Incubation Period and Latent Period of Wheat for Resistance to *Leptosphaeria nodorum*

D. E. STOOKSBURY, Former Graduate Research Assistant, J. W. JOHNSON, Professor, Agronomy, and B. M. CUNFER, Professor, Plant Pathology, University of Georgia, Georgia Station, Griffin 30223-1797

ABSTRACT

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Seven soft red winter wheat (*Triticum aestivum*) parents and the diallel set of hybrids among them were included in a complete diallel mating design. Parents and F_1 crosses were evaluated for the inheritance of incubation period and latent period, two components of resistance to *Leptosphaeria nodorum*, cause of Septoria nodorum blotch. General combining ability (GCA) effects and specific combining ability (SCA) effects were highly significant for both incubation and latent period. Fitting GCA effects accounted for 54 and 46% of the corrected sums of squares among crosses. Coker 762 and Oasis had the largest GCA effects for latent period and should make excellent parental sources for resistance to *L. nodorum*.

Septoria nodorum blotch, caused by *Leptosphaeria nodorum* E. Müller (anamorph: *Septoria nodorum* (Berk.) Berk.), is a major cause of yield and quality reduction in soft red winter wheat (*Triticum aestivum* L.) in the southern United States (11). Incubation period, latent period, infection frequency, spore production, and disease severity are important components of resistance to *L. nodorum* and other plant pathogens (5,12,15–17). Rapilly et al (12) found that the incubation period of *L. nodorum* varied among cultivars of wheat and that the inheritance of a long incubation period was partially dominant. F_1 plants had longer incubation periods than either of the parents. Jeger et al (6) found a significant linear correlation ($r = 0.41$) between incubation period and latent period.

Nelson (9) reported significant general (GCA) and specific (SCA) combining abilities for *L. nodorum* resistance. Oasis and Blueboy II had the largest GCA effect for resistance and contributed most to resistance in hybrid combinations. The objective of this study was to determine the inheritance of two resistance components, incubation period and latent period, of *L. nodorum* among soft red winter wheats grown in recent years in the southeastern United States.

Contribution from the Department of Agronomy and Department of Plant Pathology, Agricultural Experiment Stations, Georgia Station, Griffin 30223-1797.

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MATERIALS AND METHODS

Seven cultivars of soft red winter wheat that varied greatly in resistance to *L. nodorum* were used in a complete diallel cross with reciprocals. They were Coker 762 (CI 92417), Oasis (CI 15929), Florida 301 (CI 17769), Holley (CI 14579), Stacy (CI 17861), Coker 747 (CI 17923), and Omega 78 (CI 17721).

Table 1. Mean squares of analysis of variance for parents, F_1 crosses, and F_1 reciprocal crosses for latent period of *Leptosphaeria nodorum*

Source	df	Mean squares
Parents	6	13.1**[a]
Crosses	35	7.9**
Parents vs. crosses	1	3.7
F_1 crosses	16	10.5**
Reciprocal F_1	18	5.4*
F_1 vs. reciprocal F_1	1	11.7
Error	117	

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

Two seeds of each cultivar and F_1 crosses were planted in 10-cm-diameter pots in a mixture (80:20) of steamed topsoil and vermiculite. The plants received 15 hr of filtered sunlight per day in a greenhouse at temperatures of 20–32 C. One week after emergence, the plants were thinned to one per pot and fertilized weekly with one-half-strength Hoagland's solution. After the second and third weeks, a 0.1% ethirimol drench (6) was added to control powdery mildew (*Erysiphe graminis* DC.). Ethirimol is a narrow-spectrum fungicide that is effective against powdery mildew but has no activity against *L. nodorum*. A randomized complete block design was used with four replicates. Data were analyzed for a diallel series with both parents and F_1 crosses and reciprocal F_1 crosses as fixed effects (model I, method 1), according to Griffing (4). To estimate GCA and SCA effects, sum of squares of F_1 crosses was partitioned into sources of variations.

