + |   |   | + |   |   |   |   |    | +  |    |    |    |    |    |    |    |    |    |    |
| Bezostaya 1      | +                                 |   |   |   |   | + |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| NC 74-31         | +                                 |   |   |   |   |   | + |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| Zenati Bouteille | +                                 | + |   |   |   |   |   | + |   |    |    |    |    |    |    |    |    |    |    |    |    |
| Titan            | +                                 |   |   |   |   |   |   |   | + |    |    |    |    |    |    |    |    |    |    |    |    |
| Etit 38          | +                                 |   |   |   |   |   |   |   |   | +  |    |    |    |    |    |    |    |    |    |    |    |
| Lakhish          | +                                 |   |   |   |   |   |   |   |   |    |    |    | +  |    |    |    |    |    |    |    |    |
| Rolette          | +                                 | + |   |   |   | + |   |   |   |    |    |    |    | +  |    |    |    |    |    |    |    |
| PAT 19           | +                                 | + |   |   |   |   |   |   |   |    |    |    |    |    | +  |    |    |    |    |    |    |
| Beagle           | +                                 | + |   |   |   |   |   |   |   |    |    |    |    | +  |    |    |    |    |    |    |    |
| Kavkaz (KVZ)/7C  | +                                 |   |   |   |   |   |   |   |   |    | +  | +  |    |    | +  |    |    |    |    |    |    |
| Tam W 101        |                                   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    | +  | +  |    |    |
| Siete Cerros     |                                   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |
| ZN-157           | +                                 |   |   | + |   |   |   |   |   |    | +  |    |    |    |    |    |    |    |    |    |    |
| DU-75            | +                                 | + | + | + | + | + | + | + | + | +  | +  | +  |    | +  |    | +  | +  | +  | +  | +  |    |
| Yamhill          | +                                 | + | + |   | + | + |   | + | + | +  | +  | +  | +  |    |    |    |    | +  | +  |    | +  |
| 81UWWMN 2095     | +                                 | + | + |   | + | + |   | + | + | +  | +  | +  | +  |    |    |    |    | +  | +  |    | +  |
| KVZ              | +                                 |   |   |   |   | + |   |   |   |    |    |    |    |    |    |    |    |    |    |    | +  |
| Frontana         | +                                 | + |   |   | + | + |   |   |   |    | +  |    |    | +  |    |    |    |    |    |    | +  |
| Bobwhite "S"     | +                                 | + | + |   |   | + |   |   |   |    |    |    |    |    |    |    |    |    |    |    | +  |
| Red Chief        | +                                 | + | + | + | + | + | + | + | + | +  | +  | +  | +  | +  |    | +  | +  | +  | +  | +  | +  |

countries, and states are given in Table 4. The frequency of VSN1 and VSN18 (from Wampum and Siete Cerros, respectively) is uniformly high. The frequency of virulence of Kavkaz (KVZ) (VSN1 + VSN6) is rather high.

Only a few isolates from the United States, Canada, and Brazil possess genes VSN20 and VSN21, which have the lowest virulence frequency and distribution. The corresponding genes for resistance (SN20 and SN21) were detected in the highly resistant cultivars, Red Chief and Yamhill (SN20), and in 81UWWMN 2095 (SN21).

The relationship between the number of the hypothetical corresponding genes and host response (percent necrosis) is presented in Fig. 3. The linear equation  $\log \text{ percent necrosis} = 1.46 - 0.05 \text{ number of hypothetical genes}$  was highly significant ( $R^2 = 0.76^{**}$ ).

