Inheritance of Septoria Tritici Blotch Resistance in Winter Wheat

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ABSTRACT

Septoria tritici blotch (STB), a fungal foliar disease of wheat (*Triticum aestivum* L.) caused by *Septoria tritici* Rob. ex Desm., is a major constraint to wheat production worldwide. Understanding the inheritance of resistance in known resistant genotypes would potentially lead to more efficient deployment of host plant resistance. In our study, inheritance of seedling STB resistance was evaluated by an eight-parent full diallel set of crosses. Parents, F_1, and reciprocal F_1 were planted in a greenhouse on three different dates. Within each planting date, three to five seeds of each entry were planted in a randomized complete block design with three replicates. Plants at the second-leaf stage were inoculated with a bulk of six *S. tritici* isolates. Significant general combining ability (GCA), specific combining ability (SCA), and reciprocal effects were observed in the analysis of variance. The ratio of GCA sum of squares relative to SCA sum of squares suggested that GCA was more important than SCA. Additive gene effects played a major role in host response to STB, while nonadditive gene effects were also detected. General combining ability effects of individual genotypes were in a close agreement with parental performance. 'KS94U338', a genotype with putative resistance derived from *Aegilops tauschii* Coss., had the lowest STB score and the highest general combining ability. Our results suggested that KS94U338, which possesses resistance thought to be distinct from other known sources, should prove useful in breeding efforts to improve STB resistance in wheat.

Septoria tritici blotch of wheat (syn. Septoria leaf blotch or speckled leaf blotch), caused by *S. tritici* [teliomorph *Mycosphaerella graminicola* (Fuckel) J. Schrot.], causes significant losses in wheat production worldwide (Eyal et al., 1987). In highly susceptible cultivars, this disease may reduce grain yield by 50% (Eyal and Ziv, 1974). Regarded as a wet weather disease (Shaner and Finney, 1976), it is highly destructive in a number of European countries, western Australia (Eyal et al., 1973), New Zealand (Gaunt et al., 1986), the Southern Cone of Latin America (De Ackermann et al., 1995), the Pacific Northwest (Camacho-Casas et al., 1995), and eastern regions of the USA (Shaner and Finney, 1982). In the northern Great Plains of the USA, severe epidemics of septoria diseases on winter wheat have been observed during the last decade when *S. tritici* was the predominant causal species. Infection levels may have been elevated by the steady increase of minimum tillage practices.

Inheritance studies have suggested that STB resistance is controlled either qualitatively or quantitatively; however, the single dominant resistant gene model predominates (Narvaez and Caldwell, 1957; Rillo and Caldwell, 1966; Rosielle and Brown, 1979; Lee and Gough, 1984; Gough and Smith, 1985; May and Lagudah, 1992). Wilson (1985) proposed three different genes conferring resistance to STB, designated *Slb1*, *Slb2*, and *Slb3*. A second inheritance model proposes that resistance is conditioned by more than one major gene (Eyal et al., 1987). Resistance to STB also has been considered as a quantitative trait, as intermediate resistance has been commonly identified in wheat and a continuous distribution of phenotypes in the F_2 population for disease reaction was observed in the field (Camacho-Casas et al., 1995). Jlibene et al. (1994) and Simon and Cordo (1998) reported significant GCA for resistance to STB. Evidently, resistance to STB could be regarded as a qualitative or quantitative trait depending on host genotype, pathogen isolate, environmental conditions, disease assessment methods, or some combination thereof.

A better understanding of the relative importance of general and specific combining abilities of resistance would potentially lead to more efficient development of resistant cultivars and deployment of germplasm resources. Therefore, our objective was to estimate the combining abilities for STB resistance in several genotypes exhibiting various levels of STB resistance.

MATERIALS AND METHODS

Plant Materials

Eight hard red winter wheat genotypes were selected based on preliminary field and greenhouse observations of their reactions to *S. tritici*. Their pedigrees, origins, and STB infection responses are presented in Table 1. All possible crosses, including F_1 and reciprocal F_1, were obtained by hand emasculation and pollination in the greenhouse. About 50 hybrid seeds were obtained for each cross combination.

