Euphytica 38: 31–37 (1988)

Diallel analysis of resistance to *Septoria tritici* isolates in durum wheat

M. van Ginkel[1] & A.L. Scharen[2]
[1] *CIMMYT, Apartado postal 6-641, Mexico;* [2] *USA, ARS, Department of Plant Pathology, Montana State University, Bozeman, MT 59717 – 0002, USA*

Received 24 March 1987; accepted 7 May 1987

Key words: Triticum durum, durum wheat, *Septoria tritici,* resistance, diallel analysis

Summary

All crosses, except for reciprocals, were made among ten cultivars originating from crop improvement programs in North Africa and the Middle East. The entries varied widely in reaction to *Septoria tritici.* F_1 and F_2 progenies of the crosses were evaluated using eight *S. tritici* isolates from seven countries in the Mediterranean area. Thus, sixteen separate combining ability analyses were excecuted. General combining ability (GCA) was the major component of variation, although specific combining ability (SCA) was present in most cases. Additive variance thus appears to be of predominant importance. Nevertheless, non-additive variance may interfere when line selection in a breeding program is practiced. While differing greatly among cultivars, specific GCA effects for each cultivar separately were of similar magnitude for all isolates. Ranking statistics determined that cultivars were ranked in similar order for both means and specific GCA effects independent of the isolate used. Different isolates may therefore interact with similar or identical genetically controlled mechanisms in a particular cultivar. This could indicate the absence of differential gene-for-gene relationships and suggests that isolates vary in aggressiveness rather than in virulence.

Introduction

Mycosphaerella graminicola (Fückel) Schroeter, (anamorph, *Septoria tritici* Rob. ex Desm.) is a pathogen of wheat and causes septoria tritici blotch. Under natural conditions, it can lead to yield losses as high as 60 percent (Eyal, 1972; Shipton et al., 1971). It can infect all above ground parts of the plant, although the symptoms and signs are usually confined to the foliage. Root production may also be affected (Gough, 1976). In the last twenty-five years, regional epidemics especially in the Mediterranean basin, have made resistance to *S. tritici* an important criterion in national breeding programs (Dubin & Rajaram, 1981; Eyal, 1972; Krupinsky et al., 1977; Saari, 1974).

Although the increase in disease occurrence and infections have to a large extent affected the durum wheat germplasm in the Mediterranean region, most of the research on the inheritance of resistance has been limited to the bread wheats, *Triticum aestivum* spp. In certain countries in North Africa and the Middle East bordering the Mediterranean Sea, more than 70% of the wheat area may be devoted to the cultivation of durum wheat.

Most of the field and greenhouse experiments on *Septoria tritici* have concentrated on the study of presumed major genes. Often a single isolate or a

Cooperative investigations of the Agricultural Research Service, U.S. Department of Agriculture and the Montana Agricultural Experiment Station, Journal Paper #1950. Partially supported by grant No. I269-81 from BARD.

bulk collection of *S. tritici* isolates have been used for inoculation. The importance of utilizing various isolates separately has become especially important since a report of physiologic specialization in *S. tritici* was published by Eyal et al. (1973), bearing clear implications for breeding research (Eyal, 1981).

The objective of this research was to quantify genetic components of resistance in durum wheat to various distinct isolates of *S. tritici* in the practically relevant terms of additive and non-additive variance.

Materials and methods

The host

Dr. H. Ketata, at the time working with INAT, Tunisia, supplied us with seed of durum wheat entries considered of value to the local crop improvement program. Several of these cultivars are also used in other breeding programs in the Mediterranean region. The following germplasm was selected, representing various levels of resistance to *S. tritici,* yielding ability, agronomic quality, regional adaptability and combining ability: Kyperounda, Badri, BD 2131, BD 2127, 65150-Lds, D75-9-6B-5B-4B-10B, D75-40-11B-4B-2B, Ben Bechir 79, Karim 80, and Maghrebi 72. All possible single crosses were made among the ten cultivars, excluding reciprocals. Subsequently, F_2 generations were obtained.