A virulent single-spore isolate of *L. nodorum* was grown on V-8 agar at 19 C with 12 hr/day of fluorescent light (2). Inoculum was prepared by aseptically scraping sporulating colonies with a scalpel and suspending conidia in deionized water. The turbidity of conidial suspensions was adjusted to 0.10 absorbance at 520 nm with a Spectronic 20 spectrophotometer (Bausch & Lomb, Inc., Rochester, NY). This resulted in a suspension with 10^6 conidia per milliliter based on a previously determined standard curve. One-tenth milliliter of Tween 20 (polyoxyethylene sorbitan monolaurate) was added to each liter of inoculum to reduce surface tension.

Three-week-old plants at the five- to seven-leaf stage were sprayed to runoff with the inoculum suspension and placed in large polyethylene bags to maintain 100% relative humidity. Plants were shaded to maintain temperatures below 25 C. Temperature was monitored by thermometers placed inside the bags. The bags were removed after 48 hr, and the plants were placed on a greenhouse bench. After inoculation, a temperature range of 18–25 C was maintained throughout the experiment.

Incubation and latent periods were recorded for each plant. Incubation period was measured in days as the time from inoculation until the first appearance of chlorotic and/or necrotic lesions. Latent period was measured as the time from inoculation of conidia until the appearance of pycnidia containing viable conidia observable by a 10× hand lens. By this time, about 50% of the pycnidia in a lesion had formed. Leaves with pycnidia were sampled randomly, and the pycnidia were examined microscopically for viable conidia. All young pycnidia observed contained viable conidia. Plants were observed daily after inoculation to determine incubation and latent period.

Table 2. Mean squares of analysis of variance for general combining ability (GCA) and specific combining ability (SCA) for incubation and latent periods of *Leptosphaeria nodorum* in the complete diallel

		Mean squares	
Source	df	Incubation period	Latent period
Crosses	20	0.9**[a]	5.8**
GCA	6	0.8	10.4**
SCA	14	0.9**	3.8**
Error	60		

[a] ** = Significant at $P = 0.01$.

Table 3. Average latent period (LP) of *Leptosphaeria nodorum* of crosses, midparents, differences between crosses and midparents, and specific combining ability (SCA) effects

		Days			
Crosses		LP	Midparent LP	Difference	SCA
Florida 301	× Fla. 301	11.3	...	...	...
	× Holley	12.8	10.8	2.0	4.87
	× Coker 747	11.8	13.4	−1.6	−2.33
	× Coker 762	11.0	12.1	−1.1	−5.33
	× Omega 78	13.5	12.9	0.6	4.67
	× Stacy	10.8	11.8	−1.0	−6.33
	× Oasis	10.8	12.3	−1.5	−3.13
Holley	× Holley	10.3	...	...	...
	× Coker 747	11.5	12.9	−1.4	−4.73
	× Coker 762	12.5	11.6	0.9	−0.73
	× Omega 78	12.8	12.4	0.4	0.27
	× Stacy	11.5	11.3	0.2	2.87
	× Oasis	11.3	11.8	−0.5	−2.53
Coker 747	× Coker 747	15.5	...	...	...
	× Coker 762	15.0	14.2	0.8	6.07
	× Omega 78	13.5	15.0	−1.5	0.07
	× Stacy	11.5	13.9	−2.4	−0.33
	× Oasis	13.0	14.4	−1.4	1.27
Coker 762	× Coker 762	12.8	...	...	...
	× Omega 78	12.8	13.7	−0.9	−2.93
	× Stacy	11.0	12.6	−1.6	−2.33
	× Oasis	14.0	13.1	0.9	5.27
Omega 78	× Omega 78	14.5	...	...	...
	× Stacy	11.3	13.4	−2.1	−1.33
	× Oasis	12.5	13.9	−1.4	−0.73
Stacy	× Stacy	12.3	...	...	...
	× Oasis	10.8	12.8	−2.0	−0.13
Oasis	× Oasis	13.3	...	...	...

RESULTS

Highly significant differences in latent period were detected among parents and F_1 crosses and significant ($P > 0.05$) differences were found among reciprocal F_1 crosses (Table 1). F_1 crosses versus reciprocal F_1 crosses did not differ significantly for latent period, indicating that maternal and/or cytoplasmic inheritance was not involved in resistance. Therefore, the data for reciprocal F_1 crosses were combined in the F_1 crosses data. Differences among parents and among F_1 crosses were highly significant; however, the comparison of parents vs. crosses was not significant.

