Diallel Analysis of Components of Partial Resistance to *Septoria nodorum* in Wheat

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ABSTRACT

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A five-parent full diallel and a nine-parent half diallel including adapted and exotic wheats (*Triticum aestivum*) of both winter and spring types were evaluated in the greenhouse for components of partial resistance to *Septoria nodorum*. F_1 seedlings and parents were inoculated with a mixture of isolates of *S. nodorum* and evaluated for inheritance of incubation period and infection frequency. Significant general combining ability effects were found for incubation period and infection frequency. Significant specific combining ability effects were found for incubation period, but were observed in only 40% of the hybrid combinations in the full diallel and 16% of the hybrid combinations in the half diallel. Additive gene effects were most important in the inheritance of both components. Reciprocal and maternal effects were nonsignificant for both components of partial resistance measured in the full diallel. Partially resistant genotypes Coker 916 and MT71-1000-11 contributed to resistance by increasing incubation period and decreasing infection frequency. Another partially resistant parent (PAT 72-180) contributed to resistance through an increased incubation period only.

Septoria nodorum Berk. (anamorph of *Leptosphaeria nodorum* E. Müller), the causal agent of glume blotch of wheat (*Triticum aestivum* L.), can limit wheat production in locations where frequent precipitation, high humidity, and temperatures from 18 to 25 C occur during the grain-filling period (13). In the southeastern United States, yield losses occur when lesions develop on upper leaves and glumes. The resulting decrease in photosynthetic area leads to reduced kernel weight (13). Under optimum conditions for development of *S. nodorum*, all cultivars may become infected; but wheat genotypes expressing different levels of partial resistance have been identified (11,16,21,25–27). Partial resistance, defined as a reduction in the rate of an epidemic, is characterized by any or all of the following: reduced infection frequency, lengthened latent period, and decreased spore production (23).

Resistance or tolerance to *S. nodorum* by seedlings and adult plants is reported to be quantitatively inherited (1,2,10, 18,20,21), with the exception of a single dominant gene for resistance located in the cultivar Atlas 66 (7,14). Bronniman (1,2) and Kleijer et al (15) found that tolerance is polygenically and additively

inherited in adult spring wheat. Resistance, measured by disease severity on adult wheat plants, was determined to be governed primarily by additive gene effects (21,22). Mullaney et al (20) reported that additive gene action is most important in the inheritance of infection frequency and percentage of necrotic leaf area in spring wheat seedlings. Significant general combining ability (GCA) effects and specific combining ability (SCA) effects were reported by Stooksbury et al (30) for latent period measured on soft red winter wheat cultivars. Jeger (10) and Jeger et al (11) hypothesized that four independent groups of genes are involved in partial resistance to *S. nodorum*. These genes are believed to govern susceptibility to a toxin associated with the fungus, resistance to pathogen reproduction, susceptibility to pathogen growth, and susceptibility to pathogen establishment.

Resistance in adult plants has frequently been associated with increased plant height (13,28), late maturity (13,28), and winter growth habit (4,13,24). As a result, selection among adult plants in a wheat breeding program is complicated by a tendency to select late maturing, tall genotypes—genotypes that appear more resistant than the agronomically desirable early-maturing, short-statured genotypes whose microclimate and plant architecture favor spread of the pathogen (13). The screening of wheat seedlings in greenhouses has been reported to be an effective strategy for identifying reaction to *S. nodorum* (5,12,17,24). This type of screening permits use of quantitative inoculation techniques, and eliminates the influence of

undesirable agronomic traits such as plant height and late maturity on selection.

In a preliminary study (31), we identified significant variation for incubation period (7.4–16.6 days) and infection frequency (0.59–1.82 lesions per square centimeter) among an array of adapted and exotic wheat lines screened in the seedling stage using a mixture of *S. nodorum* isolates from the southeastern United States. In addition to adapted lines, we identified several exotic lines with high levels of partial resistance to *S. nodorum* (incubation period longer than 10 days; infection frequency fewer than 1.2 lesions per square centimeter). These lines were developed either outside the United States or from breeding programs within the United States that use germ plasm different from that used in the Southeast.

Our study determined the inheritance among seedlings of two components of partial resistance: incubation period and infection frequency. We used a geographically diverse subset of wheat lines exhibiting different levels of partial resistance to *S. nodorum*. Of particular interest was the breeding behavior of partially resistant exotic lines, with potentially novel genes for resistance, when combined with both susceptible and partially resistant adapted genotypes from the southeastern United States.