**Relationship between *L. nodorum* and *M. graminicola*.** The host response of 42 wheat and triticale accessions to 33 isolates of *L. nodorum* and to 97 isolates of *M. graminicola* secured worldwide is presented in Table 5. Resistant host response to *L. nodorum* was

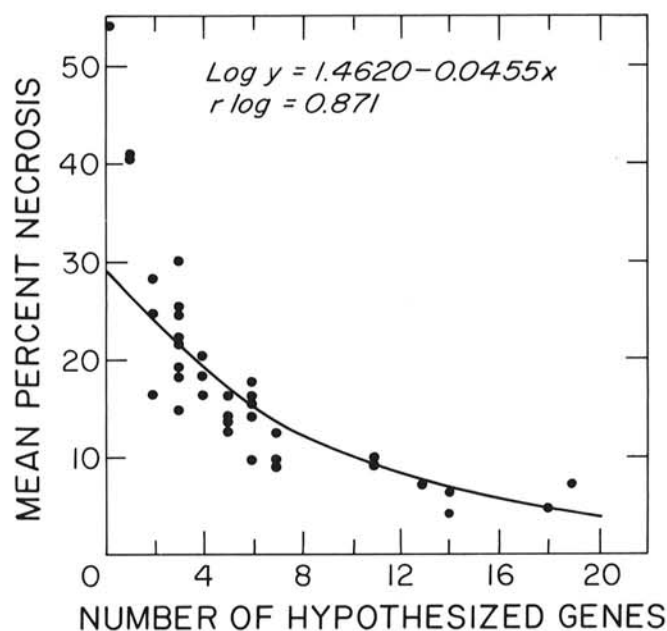


Fig. 3. The relationship between the numbers of hypothesized corresponding genes for resistance and measured host response.

calculated to be  $\leq 17.9\%$  necrosis, and that to *M. graminicola* to be  $\leq 16.6\%$  necrosis. In Table 5, only the resistant and some susceptible lines of the 38 accessions are presented. Cultivars DU-75 (triticale), JCR-979 (winter hexaploid wheat), MTN 71-8-11 (winter hexaploid wheat), and Bobwhite "S" (spring hexaploid wheat) expressed low seedling necrosis in response to infection by populations of both pathogens.

The linear relationship between seedling host response to *L. nodorum* and *M. graminicola* in the 38 tested accessions is presented in Fig. 4. The relationship between seedling host response is highly significant ( $R^2 = 0.656^{**}$ ); however, while certain wheats and triticale accessions expressed low percent necrosis in response to infection by both pathogens, some accessions were resistant to one and not to the other, or susceptible to both.

## DISCUSSION

The supposition, though experimentally unproven, was that a gene-for-gene relationship is operative in *L. nodorum* and wheat. Extension of this idea would require placing host responses into two distinct categories: resistant and susceptible. A statistical

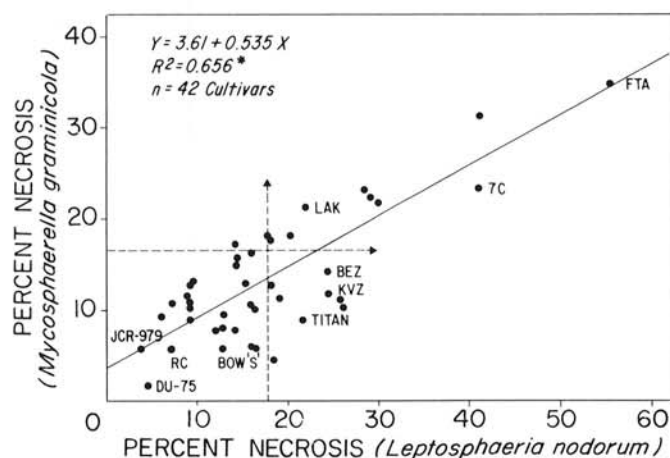


Fig. 4. The relationship between host response (percent necrosis) of 42 cultivars to populations of *Leptosphaeria nodorum* and *Mycosphaerella graminicola*: DU-75 (triticale); RC = Red Chief; Bow "S" = (Bobwhite "S"); 2024 = (81UWWMN 2024); 2095 = (81UWWMN 2095); MTN 81-8-11; AUR = (Aurora); KVZ = (Kavkaz); Bez = (Bezostaya 1); LAK = (Lakhish); 7C = (Siete Cerros); and FTA = (Fortuna).