GCA and SCA mean squares were highly significant for latent period (Table 2). Florida 301 and Holley had cross averages for latent period that were longer than the parental averages. Coker 747 × Coker 762 had the longest latent period of any cross or parent in this study (Table 3). For the Florida 301 single-cross array, the cross with the longest latent period was one with Omega 78; for the Omega 78 array, Florida 301 or Coker 747; for both Coker 747 and Oasis arrays, Coker 762; for the Coker 762 array, Coker 747; for the Holley array, Omega 78; and for the Stacy array, Holley or Coker 747. These results are what one would expect knowing that Coker 747, Coker 762, and Omega 78 all had a GCA effect of 2.66.

Large SCA effects were found for crosses of Florida 301 × Holley, Florida 301 × Omega 78, and Coker 762 × Oasis. The largest SCA effects for resistance were detected for Coker 747 × Coker 762. Coker 747, Coker 762, and Omega 78 all had large positive GCA effects (Table 4). Florida 301 had a large negative value for GCA effects.

Crosses and SCA effects for incubation period were highly significant ($P<0.01$) (Table 2). GCA effects for incubation period were not significant ($P>0.05$). No array of single crosses with a common parent had a longer incubation period than the longest incubation period of a parent, 5 days (Table 5). Coker 747 was the best general combiner (highest positive GCA effect), whereas Stacy and Florida 301 were the poorest. Coker 747 was the best parent for increasing the incubation period of Florida 301, Coker 762, Omega 78, and Stacy. The largest positive SCA effect was for Holley × Coker 762, and the most negative was for Coker 762 × Omega 78 (Table 6). Coker 762 had the higher GCA of the parents of Holley × Coker 762.

DISCUSSION

Other research conducted in the field involving these cultivars showed that Coker 747 and Coker 762 consistently had the longest incubation period, whereas Stacy, Omega 78, Holley, and Florida 301 had the shortest. Oasis had an intermediate incubation period (13). Similar responses were found among the cultivars in these tests conducted in the greenhouse.

Neither maternal nor reciprocal effects were observed, thus inheritance is nuclear. This agrees with findings by Nelson (9) and Nelson and Gates (10), who rated foliage and heads on a scale of 0 (no damage) to 9 (killed) for plant reaction to Septoria nodorum blotch. Rapilly et al (12), however, found inheritance of resistance to *L. nodorum* to be cytoplasmic and nuclear. Mullaney et al (8) reported that resistance was explained by additive gene effects and that the cytoplasm did not play a significant role for resistance. The longer incubation period for several crosses than that of the parents (Table 1) in our study agrees with results reported by Rapilly et al (12). Although the range of incubation periods we observed in the greenhouse was small, our observations on the cultivar rankings for resistance in a subsequent field study were the same (3). Inoculation in the field gave a wider range of differences for incubation period in reaction to *L. nodorum*. We observed in the earlier study an effect of microclimate (leaf position) and leaf age rather than large year effects (3).

Latent periods of F_1 crosses (9–12 days) were very similar to those of the parents (12.2 days) (Table 4). However, the most susceptible cultivars, Holley and Florida 301, with the shortest latent periods, had the greatest differences between the values for the parents and their single-cross array means. The two cultivars with the longest latent periods, Coker 747 and Omega 78, had a decrease in their cross averages compared with their parental averages. Nelson (9) reported that additive gene effects were probably most important in the

Table 4. Average latent period of *Leptosphaeria nodorum* for seven wheat cultivars, mean of single crosses with common parent, difference between parents and single crosses with common parent, and general combining ability (GCA) effects

Cultivar	Latent period (days)			
	Parent	Single cross	Difference	GCA
Coker 747	15.5	12.7	−2.8	2.66
Omega 78	14.5	12.7	−1.8	2.66
Coker 762	12.8	12.7	−0.1	2.66
Holley	10.3	12.0	1.7	−0.54
Florida 301	11.3	11.8	0.5	−1.94
Oasis	13.3	12.0	−1.3	−0.54
Stacy	12.3	11.3	−1.0	−0.94