MATERIALS AND METHODS

Nine wheat lines were selected as parents (Table 1). Four of these—Coker 916, Caldwell, FL 302, and NK 81W701—are soft red winter wheats adapted to or grown commercially in North Carolina. The other five parents are classified as unadapted or exotic genotypes. Two parents, MT7819 and PAT72-180, are spring wheats, while the remainder are winter types.

The first five parents in Table 1 were crossed in all possible combinations, including reciprocals, in a full-diallel design (20 F_1 hybrids) to examine the significance of reciprocal and maternal effects on inheritance of resistance components. All nine parents were crossed in all possible combinations, excluding reciprocals, in a half-diallel design (36 F_1 hybrids) to examine the relative importance of additive and nonadditive gene effects on inheritance of resistance components. Parents were included in

the experiments, for a total of 25 entries in the full diallel and 45 entries in the half diallel.

All experiments were conducted in the greenhouse. The experimental design was a randomized complete block with four replications. An experimental unit consisted of two 10-cm clay pots; a third pot of each entry was used as a water-sprayed control. The pots were over-planted and then thinned to three plants per pot when seedlings emerged. Pots were filled with Terra-Lite Metromix, 6 g of Osmocote (a 14-14-14 slow-release fertilizer), and 0.04 g of disulfoton (a systemic insecticide).

When the seedlings reached the two-to three-leaf stage, the last fully emerged leaf on each plant was marked at the base with a nonphytotoxic felt tip pen and its length and width recorded. Plants were then inoculated using a composite of five isolates collected from Maryland (SN 82-12), Virginia (SN 83-32), North Carolina (BR 2-3), Georgia (SN 82-04), and Florida (SN 84-53). Isolates were grown on potato-dextrose agar in 9-cm petri dishes for 7 days at 20 C, approximately 15 cm below constant cool-white fluorescent light (Sylvania 34W). Plates were flooded with 5–10 ml of sterile distilled water and the agar surface was scraped with a rubber policeman. The resulting spore suspension consisted of

equal amounts of each isolate, adjusted to a concentration of 1×10^6 spores per milliliter using a hemacytometer. Tween 80 (0.001%) was added to the suspension as a surfactant.

In each replication, two pots of each entry were transferred to a rotating table in a settling tower and inoculated with the spore suspension—atomized through an air brush at 1.38×10^5 Pa (20 psi) pressure—for seven revolutions (5,24). Approximately 41 spores were deposited per square millimeter, determined by substituting glass microscope slides for clay pots in the settling tower. After inoculation, plants were placed in a moisture chamber for 72 hr with 98 ± 2% relative humidity to provide an atmosphere conducive to infection. After the initial 72-hr period, 12-hr periods of ambient air (days) were alternated with 12-hr periods of high-humidity air (nights) (29). The greenhouse temperature was maintained at 18–25 C; supplementary lighting was used to provide a 16-hr photoperiod ($350 \pm 50\ \mu E \cdot m^{-2} \cdot s^{-1}$). The procedure and spore mixture described here were also used to classify the reaction of the selected parents to *S. nodorum* (31).

The components of partial resistance measured in our study were incubation period (the number of days from inoculation to the first appearance of symp-

toms) and infection frequency (the number of lesions per square centimeter of leaf at the end of the incubation period). Full-diallel and half-diallel analyses were performed according to Griffing (9) for a fixed-effects model with parents included (methods 1 and 2, respectively). Genotypic effects were considered fixed, and parental lines made up the population about which inferences were made. The full-diallel analysis was modified with extensions for maternal and reciprocal effects (3). Component heritabilities were calculated by regressing F_1 progeny means on midparent means (6). Pearson product-moment correlations among resistance components were computed using both parent and progeny means.

RESULTS AND DISCUSSION

The significance levels of mean squares for comparable sources of variation measured in both the full and half diallels were almost identical (Table 2). In the full diallel, maternal and reciprocal effects were nonsignificant for incubation period and infection frequency. The mean squares for pooled maternal and reciprocal effects were also nonsignificant for the same components. Maternal effects are generally attributed to differences in heritable extranuclear factors such as mitochondrial and chloroplast DNA; reciprocal effects are generally attributed to interactions between nuclear and extranuclear factors. Results similar to ours were obtained by Nelson (21) and Nelson and Gates (22) when they measured disease severity among adapted adult wheat plants inoculated at the milk stage in the greenhouse. Likewise, Stooksbury et al (30) found that neither reciprocal nor maternal effects were significant for incubation period or latent period when measured on adapted soft red wheat cultivars commonly grown in the southeastern United States.