Sixty-four genotypes including parents, F_1, and reciprocal F_1, were included in the tests. 'Newton' was used as a susceptible check. The study consisted of three planting dates at three-day intervals. For each planting, three to five seeds of each genotype were planted in a 21-cm-long plastic Cone-tainer (Stuewe and Sons, Inc., Corvallis, OR) filled with a peat moss:perlite mixture (Sunshine Mix 1; Sun Gro Horticulture Inc., Bellevue, WA). Each Cone-tainer represented one experimental unit. Each planting date consisted of three replicates arranged in a randomized complete block design. At planting, each Cone-tainer was fertilized with 3 g of slow release granular fertilizer (Osmocote 14-14-14 NPK, Sierra Chemical Co., Milpitas, CA). Before inoculation, plants were grown in a greenhouse with a photoperiod of 16 h (supplemented by high pressure sodium lights) at 20 to 25°C. To avoid leaf damage by direct overhead irrigation, the plants were watered by placing the plastic trays supporting the plastic Cone-tainers in an aluminum pan filled with water.

Pathogen Production and Disease Evaluation

A mixture of six *S. tritici* isolates originating from field collections in South Dakota was used. Fresh inoculum was

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Abbreviations: GCA, general combining ability; MR, moderately resistant; MS, moderately susceptible; R, resistant; S, susceptible; SCA, specific combining ability; STB, Septoria tritici blotch.

Table 1. Origin, pedigree, and *Septoria tritici* infection response of hard red winter wheat parents used.

Genotype	Origin or source	Pedigree	Infection response†
KS94U338	KS	KS90WGRC10 sib*2/TA2455	R
Jagger	KS	KS82W418/Stephens	R
KS91W005-1-4	KS	KS85W663-3-2/Karl/3/Karl′S′/VE1110/1PV118	R
KS91W0935-29-1	KS	2180/Karl//2163	MR
KS87822-2-1	KS	KS831374-154B/OR8300764	MR
SD93493	SD	Redland/Centurk78	S
Tandem	SD	Brule/Agate	S
SD93500	SD	Judith/Redwin	S

† R = resistant, MR = moderately resistant, S = susceptible.

prepared prior to each inoculation. Conidia of individual isolates were streaked on PDA (39 g potato dextrose agar, 1 L water) petri plates with a sterile wire loop. The plates were placed on a laboratory bench and exposed to cool white fluorescent lights for 12 h each day at room temperature (20 ± 2°C). When the edge of the pink colony began to darken, the conidia were ready to harvest. Growth rates of the six isolates varied, and as cultures of the faster growing isolates reached harvest stage, the plates were stored in a 4°C refrigerator until the slower growing isolates had produced sufficient inoculum. Conidia of each isolate were collected by flooding the plates with double-distilled water and gently scraping the colonies with a rubber policemen. A conidial suspension was prepared using equal quantities of the six isolates, filtered through two layers of cheesecloth, and adjusted to approximately 5 to 10 × 10^6 conidia mL^{-1} as determined by hemacytometer counts.

Plants were inoculated when the second leaf was fully expanded. A volume of 100 mL of the conidial suspension was sprayed evenly onto 300 plants with an atomizer. Plants were placed into a mist chamber where a cool mist ultrasonic humidifier was used to supply moisture. To avoid leaf senescence due to high humidity, the mist chamber was opened for 30 min every 24 h. After 96 h incubation at 21°C under a 12-h photoperiod, the inoculated plants were moved to a growth chamber with a 12-h photoperiod at 21 ± 1°C.

Twenty-one days after inoculation, disease ratings of the second leaf were recorded based on a 1 to 9 scale. This scale was established on the basis of the infection response (amount of necrosis and chlorosis) and on the density of pycnidia (Zhang et al., 1999). The genotypes were classified into four categories on the basis of mean STB scores: resistant (R, average disease scores ranged from 1.0–4.9); moderately resistant (MR, average disease scores ranged from 5.0–6.9), moderately susceptible (MS, average disease scores ranged from 7.0–7.9), and susceptible (S, average disease scores ranged from 8.0–9.0).

Data Analysis

The data were subjected to analysis of variance (ANOVA) by split-plot design, with different planting dates as the main plot and genotypes (parents and F_1) as the subplot. No genotype × planting date interaction was detected from the above procedure. Therefore, for further diallel analysis, planting dates were treated as replicates, and the mean value of the three observations within each planting date represented the estimated STB score of the replicate.

The data were analyzed with the "Diallel Analysis and Simulation" program designed by Burow and Coors (1994) according to Griffing's Model 1 (parents were considered fixed), Method 1 (Griffing, 1956). The general linear model for the analysis is: $X_{ijk} = m + g_i + g_j + s_{ij} + r_{ij} + b_K + e_{ijk}$, where X_{ijk} = observed value of the experimental unit, m = population mean, g_i = general combining ability (GCA) effect for the ith parent, g_j = general combining ability for the jth parent, s_{ij} = specific combining ability (SCA) for the cross involving Parents i and j, r_{ij} = reciprocal effect for the cross involving Parents i and j, b_k = replication (block) effect, and e_{ijk} = error. The t-test was used to test whether GCA, SCA, and reciprocal effects were significantly different from zero. The degrees of freedom for estimable GCA effects (g_i) were $(p - 1)$, where p = number of parents. The degrees of freedom for estimable SCA effects (s_{ij}) and estimable reciprocal effects (r_{ij}) were $p(p - 1)/2$ (Kang, 1994).