The pathogen

Eight isolates were selected from seven countries in the Mediterranean region, including the Iberian Peninsula: Tunisia (TUN 8202 and TUN 8204-1), Turkey (TKY 8201), Israel (ISR 80-8), Syria (SYR 8209), Portugal (POR 81199-1), Italy (ITL 82024) and Spain (SPN 81299). The isolates were obtained by mass spore transfer from a single pycnidium, cultured on solid yeast-malt agar and increased in liquid yeast extract medium for inoculation purposes, according to Krupinsky (1976).

Disease assessment

Each entry was represented by four F_2 seedlings per replication. The seeds of cross progenies and the ten parent cultivars were planted in square $21 \times 21 \times 6$ cm aluminum trays. Ten days after planting, the seedlings had developed fully extended first leaves and partially emerged second leaves. The seedlings were then inoculated with a suspension containing 10^7 spores/ml using the quantitative method described by Eyal & Scharen (1977). The disease symptoms were visually assessed three weeks after inoculation as percentage necrotic tissue of the total leaf area, according to Eyal & Scharen (1977).

A total of twelve replications was run for the diallel analysis involving a single *S. tritici* isolate. A separate set of such trials was executed for each of the eight selected isolates. In the case of isolate TUN 8204-1, the number of seedlings assessed in the trials was twenty per each of six replications, since that particular experiment was part of a dual purpose study (M. van Ginkel & A.L. Scharen, 1987a and b). One week after disease assessment, presence or absence of pycnidia on the individual F_2 seedlings in the trials with isolate TUN 8204-1 was recorded. The percentage of seedlings with pycnidia for twenty seedlings per cross per replication was calculated.

Similar diallel analyses were carried out on F_1 seedlings. Each of the fifty-five entries, crosses and parental cultivars, was represented by two seedlings and the experiment replicated four times. Again, eight separate sets of trials were executed using the individual *S. tritici* isolates. The trial involving isolate TUN 8204-1 was replicated six times with five seedlings per replication.

Statistical analyses

Means were calculated per generation per replication and used in the analyses of variance. Overall means of all replications involved were used in multiple regression analyses to determine the general combining ability (GCA), specific combining ability (SCA) and other variance components, and

the individual combining ability effects, according to Analysis III by Gardner & Eberhart (1966).

The relative importance of GCA and SCA was studied by calculating ratios of relevant mean squares and sums of squares, as suggested by Baker (1978) and Auld et al. (1983):

Baker: $2\ MS_{GCA}/(2\ MS_{GCA} + MS_{SCA})$

Auld et al.: $SS_{GCA}/(SS_{GCA} + SS_{SCA})$.

Ranking of the cultivars for mean performance and GCA effects by isolates was tested using the Friedman test statistics and Kendall's coefficient of concordance between *S. tritici* isolates. Similarly, the SCA effects of the forty-five crosses in the 10×10 diallel were tested for possible systematic ranking by the eight isolates.

Results

The analyses of variance for combining abilities, listing mean squares, levels of significance and relative importance of GCA and SCA for the individual isolates are presented in Table 1 for the F_2 data and in Table 2 for the F_1 data.

Table 1. Analyses of variance for combining ability of a 10×10 diallel of durum wheat cultivars (based on F_2 seedling data) inoculated with eight selected *S. tritici* isolates.

Source	df	Isolate code					
		TUN 8202 MS[1]	TKY 8201 MS	ISR 80-8 MS	SYR 8209 MS	POR 81199-1 MS	ITL 82024 MS
Entries	54	7057.9***	4200.4***	7383.8***	5749.5***	5100.6***	3615.6***
Parents	9	9630.0***	6576.1***	13482.7***	9478.5***	7597.9***	5138.1***
Parents vs. Crosses	1	1650.4*	1476.4	157.5	442.2	38.0	1195.1
Crosses	44	6652.0***	3761.2***	6302.0***	5097.2***	4704.0***	3354.7***
GCA	9	27917.2***	15002.0***	27278.1***	20763.5***	20028.7***	13605.3***
SCA	35	1180.4***	851.5***	910.0***	1055.7***	762.3***	713.0**
Relative importance of GCA and SCA:							
(a) $2MS_{GCA}/(2MS_{GCA} + MS_{SCA})^2$		0.98	0.97	0.98	0.98	0.98	0.97
(b) $SS_{GCA}/(SS_{GCA} + SS_{SCA})^3$		0.86	0.82	0.89	0.83	0.87	0.83