Among parents and crosses, we observed significant differences for incubation period and infection frequency in the full-diallel and half-diallel analyses (Table 2). Water-sprayed control plants displayed no disease symptoms. Parental means for incubation period ranged from 8.3 to 13.9 days; for infection frequency, means ranged from 0.8 to 2.0 lesions per square centimeter (Tables 3 and 4). Incubation periods and infection frequencies of the three exotic resistant parents (VPM/MOS, PAT72-180, MT71-1000-11) were comparable to those observed in the two adapted resistant parents (Coker 916, FL 302) in the half diallel. A partially resistant parent is expected to have a long incubation period, a low infection frequency, or both; a susceptible parent is expected to have a short incubation period, a high infection frequency, or both (23). Rank orders of parents were slightly different for each

Table 1. The geographical origins and reactions to *Septoria nodorum* of the nine parental wheat genotypes

Parents[a]	Origin	Reaction[b]
MT71-1000-11	Montana	Partially resistant
Coker 916	South Carolina	Partially resistant
Caldwell (CI 117897)	Indiana	Susceptible
VPM/MOS	France	Partially resistant
MT7819	Montana	Susceptible
SK7	Yugoslavia	Susceptible
FL 302	Florida	Partially resistant
NK81W701	North Carolina	Susceptible
PAT72-180	Brazil	Partially resistant

[a] The first five parents were crossed in a full-diallel design; all nine parents were crossed in a half-diallel design.

[b] Wilkinson (31); disease reaction was determined on wheat seedlings grown under greenhouse conditions inoculated with the same spore mixture used in this study.

Table 2. Analysis of variance for components of partial resistance to *Septoria nodorum* measured on wheat seedlings under greenhouse conditions in a five-parent full-diallel and nine-parent half-diallel design

Source	df	Full-diallel mean squares		df	Half-diallel mean squares	
		Incubation period (days)	Infection frequency (lesions per cm²)		Incubation period (days)	Infection frequency (lesions per cm²)
Replications	3	99.56**[a]	4.04**	3	157.25**	4.01**
Entries	24	10.14**	0.56**	44	10.20**	0.38**
Parents	4	22.40**	1.00**	8	18.00**	0.67**
P vs. C	1	18.90**	0.76*	1	23.82**	0.25
Crosses	9	13.49**	0.87**	35	8.03**	0.32**
GCA	4	23.67**	1.75**	8	22.66**	0.88**
SCA	5	5.33**	0.17	27	3.69*	0.16
Maternal	4	1.18	0.02	...	...	...
Reciprocal	6	1.47	0.11	...	...	...
Error	72	1.64	0.17	132	2.21	0.14
C.V. (%)	...	12.00	26.60	...	13.80	26.00

[a] * = Significant at $P = 0.05$; ** = significant at $P = 0.01$.

component of partial resistance measured; however, no change in rank between a partially resistant and a susceptible parent occurred for any component.

The ranges for cross means and parental means were similar for both incubation period and infection frequency (Tables 3 and 4). Cross means were not significantly different from midparent means for infection frequency in the half diallel (Table 2). Incubation period was partially controlled by nonadditive gene effects, as suggested by the significant parent-vs.-crosses source of variation in the full and half diallels (Table 2). Comparisons of parental and cross means (Table 4) showed a trend toward dominance for decreased incubation period (greater susceptibility) in hybrid progeny. The trend is especially evident in crosses involving the partially resistant parents with long incubation periods (MT71-1000-11, FL 302, PAT72-180) and the susceptible parent with a short incubation period (MT7819). Dominance for susceptibility has also been reported by Fried and Meister (8) for leaf and head resistance.

General combining ability (GCA), which reflects the average performance of a genotype in hybrid combination, is a function both of additive gene effects and of the average dominance effects associated with that particular parent. Our results showed that GCA effects were significant for incubation period and infection frequency in the full and half diallels (Table 2). Specific combining ability (SCA), which is detected whenever specific hybrid combinations perform better or worse than expected based on the average performance of parental lines, is a function of dominance and other nonadditive gene effects such as epistasis. We found that SCA effects were significant for incubation period only (Table 2). Only four (40%) of 10 hybrids had significant SCA effects for incubation period in the full diallel, and only six (17%) of 36 hybrids had significant SCA effects for incubation period in the half diallel (Table 5). While nonadditive gene effects were significant, they were nonetheless of minor importance in the expression of this component.