TABLE 4. The relative frequency of hypothetical virulence genes in isolates of *Leptosphaeria nodorum* among regions and within countries and states

| Source of Isolates | Isolates (no.) | Hypothetical virulence genes, VSN |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
|--------------------|----------------|-----------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
|                    |                | 1                                 | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
| United States      | 17             | 51 <sup>a</sup>                   | 39 | 36 | 27 | 33 | 30 | 21 | 24 | 24 | 27 | 33 | 27 | 24 | 12 | 12 | 21 | 18 | 49 | 15 | 6  | 6  |
| Alabama            | 3              | 18 <sup>b</sup>                   | 12 | 18 | 12 | 12 | 12 | 18 | 12 | 18 | 18 | 12 | 18 | 6  | 6  | 12 | 12 | 12 | 18 | 12 | 0  | 6  |
| Florida            | 1              | 6                                 | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  |
| Georgia            | 1              | 6                                 | 6  | 6  | 6  | 0  | 0  | 0  | 0  | 0  | 0  | 6  | 6  | 6  | 0  | 0  | 0  | 0  | 6  | 0  | 0  | 0  |
| Louisiana          | 1              | 6                                 | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 6  | 0  |
| Montana            | 1              | 65                                | 47 | 35 | 29 | 41 | 35 | 18 | 23 | 18 | 23 | 35 | 23 | 29 | 12 | 6  | 18 | 12 | 54 | 6  | 0  | 0  |
| Canada             | 3              | 9                                 | 9  | 6  | 0  | 9  | 9  | 3  | 6  | 6  | 3  | 9  | 6  | 9  | 9  | 6  | 0  | 3  | 9  | 0  | 3  | 3  |
| Saskatchewan       | 3              | 9                                 | 9  | 6  | 0  | 9  | 9  | 3  | 6  | 6  | 3  | 9  | 6  | 9  | 9  | 6  | 0  | 3  | 9  | 0  | 3  | 3  |
| Europe             | 4              | 9                                 | 3  | 6  | 0  | 3  | 0  | 6  | 0  | 6  | 9  | 6  | 3  | 0  | 0  | 0  | 0  | 3  | 12 | 0  | 0  | 0  |
| Netherlands        | 3              | 75                                | 0  | 25 | 0  | 25 | 0  | 50 | 0  | 50 | 75 | 50 | 25 | 0  | 0  | 0  | 0  | 0  | 75 | 0  | 0  | 0  |
| Portugal           | 1              | 0                                 | 25 | 25 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 25 | 25 | 0  | 0  | 0  |
| Africa             | 1              | 3                                 | 3  | 3  | 3  | 0  | 3  | 3  | 3  | 3  | 3  | 3  | 3  | 0  | 0  | 0  | 3  | 3  | 3  | 0  | 0  | 0  |
| Tanzania           | 1              | 3                                 | 3  | 3  | 3  | 0  | 3  | 3  | 3  | 3  | 3  | 3  | 3  | 0  | 0  | 0  | 3  | 3  | 3  | 0  | 0  | 0  |
| South America      | 8              | 24                                | 21 | 15 | 24 | 21 | 21 | 12 | 15 | 6  | 21 | 24 | 21 | 12 | 15 | 15 | 6  | 15 | 24 | 15 | 3  | 3  |
| Brazil             | 5              | 62                                | 50 | 38 | 62 | 50 | 50 | 50 | 38 | 25 | 50 | 62 | 50 | 25 | 38 | 25 | 12 | 50 | 62 | 50 | 12 | 12 |
| Chile              | 2              | 25                                | 25 | 12 | 25 | 25 | 25 | 0  | 12 | 0  | 25 | 25 | 25 | 12 | 12 | 12 | 0  | 25 | 0  | 0  | 0  | 0  |
| Ecuador            | 1              | 12                                | 12 | 12 | 12 | 12 | 12 | 0  | 12 | 0  | 12 | 12 | 12 | 12 | 12 | 12 | 0  | 12 | 12 | 12 | 0  | 0  |
| Total              | 33             | 97                                | 76 | 67 | 54 | 67 | 64 | 45 | 48 | 45 | 64 | 76 | 61 | 45 | 36 | 36 | 30 | 42 | 97 | 30 | 12 | 12 |

<sup>a</sup>Number of compatible interactions per region divided by total number of isolates of *L. nodorum*.