Source	df	Isolate code		
		SPN 81299 MS	TUN 8204-1 MS	(pycnidia) TUN 8204-1 MS
Entries	54	1721.2***	1144.2***	314.5*
Parents	9	2097.2***	1320.6***	310.8
Parents vs. Crosses	1	144.0	1.0	209.2
Crosses	44	1669.8***	1137.9***	319.7*
GCA	9	5501.0***	4422.9***	839.8***
SCA	35	671.5*	297.9	188.5
Relative importance of GCA and SCA:				
(a) $2MS_{GCA}/(2MS_{GCA} + MS_{SCA})^2$		0.94	0.97	0.90
(b) $SS_{GCA}/(SS_{GCA} + SS_{SCA})^3$		0.68	0.79	0.53

*, **, *** = Significant at the 0.05, 0.01, and 0.005 level of probability, respectively.

[1] MS = Mean Squares.

[2] Ratio suggested by Baker (1978).

[3] Ratio suggested by Auld et al. (1983).

Mean cultivar performance, specific GCA effects and their standard errors are presented in Table 3 for the F_2 seedlings and in Table 4 for the F_1 data. Differences among parents and among crosses were highly significant in almost every case. For one and three isolates respectively, significance was indicated at the five percent level for the parents versus crosses component in the F_2 and F_1 analyses. Friedman test statistics were highly significant for systematic ranking of cultivar means by the eight isolates and Kendall's coefficient of concordance was respectively 0.86 and 0.85 for the F_2 and F_1 data.

For all isolates, GCA was the major component of variation among crosses and was highly significant. Despite the minor importance of SCA, its presence could significantly be detected for seven out of eight *S. tritici* isolates in the F_2 analyses. Presumably, the decrease in number of replications used for the F_1 seedlings, four versus twelve for the F_2 seedlings, resulted in the inability to show consistently significant SCA's in the F_1 analyses.

The specific GCA effects of a particular cultivar were remarkably similar in size and sign for all isolates tested. The Friedman test statistics were highly significant and Kendall's coefficient of con-

Table 2. Analyses of variance for combining ability of a 10 × 10 diallel of durum wheat cultivars (based on F_1 seedling data) inoculated with eight selected *S. tritici* isolates.

Source	df	Isolate code					
		TUN 8202 MS[1]	TKY 8201 MS	ISR 80-8 MS	SYR 8209 MS	POR 81199-1 MS	ITL 82024 MS
Entries	54	1171.4***	1872.1***	2266.4***	2099.6***	3003.6***	1944.8***
Parents	9	2369.6***	2724.8***	1733.5***	1401.8	3493.3***	2199.2***
Parents vs. Crosses	1	1396.9	156.8	1034.5	7072.0***	70.4	611.4
Crosses	44	926.9***	1810.4***	2449.0***	2130.5***	2978.1***	1940.3***
GCA	9	1942.7***	6776.7***	7093.1***	6965.0***	10335.0***	6502.4***
SCA	35	672.8	626.1	1312.2***	888.6	1096.4	788.8
Relative importance of GCA and SCA:							
(a) $2MS_{GCA}/(2MS_{GCA} + MS_{SCA})^2$		0.85	0.96	0.92	0.94	0.95	0.94
(b) $SS_{GCA}/(SS_{GCA} + SS_{SCA})^3$		0.43	0.74	0.58	0.67	0.71	0.68

Source	df	Isolate code	
		SPN 81299 MS	TUN 8204-1 MS
Entries	54	1900.9***	1576.0***
Parents	9	2242.0***	1320.6***
Parents vs. Crosses	1	2926.1*	4005.9***
Crosses	44	1812.2***	1571.0***
GCA	9	6240.7***	5977.2***
SCA	35	678.7	435.3
Relative importance of GCA and SCA:			
(a) $2MS_{GCA}/(2MS_{GCA} + MS_{SCA})^2$		0.95	0.96
(b) $SS_{GCA}/(SS_{GCA} + SS_{SCA})^3$		0.70	0.78

*, *** = Significant at the 0.05 and 0.005 level of probability, respectively.

[1] MS = Mean Squares.

[2] Ratio suggested by Baker (1978).

[3] Ratio suggested by Auld et al. (1983).