RESULTS AND DISCUSSION

Means of F_1 hybrids of parents grouped by infection responses are given in Table 2. In most cases, the average disease scores of F_1 hybrids between different infection response categories were close to the mid-point parent values. F_1 hybrids of crosses between parents of the same STB infection response had the same infection responses as their parents (Table 2). The F_1 hybrids of S/MR or MR/S were MS (with an average infection response of 7.3 for S/MR and 7.7 for MR/S). Average infection response of F_1 hybrids of S/R, regardless of the direction of the cross, were generally similar (7.1 for S/R and 7.2 for R/S), except for the cross of 'Tandem'/KS94U338 which was 3.8. This cross was not included in

Table 2. Means and ranges of septoria tritici blotch scores for winter wheat crosses (F_1) among infection response groups.

Combination	No. of crosses	F_1 Disease score		Mean	Infection response†
		Maximum	Minimum		
S/S	6	8.1	8.6	8.4	S
MR/MR	2	6.1	7.0	6.5	MR
R/R	6	1.6	3.4	1.9	R
S/MR	6	7.2	8.0	7.3	MS
MR/S	6	7.5	8.3	7.7	MS
S/R‡	8	5.0	7.8	7.2	MS
R/S	9	5.7	8.3	7.1	MS
MR/R	6	2.0	5.7	2.2	R
R/MR	6	1.3	6.8	2.9	R

† R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible.
‡ Cross of Tandem/KS94U338 was excluded.

Table 3. Analysis of variance of septoria tritici blotch scores for eight parents and 56 F_1 crosses.

Source	df	Sum of squares	Mean squares
Replicate	2	0.3	0.2
Cross	63	1165.5	18.5**
GCA	7	899.5	128.5**
SCA	28	210.0	7.5**
Reciprocal	28	56.0	2.0**
Error	126	72.2	0.6

** Significant at the 0.01 level of probability.

the estimate of mean values of S/R due to the reciprocal effect. The F_1 results indicated that resistance to STB is conditioned mainly by a set of genes with additive effects. However, as the means of F_1 of S/R and R/S were closer to the susceptible parents, the existence of recessive gene effects cannot be excluded.

Highly significant effects ($P < 0.01$) due to general combining ability (GCA), specific combining ability (SCA), and reciprocal effects were observed (Table 3). Traditionally, the ratio of GCA and SCA mean squares has been used to assess the relative importance of general combining ability and specific combining ability. However, in a model with fixed effects, Kang (1994) suggested the use of the ratio of GCA to SCA sum of squares to determine their relative importance. In this study, the ratio of GCA to SCA sum of squares was 4.3. Since GCA effects accounted for the largest portion of the phenotypic variation, additive gene effects were most important in the inheritance of resistance to STB. This conclusion is also supported by the F_1 data discussed above. Thus, performance of single cross progeny can be predicted on the basis of GCA of the parents. Similar conclusions were reached in other studies (Van Ginkel and Scharen, 1988; Jlibene et al., 1994; Simon and Cordo, 1998) using different sets of genotypes.

GCA effects were generally in agreement with parental performance (Table 4). A negative value of GCA indicated that the corresponding parent was resistant while a positive value was associated with susceptibility. KS94U338 had the lowest GCA value (−2.2) and the lowest STB score (1.4), indicating that resistance to STB was consistently inherited in crosses with this parent. This genotype, with resistance derived from *T. tauschii*, may prove useful in breeding efforts to improve septoria tritici blotch resistance in wheat. The other two resistant genotypes, 'Jagger' and 'KS91W005-1-4' also had highly significant negative GCA effects. Of the two MR parents, 'KS91W0935-29-1' and 'KS87822-2-1', the latter had negative GCA effects. Each of the susceptible parents ('SD93493', 'SD93500', and Tandem) had large positive GCA estimates.

Table 4. Parental means of septoria tritici blotch (STB) scores and general combining ability (GCA) effects in an eight-parent diallel.