<sup>b</sup>Number of compatible interactions per country divided by number of total isolates per region.



procedure developed for *Septoria tritici* blotch of wheat (3) was used in the analysis of the host response to isolates of *L. nodorum* secured from eight countries. In a previous study, Scharen and Eyal (15) used a multiple range test to distinguish among host response classes. Thus, the classification of host response into resistant and susceptible groups is dependent on the outcome of the multiple range test and difficulties may be encountered if the range is subdivided into many significance groups. The cutpoint between resistant and susceptible host response in the Scharen and Eyal study (15) was found to be about 25% necrosis. That cutpoint differs from the cutpoint calculated in the present study (about 18% necrosis). The use of different procedures to differentiate between two response classes (resistant and susceptible) may thus result in different cutpoint values. Yet, it is rather interesting that the work presented here and in the previous report (15) resulted in cutpoints of 18 and 25%, respectively, which are rather similar. In the future, researchers working with these diseases might consider using a single differentiating value within the range of 18–25% necrosis. In the previous study, no attempt was made to analyze the isolate × cultivar matrix as was done in the present study by using a gene-for-gene analysis program. The assignment of 21 different hypothetical interacting genes to the 33-isolate × 38-cultivar matrix may be partly due to the size of the matrix. Unlike the studies on *M. graminicola* (3,18), many of the accessions and isolates of *L. nodorum* were assigned a complex gene profile rather than a single gene, or only a few genes (3). The differences in percent necrosis between cultivars were not large, and any small variation caused assignment of a different gene. The large number of assigned genes for virulence may be due to the assignment of a differentiating value, which is the core of the analytical procedure, and assumption that the gene-for-gene system is operative.

Single and oligogenic control of resistance to *L. nodorum* was reported by several investigators (17). Mullaney et al (7) reported seedling resistance to be polygenic and that it could be explained by additive gene effects. Nelson and Gates (9) reported that resistance to *L. nodorum* was inherited in a very complex manner and that several genes may be involved. Although different isolates of *L. nodorum* and different wheat cultivars were used in the present study, the matrix analysis hypothesized several genes in the highly resistant cultivars (Table 2). The hypothetical genes were used to calculate overall virulence frequencies and geographical distribution of virulence. Owing to limitations in sampling of the pathogen and selection of cultivars, results of the present study provide an insight into virulence patterns rather than an exhaustive virulence survey.

The relative frequency of hypothetical genes for resistance varied rather markedly among the regions, countries, and states. The relative frequency of several hypothetical genes for virulence was low in certain locations. Isolates of *L. nodorum* from the United States expressed a wide spectrum of virulence, with VSN20 and VSN21 being the lowest. Similarly, virulence patterns were revealed in the South American populations of *L. nodorum*, with the addition of VSN9 and VSN16.

All the lines derived from cultivar Kavkaz possessed the hypothetical resistance genes SN1 and SN6. The relative frequency of the corresponding hypothetical virulence genes (VSN1 and VSN6) was rather high in most regions except Europe and Africa.

The relationship between the number of hypothetical corresponding genes and host response of the 38 accessions was best expressed by a transformed linear function (log percent necrosis = intercept + regression coefficient × number of hypothetical genes). The logarithmic relationship suggests that the quantitative host response may be affected by differential gene interactions that are not necessarily arithmetic (10). The action of these supposed polygenes controlling quantitative host response may not be additive, but multiplicative or geometric (9).

Some cultivars responded more readily (tissue collapse or its retardation) than others to the same isolate of *L. nodorum* (Fortuna and Red Chief). A consequence of the multiplicative gene action is that values in a segregating population (although such populations were not used here) may not follow a normal probability distribution (4).