Table 3. Mean percentage necrotic leaf area of durum wheat cultivars and general combining ability (GCA) effects for reactions of F_2 seedlings to inoculation with eight selected *S. tritici* isolates.

Cultivar	Isolate code																	
	TUN 8202		TKY 8201		ISR 80-8		SYR 8209		POR 81199-1		ITL 82024		SPN 81299		TUN 8204-1		TUN 8204-1	
	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^2$	GCA effect	$\bar{x}^3$	GCA effect
Kyperounda	56	3.8	70	5.2	59	4.3	90	12.5	47	−5.2	56	−1.9	62	0.5	76	6.3	9	−2.5
Badri	99	22.5	84	14.9	90	24.2	79	17.0	81	15.0	61	13.1	81	8.5	98	7.6	17	−0.4
BD 2131	33	−18.1	28	−13.5	20	−17.6	42	−12.4	22	−18.4	18	−11.7	55	−7.2	62	−12.3	26	4.2
BD 2127	33	−11.6	34	−11.5	13	−18.4	21	−15.6	29	−12.6	20	−12.9	50	−11.6	63	−5.3	24	8.4
65150-Lds	96	24.7	92	21.0	96	24.1	99	21.9	94	20.5	78	22.6	87	11.4	99	16.3	23	1.1
D75-9-6B-5B-4B-10B	29	−9.2	44	−8.7	17	−9.4	54	−5.4	33	−7.1	41	−5.2	52	1.0	76	−6.0	6	−3.1
D75-40-11B-4B-2B	95	20.6	84	11.6	96	17.5	98	14.0	79	22.9	71	12.6	77	8.5	94	10.6	17	−1.5
Ben Bechir 79	54	−2.8	43	0	50	−0.2	50	−6.3	45	−0.7	35	−4.2	52	−2.8	81	−3.8	15	−2.9
Karim 80	34	−20.7	42	−12.2	30	−16.3	35	−16.8	30	−11.0	34	−8.0	60	−6.5	59	−11.0	20	0.9
Maghrebi 72	66	9.2	46	6.8	29	8.2	43	8.9	46	3.4	58	4.4	63	1.8	73	2.4	11	4.2
Standard error:	6.8	2.0	5.9	2.0	6.1	2.0	6.1	2.3	5.6	1.9	6.1	2.0	5.9	2.0	6.9	2.3	6.0	1.9

[1] Mean percentage necrotic leaf area (12 replications).
[2] Mean percentage necrotic leaf area (6 replications).
[3] Mean percentage of seedlings with pycnidia (6 replications).

Table 4. Mean percentage necrotic leaf area of durum wheat cultivars and general combining ability (GCA) effects for actions of F_1 seedlings to inoculation with eight selected *S. tritici* isolates.

Cultivar	Isolate code															
	TUN 8202		TKY 8201		ISR 80-8		SYR 8209		POR 81199-1		ITL 82024		SPN 81299		TUN 8204-1	
	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^1$	GCA effect	$\bar{x}^2$	GCA effect
Kyperounda	68	−6.0	61	−1.0	70	−10.0	98	0.3	64	−4.1	68	−4.2	97	9.8	76	11.2
Badri	100	12.0	100	19.5	100	20.7	100	12.6	100	25.5	99	15.5	100	13.8	98	6.6
BD 2131	69	−2.9	32	−2.0	35	−18.2	49	−21.4	20	−24.4	63	−14.8	38	−14.8	62	−14.7
BD 2127	78	−3.6	49	−8.5	77	−10.0	68	−3.6	50	−10.4	63	−6.7	73	−7.8	63	−11.7
65150-Lds	100	12.6	100	11.6	100	17.2	100	18.8	97	24.0	100	14.7	100	15.3	99	18.4
D75-9-6B-5B-4B-10B	32	−3.0	54	−8.3	66	−12.4	66	−12.7	55	−13.1	30	−13.3	42	−18.4	76	−6.0
D75-4011B-4B-2B	100	5.3	99	16.4	100	13.8	100	20.2	100	20.7	100	21.3	100	16.2	94	9.0
Ben Bechir 79	99	2.5	98	0.8	98	9.3	91	6.1	81	−0.8	94	7.7	91	1.1	81	−1.7
Karim 80	44	−8.9	52	−31.2	75	−16.6	86	−19.2	23	−19.0	55	−20.1	68	−18.4	59	−11.8
Maghrebi 72	78	8.0	86	−2.7	85	−6.2	65	1.1	70	−1.6	75	0.1	86	−3.2	73	−0.7
Standard error:	13.7	3.7	12.6	4.0	11.2	3.8	11.9	4.6	13.7	4.6	11.3	4.2	11.0	3.8	8.4	2.8

[1] Mean percentage necrotic leaf area (4 replications).
[2] Mean percentage necrotic leaf area (6 replications).