Table 5. Average incubation period of *Leptosphaeria nodorum* on seven wheat cultivars (parents), mean of single crosses with common parents, difference between parents and single crosses with common parent, and general combining ability (GCA) effects

Cultivar	Incubation period (days)			
	Parent	Single cross	Difference	GCA
Coker 747	5.0	4.0	1.0	1.51
Omega 78	3.8	3.7	−0.1	0.31
Coker 762	3.8	3.6	−0.2	−0.29
Holley	3.0	3.7	0.7	0.31
Florida 301	3.5	3.5	0.0	−0.69
Oasis	3.5	3.5	0.0	−0.49
Stacy	3.3	3.5	0.2	−0.69

Table 6. Average incubation period (IP) of *Leptosphaeria nodorum* on crosses, midparents, differences between crosses and midparents, and specific combining ability (SCA) effects

Crosses		Days			
		IP	Midparent IP	Difference	SCA
Florida 301	× Fla. 301	3.5	...	...	...
	× Holley	3.3	3.3	0.0	−1.2
	× Coker 747	3.8	4.3	−0.5	−0.4
	× Coker 762	3.3	3.7	−0.4	−0.6
	× Omega 78	3.5	3.7	−0.2	−0.2
	× Stacy	3.5	3.4	0.1	0.8
	× Oasis	3.8	3.5	0.3	1.6
Holley	× Holley	3.0	...	...	...
	× Coker 747	4.0	4.0	0.0	−0.4
	× Coker 762	4.5	3.4	1.1	3.4
	× Omega 78	4.3	3.4	0.9	1.8
	× Stacy	3.0	3.3	−0.3	−2.2
	× Oasis	3.3	3.3	0.0	−1.4
Coker 747	× Coker 747	4.0	...	...	...
	× Coker 762	4.3	4.4	−0.1	1.2
	× Omega 78	4.5	4.4	0.1	1.6
	× Stacy	4.0	4.2	−0.2	0.6
	× Oasis	3.3	4.3	−1.0	−2.5
Coker 762	× Coker 762	3.8	...	...	...
	× Omega 78	3.0	3.8	0.0	−2.6
	× Stacy	3.0	3.6	−0.6	−1.6
	× Oasis	3.5	3.7	−0.2	0.2
Omega 78	× Omega 78	3.8	...	...	...
	× Stacy	3.5	3.6	−0.1	−0.2
	× Oasis	3.5	3.7	−0.2	−0.4
Stacy	× Stacy	3.3	...	...	...
	× Oasis	4.0	3.4	0.6	2.6
Oasis	× Oasis	3.5	...	...	...

inheritance of resistance to *L. nodorum.*

Neither maternal nor reciprocal inheritance effects were found for latent period. A larger portion of the variation was accounted for by GCA. Because the seven cultivars in this study are not a random sample of a population, the variations are only representative of the seven cultivars (14). One would expect to produce the best combination with a parent that had a large positive GCA effect. Although this would not be expected from the calculated GCA effects, Briggs and Knowles (1) state that, with other crop plants, GCA correlations between effects and SCA effect vary from 0.53 to 0.90. Coker 762 should make a good germ plasm source for the development of lines with longer latent periods. Coker 762 has also showed good field resistance to *L. nodorum.* Significant SCA effects on resistance to *L. nodorum* were observed for Holley × Ga #69-5611-1, Oasis × McNair 1813, and Holley × Blueboy II (9).

Leonard and Mundt (7) studied the importance of latent period in quantitative resistance using mathematical models. Several of their examples are based on data from diseases of small grains. They concluded that for diseases with long latent periods (greater than 8–10 days), selection for increased latent period is more important than selection for reduced pathogen sporulation. *L. nodorum* fits this category well. A significant range in latent period exists in the wheat cultivars grown in the southeastern United States. Coker 762 had long latent periods and good GCA effects. Coker 747 and Oasis increased latent period in various combinations with other cultivars. In the field, latent periods of the resistant cultivars Oasis, Coker 747, and Coker 762 may be as long as 18–25 days (3). Our results show that parents with extended latent periods can be selected and that this increase in latent period is probably heritable.

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