TABLE 5. Cultivars resistant to 33 isolates of *Leptosphaeria nodorum* and 97 isolates of *Mycosphaerella graminicola*<sup>a</sup>

| Cultivar     | Class <sup>b</sup> | Mean necrosis (%) |                       | Response <sup>c</sup> |
|--------------|--------------------|-------------------|-----------------------|-----------------------|
|              |                    | <i>L. nodorum</i> | <i>M. graminicola</i> |                       |
| DU-75        | TCL                | 4.7               | 1.9                   | 3.3                   |
| JCR-979      | WBW                | 3.9               | 5.8                   | 4.8                   |
| Red Chief    | WBW                | 7.1               | 5.6                   | 6.3                   |
| 81UWWMN 2095 | WBW                | 6.0               | 9.4                   | 7.7                   |
| MTN 71-8-11  | WBW                | 7.4               | 10.6                  | 9.0                   |
| Bobwhite "S" | SBW                | 12.7              | 5.8                   | 9.2                   |
| 81UWWMN 2024 | WBW                | 9.3               | 9.2                   | 9.2                   |
| Frontana     | SBW                | 9.2               | 10.1                  | 9.7                   |
| VOC 447      | SDW                | 12.2              | 7.7                   | 10.0                  |
| Weibull 7389 | WBW                | 12.7              | 7.8                   | 10.2                  |
| EA-7         | WBW                | 9.3               | 11.2                  | 10.3                  |
| MTN 72-11-9  | WBW                | 9.0               | 11.9                  | 10.5                  |
| Beagle       | TCL                | 14.1              | 7.6                   | 10.9                  |
| Yamhill      | WBW                | 9.2               | 13.0                  | 11.1                  |
| Bet Lehem    | SBW                | 12.7              | 7.8                   | 11.3                  |
| PAT 19       | SBW                | 9.7               | 13.0                  | 11.4                  |
| ZN-157       | SBW                | 13.3              | 9.5                   | 11.4                  |
| Kavkaz (KVZ) |                    |                   |                       |                       |
| K4500.L.A.4  | SBW                | 16.1              | 6.9                   | 11.5                  |
| Mapache      | TCL                | 16.5              | 6.7                   | 11.6                  |
| Aurora       | WBW                | 16.1              | 10.1                  | 13.1                  |
| Titan        | SBW                | 21.8              | 9.1                   | 15.5                  |
| KVZ          | WBW                | 24.6              | 11.9                  | 18.2                  |
| Bezostaya 1  | WBW                | 24.7              | 14.3                  | 19.5                  |
| Siete Cerros | SBW                | 41.3              | 23.7                  | 32.5                  |
| Wampum       | WBW                | 41.3              | 31.1                  | 36.2                  |
| Fortuna      | SBW                | 55.9              | 35.0                  | 45.4                  |

<sup>a</sup>Seedling response to *L. nodorum* and *M. graminicola*.

<sup>b</sup>Cultivar class: TCL = triticale, WBW = winter bread wheat, SBW = spring bread wheat; and SDW = spring durum wheat.

<sup>c</sup>Cutpoint between resistant and susceptible response as follows: *L. nodorum* equal to or less than 17.9% necrosis; *M. graminicola* equal to or less than 16.6% necrosis.

In previous studies (15), the comparison between cultivar responses to *L. nodorum* and *M. graminicola* was based on two different assessment methods (percent leaf surface covered by pycnidia of *M. graminicola*, and percent necrosis caused by *L. nodorum*). These two disease assessment parameters were not strongly associated. In the present study, the relationship between host responses was based on percent leaf necrosis for both *L. nodorum* and *M. graminicola* and the association between the 42 selected cultivars was much stronger ( $R^2 = 0.656^{**}$ ).

The wheat and triticale accessions were selected among cultivars previously recorded as resistant to either one or both of the pathogens. This relationship might not hold true if cultivars were randomly selected from diverse populations of cultivars. The apparent high level of resistance expressed by some cultivars to the two major *Septoria* diseases of wheat to a wide virulence spectrum should be tested further. Utilization of these resistant cultivars in breeding for resistance programs should be encouraged. Strategies for incorporation and accumulation and future deployment of the resistance genes identified here need to be developed.

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