Table 5. Correlation coefficients between GCA effects derived from F_1 and F_2 durum wheat seedling reaction data for eight selected *S. tritici* isolates.

Isolate code	Correlation coefficient
TUN 8202	0.87***
TKY 8201	0.79**
ISR 80-8	0.88***
SYR 8209	0.82***
POR 81199-1	0.96***
ITL 82024	0.83***
SPN 81299	0.77**
TUN 8204-1	0.96***

, * = Significant at the 0.01 and 0.005 level of probability, respectively.

cordance was high for both F_2 and F_1 data, respectively 0.94 and 0.85. Although SCA was not significant in all analyses of variance, the ranking of SCA effects by isolates was studied. Again, rankings were systematic between isolates although concordance was less than with GCA effects.

Correlation coefficients between GCA effects calculated on the basis of F_2 seedling reactions and those from F_1 data analyses were calculated and are listed in Table 5. These were highly significant and large for all isolates.

Discussion

Two kinds of combining ability estimates can be made. General combining ability (GCA) describes the average performance of a line in hybrid combinations and contains mainly additive effects. Specific combining ability (SCA) is a measure of the deviation of crosses from the value expected on the basis of the performance of the parents and includes dominance, additive × dominance, dominance × dominance and higher order epistatic variance (Matzinger & Kempthorne, 1956; Sokol & Baker, 1977; Sprague & Tatum, 1942).

Given the highly significant differences among entries, it was relevant to further analyze the data for combining ability variance components. Parents versus crosses as a source of variation tests the importance of non-additive effects. This component was significant in four cases, indicating a certain measure of average heterosis contributed by all selected cultivars in the crosses.

Judging the ratios expressing the relative importance of GCA and SCA, additive variance was of overriding importance. This signifies that the progeny performance can be effectively estimated on the basis of GCA effects, as reaction to disease appears to be rather uniformly transmitted to all offspring. Line selection in a crop improvement program should be successful in developing more resistant lines.

The objective of the ranking tests was to determine if the isolates, originating from very different locations, would nevertheless rank cultivars in a similar order for mean disease reaction and for combining ability effects. For mean values and GCA effects especially, this seemed to be clearly the case. However, even for the SCA effects, which measure unique 'nicking' of certain parental combinations, systematic rankings were highly significant for all eight isolates.

In both F_2 and F_1 data sets for all isolates the following four cultivars constituted the most resistant group on the basis of mean performance, GCA effects and their behavior in the ranking tests: BD 2131, Karim 80, BD 2127, and D75-9-6B-5B-4B-10B.

While no significant correlation could be shown to exist between GCA effects respectivly derived from percentage necrotic leaf area and pycnidial presence due to isolate TUN 8204-1, a noteworthy observation was made. Three of the cultivars identified as relatively resistant showed an above average ability to allow pycnidia development in the small necrotic lesions. Data reported by Eyal et al. (1985) display similar examples. Should this phenomenon of a relatively low infection level coupled with a relatively high production of fungal fruiting structures also occur in the field, then ramifications for the epidemiological behavior of such isolates may be immense. The impediment of successful fungal invasion could be offset by the pathogen by a more prompt and profuse production of inoculum.

This study indicated a major role for general combining ability and associated effects, generally regarded as measures of additive gene effects. Spe-

cific combining ability remained relatively small though often significant, probably due to dominance gene effects and rare epistatic gene effects (M. van Ginkel & A.L. Scharen, 1987a and b). The GCA's and SCA's were generally of comparable size and significance for different isolates, as was their relative importance. Individual GCA and SCA effects of a particular cultivar for the reaction to infection by various *S. tritici* isolates were similar, apparently independent of which isolate was used. In fact, the isolates ranked the cultivars in almost identical fashion on the basis of their mean infection levels. While the isolates incited very different levels of disease in the set of hosts, they thus appeared to activate similar genetic mechanisms in a particular host. Such similarities between isolates may suggest that differential gene-for-gene relationships did not operate in the material studied, but rather the isolates varied in agressiveness, sensu van der Plank (1968).