A parent that exhibits large positive GCA effects for incubation period and large negative GCA effects for infection frequency would be desirable in a breeding program intended to improve resistance. Three of the five partially resistant parents significantly increased incubation period between 0.7 days (MT71-1000-11, PAT72-180) and 1.5 days (Coker 916) (Table 6). Three of the four susceptible parents significantly decreased incubation period between 0.6 days (Caldwell, NK81W701) and 1.6 days (MT7819). Three partially resistant parents (MT71-1000-11, FL 302, Coker 916) significantly reduced infection fre-

quency by 0.1 to 0.2 lesions per square centimeter, while two susceptible parents (Caldwell, MT7819) significantly increased infection frequency by 0.3 lesions per square centimeter. Only two partially resistant parents (MT71-1000-11, Coker 916) contributed to resistance in their progeny by significantly altering both components. In contrast, two others (PAT72-180, FL302) altered one component each: PAT72-180 contributed to resistance through a lengthened incuba-

tion period; FL 302 contributed through a reduced infection frequency. Only two susceptible parents (Caldwell, MT7819) significantly altered both components.

Parlevliet (23) and Leonard and Mundt (19) have suggested that breeding programs for partial resistance should emphasize selection for decreased sporulation and inoculum efficiency and increased latent period. The relative importance of each component depends on the particular pathosystem, the environ-

Table 3. Parental (in italics) and F_1 progeny means for components of partial resistance measured on wheat seedlings inoculated with *Septoria nodorum* under greenhouse conditions in a five-parent full-diallel design

Parent	1	2	3	4	5
	Incubation period (days)				
1 MT71-1000-11	*13.9*	12.9	10.7	10.0	9.8
2 Coker 916	13.6	*13.0*	11.1	10.0	9.4
3 VPM/MOS	11.5	12.0	*12.6*	10.3	9.7
4 Caldwell	9.3	11.0	11.2	*9.8*	9.2
5 MT 7819	9.4	10.2	8.3	9.2	*8.3*
	Infection frequency (lesions cm²)				
1 MT71-1000-11	*0.8*	1.0	1.4	2.1	1.5
2 Coker 916	1.0	*1.2*	1.2	1.5	1.7
3 VPM/MOS	1.3	1.1	*1.1*	2.0	1.7
4 Caldwell	1.7	1.8	1.6	*2.0*	2.2
5 MT 7819	1.5	1.7	1.8	2.0	*1.8*

Table 4. Parental means (in italics) and F_1 progeny means for incubation period (top number) and infection frequency (bottom number) measured on wheat seedlings inoculated with *Septoria nodorum* under greenhouse conditions in a nine-parent half-diallel design

Parent	1	2	3	4	5	6	7	8	9
1 MT71-1000-11	*13.9*[a]	13.6	11.5	9.3	9.4	13.0	12.6	10.8	9.5
	0.8[b]	1.0	1.3	1.7	1.5	1.1	1.2	1.5	1.3
2 Coker 916	···	*13.0*	12.0	11.0	10.2	13.2	12.1	12.4	10.5
	···	*1.2*	1.1	1.8	1.7	1.1	1.0	1.3	1.3
3 VPM/MOS	···	···	*12.6*	10.3	8.3	8.4	12.1	12.1	9.1
	···	···	*1.1*	2.0	1.8	1.8	1.3	1.2	1.5
4 Caldwell	···	···	···	*9.8*	9.2	9.6	10.8	10.0	10.2
	···	···	···	*2.0*	2.0	1.3	1.8	1.6	1.4
5 MT 7819	···	···	···	···	*8.3*	8.7	9.8	8.7	9.4
	···	···	···	···	*1.8*	1.7	1.7	1.8	1.5
6 FL 302	···	···	···	···	···	*13.8*	10.5	10.2	11.2
	···	···	···	···	···	*0.9*	1.4	1.1	1.1
7 PAT72-180	···	···	···	···	···	···	*12.8*	11.6	10.0
	···	···	···	···	···	···	*1.5*	1.7	1.3
8 SK 7	···	···	···	···	···	···	···	*10.0*	10.5
	···	···	···	···	···	···	···	*1.7*	1.4
9 NK81W701	···	···	···	···	···	···	···	···	*9.4*
	···	···	···	···	···	···	···	···	*1.3*

[a] Incubation period in days.
[b] Infection frequency in number of lesions per square centimeter.