Parent	STB mean†	GCA
KS94U338	1.4 ± 0.5	−2.2**
Jagger	1.4 ± 0.8	−1.6**
KS91W005-1-4	1.9 ± 0.8	−1.1**
KS91W0935-29-1	5.8 ± 2.3	−0.5**
KS87822-2-1	5.8 ± 3.2	0.0
SD93493	8.0 ± 0.7	1.8**
Tandem	8.3 ± 0.7	1.6**
SD93500	8.7 ± 0.5	1.8**

** Significantly different from zero at the 0.01 level of probability.
† Mean STB reaction score and standard error of nine observations.

Significant SCA effects were detected in 20 of the 28 possible F_1 combinations (Table 5), indicating that nonadditive effects may be important at the seedling stage resistance. Crosses with negative SCA effects should be more resistant than predicted by the GCA of the parents. Among the hybrids in this study, crosses of Jagger (R) with KS87822-2-1 (MR) and KS91W005-29-1 (R) with KS91W005-1-4 (MR) had the lowest SCA effects (−2.0). SCA effects in the S/S combinations were always significantly negative, suggesting that S/S crosses could conceivably produce hybrids with lower STB scores. However, all F_1 hybrids of S/S crosses were still highly susceptible to STB.

Reciprocal effects were present in five of the seven combinations involving KS94U338, the crosses of KS 91W005-1-4 with Jagger, and the cross of Tandem with KS91W0935-29-2 (Table 5). When crossed with KS94 U338 (R) as female, the hybrids of KS91W005-1-4 (R), and the two susceptible parents (SD93500, and Tandem) had significantly lower disease scores than those of the reciprocal crosses (with reciprocal effects of −0.9, −1.1, and −1.2). Apparently, KS91W005-1-4, Tandem, and SD93500 contribute additional resistance when used as female. The possible reciprocal effects in combinations of KS94U338 with Jagger and KS94U338 with KS91 W0935-29-2 are ascribed to KS94U338 because of the positive reciprocal effects between crosses of KS94U338 used as male and female. Reciprocal effects of SD93500 were also observed when it was crossed with KS91W 0935-29-1. Reciprocal effects for resistance to STB was

Table 5. Specific combining ability (SCA), and reciprocal effects of septoria tritici blotch scores on the second leaf in an eight-parent winter wheat diallel.

	Resistant			Moderately resistant		Susceptible		
Parent	1	2	3	4	5	6	7	8
1 KS94U338	–†	0.5	0.1	0.3	−1.9**	0.9**	0.6*	−0.6*
2 Jagger	0.8*	–	−0.5	−1.0**	−2.0**	1.0**	1.1**	2.0**
3 KS91W005-1-4	−0.9*	−0.9*	–	−2.0*	1.6**	0.8**	1.0**	0.7*
4 KS91W0935-29-1	1.3**	−0.6	0.0	–	1.3**	0.4	0.5	−0.6*
5 KS87822-2-1	0.3	0.1	−0.6	−0.5	–	0.1	0.3	0.5
6 SD93493	−0.1	−0.4	−0.2	0.1	0.2	–	−0.8*	−1.3**
7 Tandem	−1.1*	0.3	0.2	−0.2	0.1	−0.2	–	−0.9*
8 SD93500	−1.2**	−0.3	−0.1	−1.1**	−0.2	−0.2	−0.1	–

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
† SCA effects are above the diagonal. Reciprocal effects are below the diagonal.

previously observed by Jlibene et al. (1994) in two wheat crosses. Reciprocal effects in reaction to *S. tritici* may have been overlooked because most of the genetic studies on STB resistance were not designed to detect the reciprocal effects. In this study, KS91W005-1-4, Tandem, and SD93500 had significant reciprocal effect for STB resistance. Further research is needed to determine the relative importance between maternal or extranuclear factors in those genotypes.

Septoria tritici blotch resistant sources have been identified in both common wheat and its alien relatives (Rosielle, 1972; Krupinsky et al., 1977; Gough and Tuleen, 1979; Shaner and Finney, 1982; Eyal et al., 1983; Yechilevich-Auster et al., 1983; McKendry and Henke, 1994). In winter wheat, 'Bulgaria 88' has been an important source of STB resistance in the development of cultivars with early maturity, high yield, good soft wheat quality, and resistance to other diseases and insects in the eastern soft red wheat region of the USA (Shaner and Finney, 1982). This study revealed that KS94U338, Jagger, and KS91W005-1-4 contributed positively to resistance in hybrids and should be good parents for improving STB resistance in the hard winter wheat region. KS94U338 with resistance derived from *T. tauschii*, which is different from the previously reported materials, should be useful for improving resistance to STB and for diversifying the current breeding gene pool.

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