References

Auld, D.L., Adams, K.J., Swensen, J.B. & Murray, G.A. 1983. Diallel analyses of winterhardiness in peas. Crop Sci. 23: 763–766.

Baker, R.J. 1978. Issues in diallel analysis. Crop Sci. 18: 533–536.

Dubin, H.J. & Rajaram, S. 1981. The strategy of the International Maize and Wheat Improvement Center (CIMMYT) for breeding disease resistant wheat: an international approach. Pages 27–35. In: Strategies for the Control of Cereal Disease. J.F. Jenkyn & R.T. Plumb, eds. Blackwell Scientific Publications, Oxford, London, Edinburgh, Boston and Melbourne. 219 pp.

Eyal, Z. 1972. Effect of Septoria leaf blotch on the yield of spring wheat in Israel. Plant Dis. Rep. 56 (11): 983–986.

Eyal, Z., Amiri, Z. & Wahl, I. 1973. Physiologic specialization of *Septoria tritici*. Phytopathology 63: 1087–1091.

Eyal, Z. & Scharen, A.L. 1977. A quantitative method for the inoculation of wheat seedlings with pycnidiospores of *Septoria nodorum*. Phytopathology 67 (5): 712–714.

Eyal, Z. 1981. Integrated control of Septoria diseases of wheat. Plant Dis. 65 (9): 763–768.

Eyal, Z., Scharen, A.L., Huffman, M.D. & Prescott, J.M. 1985. Global insights into virulence frequencies of *Mycosphaerella graminicola*. Phytopathology 75 (12): 1456–1462.

Gardner, C.O. & Eberhart, S.A. 1966. Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22, p. 439–452.

Gough, F.J. 1976. The effect of Septoria leaf blotch on root development of wheat. Page 48. In: Proc. of the Septoria diseases of wheat workshop, May 4–6, 1976, Experiment, GA. Edited by B.M. Cunfer & L.R. Nelson. GA. Ag. Exp. Sta. Spec. Pub. No. 4. 69 pp.

Krupinsky, J.M. 1976. Techniques for screening wheat for Septoria resistance. p. 28–33. In: Proc. of the Septoria diseases of wheat workshop, May 4–6, 1976, Experiment, GA. Edited by B.M. Cunfer & L.R. Nelson. GA. Ag. Exp. Sta. Spec. Pub. No. 4. 69 pp.

Krupinsky, J.M., Craddock, J.C. & Scharen, A.L. 1977. Septoria resistance in wheat. Plant Dis. Rep. 61 (8): 632–636.

Matzinger, D.F. & Kempthorne, O. 1956. The modified diallel table with partial inbreeding and interactions with environment. Genetics 41: 822–833.

Saari, E.E. 1974. Results of studies on Septoria in the Near East and Africa. Pages 275–283. In: Proc. of Fourth FAO/Rockefeller Foundation Wheat Seminar. Tehran, Iran, 21 May–2 June 1973. 441 pp.

Shipton, W.A., Boyd, W.J.R., Rosielle, A.A. & Shearer, B.L. 1971. The Common Septoria Diseases of Wheat. Bot. Rev. 37 (2). pp. 231–262.

Sokol, M.J. & Baker, R.J. 1977. Evaluation of the assumptions required for the genetic interpretation of diallel experiments in self-pollinating crops. Can. J. Plant Sci. 57: 1185–1191.

Sprague, G.F. & Tatum, L.A. 1942. General vs. specific combining ability in single crosses of corn. J. Am. Soc. Agron. 34: 923–932.

Van Der Plank, J.E. 1968. Disease Resistance in Plants. Academic Press, N.Y. 201 pp.

Van Ginkel, M. & Scharen, A.L. 1987a. Generation mean analysis and heritabilities of resistance to *Septoria tritici* in durum wheat. Phytopathology 77: (in press).

Van Ginkel, M. & Scharen, A.L. 1987b. Host-pathogen relationships of wheat and *Septoria tritici*. Phytopathology 77: (in press).