Table 5. Specific combining ability (SCA) effects for incubation period measured on wheat seedlings inoculated with *Septoria nodorum* under greenhouse conditions in a five-parent full-diallel design (above diagonal) and a nine-parent half-diallel (below diagonal) design (values expressed in days)

Parent	1	2	3	4	5	6	7	8
1 MT71-1000-11		1.09**[a]	-0.16	-0.84**	-0.09	···	···	···
2 Coker 916	0.83		-0.22	-0.50	-0.37	···	···	···
3 VPM/MOS	0.36	0.07		0.64*	-0.25	···	···	···
4 Caldwell	-1.32*	-0.43	0.47		0.71*	···	···	···
5 MT 7819	-0.31	-0.24	-0.55	0.81		···	···	···
6 FL 302	1.67*	1.15	-2.07**	-0.33	-0.32		···	···
7 PAT72-180	0.65	-0.63	1.01	0.14	0.12	-0.78		···
8 SK 7	-0.72	0.14	1.46**	-0.14	-0.54	-0.56	0.08	
9 NK81W701	-1.16*	-0.89	-0.74	0.81	1.05	1.24*	-0.58	1.05

[a] * = Significant at $P = 0.05$; ** = significant at $P = 0.01$.

ment, and the range of variation in resistance available in the crop species (19). We observed significant variation among both adapted and exotic parents for incubation period and infection frequency. The predominance of additive gene effects in the inheritance of both components of partial resistance to *S. nodorum* suggests that progress from selection can be expected. Heritability values based upon midparent-offspring regressions were relatively high: 0.65 ± 0.08 for incubation period and 0.67 ± 0.03 for infection frequency. Incubation period was significantly ($P = 0.01\%$) correlated with infection frequency ($r = -0.73$). This result is consistent with Parlevliet's (23) statement that association between components may be strong but not complete. The correlation suggests that incubation period may be sufficient criterion on which to base selection in an initial large-scale screening program.

Our results indicate that progress in selecting for resistance in breeding populations developed from combinations of the partially-resistant adapted and exotic germ plasm included in this study should be comparable (at least) to progress in populations developed from combinations of adapted germ plasm only, as demonstrated by Stooksbury et al (30). Work is in progress to determine whether genetic variation and transgressive segregation among progeny in populations that combine partially-resistant adapted and exotic germ plasm are significantly greater than those observed in populations containing adapted germ plasm only. Four of the five parents previously classified as partially resistant (31) significantly altered one or both components in the direction of improved resistance. Comparable results were observed for three susceptible parents. Susceptible SK7 from Yugoslavia was an exception; it had no significant GCA effects for any of the components.

In conclusion, our data indicate that additive gene effects are relatively more important in the inheritance of incubation period and infection frequency in combinations between the wheat lines of adapted and exotic origin that we studied. Nonadditive gene effects appear to be involved in the inheritance of incubation period and may play an important role in some specific crosses. Coker 916 and MT71-1000-11 had large positive GCA effects for incubation period and large negative GCA effects for infection frequency. They would be useful parents in a breeding program for improving resistance to *S. nodorum*. While selection for both components of partial resistance would be more desirable in a breeding program, our data indicate that selection based on a single component should result in progress toward more resistant genotypes.

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Table 6. General combining ability (GCA) effects for incubation period and infection frequency measured on wheat seedlings inoculated with *Septoria nodorum* under greenhouse conditions in a five-parent full-diallel design and a nine-parent half-diallel design

Diallel	Parent	Incubation period (days)	Infection frequency (lesions/cm²)
Full	MT71-1000-11	0.61*[a]	−0.20**
	Coker 916	1.12**	−0.28**
	VPM/MOS	0.22	−0.09
	Caldwell	−0.56*	0.35**
	MT 7819	−1.40**	0.22**
Half	MT71-1000-11	0.69*	−0.14*
	Coker 916	1.46**	−0.19**
	PAT72-180	0.65*	−0.04
	SK 7	0.22	0.01
	VPM/MOS	−0.15	0.07
	FL 302	−0.01	−0.14*
	NK81W701	−0.62*	−0.12
	Caldwell	−0.63*	0.26**
	MT 7819	−1.61**	0.29**

[a] * = Estimate significantly different from zero, $P = 0.05$; ** = estimate significantly different from zero, $P = 0.01$.