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Association between dwarfing genes 'Rht_1' and 'Rht_2' and resistance to *Septoria tritici* Blotch in winter wheat (*Triticum aestivum* L. em Thell)

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Summary. Differences in levels of resistance to *Septoria tritici* blotch were observed in plants with a specific height-reducing gene. When the gene 'Rht_2' was present either as an isoline or in the progeny, a higher degree of resistance was found. The most susceptible plants were observed in populations carrying the 'Rht_1' gene. Associations, as determined by phenotypic correlations, were detected between *Septoria tritici* blotch and tall stature, late heading, and maturity. Plants having short stature, early heading, early maturity, and acceptable levels of resistance were identified in the F_2 population when Rht_2 was present. Results of this study indicated that wheat breeders must select the appropriate dwarfing source that may confer resistance and grow large F_2 populations, in order to increase the probability of obtaining desired genotypes.

Key words: Winter wheat – Disease resistance – Norin 10 genes – *Septoria*

Introduction

Mycosphaerella graminicola (Fuckel) Schroeter (anamorph, *Septoria tritici* Rob. ex Desm.) is a major foliar pathogen of wheat in many parts of the world (Danon et al. 1982; Eyal 1981; Rajaram and Dubin 1977; Saari and Wilcoxson 1974). Increased severity of *Septoria tritici* blotch is thought by some to be due to the widespread replacement of tall, local cultivars by high-yielding, early maturing, semidwarf wheats (Danon et al. 1982; Eyal et al. 1987; Saadaoui 1987).

Many semidwarf cultivars possess one or both of the Norin 10 height-reducing genes (Rht_1 or Rht_2) in their parentage (Gale et al. 1981; Gale and Youssefian 1985). It has been suggested that short-strawed wheat cultivars are more susceptible to *Septoria tritici* blotch because reduced distances between consecutive leaves facilitate the ladder effect of pathogen progress up the plant (Bahat et al. 1980). However, experimental results have been inconsistent when comparisons were made between plant height and susceptibility (Danon et al. 1982; Scott et al. 1982; Scott and Benedikz 1985; Tavella 1978).

Genetic associations between short stature and susceptibility to *S. tritici* have also been suggested (Danon et al. 1982; Rosielle and Brown 1979; Tavella 1978). Pleiotropy or linkages between genes that determine plant height and susceptibility to *S. tritici* may explain such associations. However, low correlations between plant height and severity of the disease have been observed (Danon et al. 1982), which does not support the hypothesis for pleiotropy between short stature and susceptibility in wheat.

Early maturity is also frequently associated with susceptibility to *S. tritici*. This association may have both genetic and epidemiological explanations (Bahat et al. 1980). In regions where *Septoria tritici* blotch is a major problem, favorable cool temperatures and rain are more probable early in the life cycle of the plant. Thus, a vulnerable stage of development in early maturing cultivars is likely to occur during weather that is favorable for infection by the pathogen (Shaner et al. 1975). Genetic linkages between earliness and susceptibility to *S. tritici* have also been mentioned as a possible explanation for this association (Eyal 1981; Rosielle and Boyd 1985).

The tendency of short, early maturing cultivars to be more susceptible to *S. tritici* than taller, late-maturing cultivars could be a constraint to the plant breeder in developing superior wheat cultivars, as the amount of genetic variability available would be limited.

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This study was conducted to examine the following statistical relationships involving *Septoria tritici* blotch: (a) association between 'Rht_1' and/or 'Rht_2' with susceptibility, and (b) associations among plant height, heading date, and susceptibility.

Materials and methods

Experimental material consisted of four near-isogenic lines of winter wheat (*Triticum aestivum* L. em Thell.) selected from the backcross population 'Itana'/3/'Norin 10'/'Brevor 14'//6*'Itana'. The isogenic lines selected were: (1) a two-gene short semidwarf, CI 17862 (Rht_1Rht_2), (2) two one-gene medium semidwarfs, CI 17869 (Rht_1rht_2) or CI 17863 (rht_1Rht_2) and (3) a standard height line, CI 17874 (rht_1rht_2) (Allan and Pritchett 1982). The isogenic lines mature late and are moderately resistant to *Septoria tritici* blotch. Tibet Dwarf, an extremely short-statured, early maturing selection susceptible to *Septoria tritici* blotch, was used as the common parent in crosses with the isogenic lines. This selection was obtained in the People's Republic of China and named Tibet Dwarf at Oregon State University.

Crosses were made using Tibet Dwarf as the male and the four isogenic lines as the female in the 1983–1984 crop cycle. In 1984–1985, the F_1 was advanced to the F_2 generation. The parents, F_1 and F_2, were space-planted on October 20, 1985 at the Hyslop Agronomy Farm located 11 km northeast of Corvallis/OR. This site is characterized by the presence of the sexual stage of *Septoria tritici* blotch (*M. graminicola*) (A. L. Scharen, personal communication). The soil type was a fine, silty, mixed mesic Aquultic Argixeroll. Prior to fall planting, 67 kg/ha of nitrogen and 10 kg/ha of sulfur were applied as 40–0–0–6. In late spring, the fertility level was increased by the addition of 195 kg/ha of nitrogen and 30 kg/ha of sulfur. Alachlor and chlorosulfuron were applied at a rate of 1.76 l/ha and 23.35 g/ha, respectively, for weed control.

A split-plot design with three replications was used. Crosses were the main plots and parents F_1 and F_2 populations were the subplots. Parents and F_1s comprised a single row of 15 plants with 15 cm between plants and 25 cm between rows. F_2s consisted of 5 rows with 15 plants in each row. The cultivar 'Stephens,' susceptible to *Septoria tritici* blotch, was planted as a border around each replication. Infected straw collected the previous season was spread uniformly between the rows to increase the inoculum of *S. tritici*. Each plant in the trial was evaluated for five factors. These included: (a) PCS, percent coverage by symptoms in the uppermost four leaves at growth stage 11.3 of Feekes' scale (Eyal et al. 1987); (b) SPC, *Septoria* Progress Coefficient [height of disease reached on plant (cm)/plant height (cm)] (Eyal et al. 1983); (c) plant height from the soil surface to the tip of the tallest spike; (d) heading date, time from planting to when the first spike on the plant emerged from the boot; and (e) physiological maturity, time from planting to when the first spike and peduncle lost their green color.

The per plant values were averaged because of unequal sample sizes and the analyses of variance were conducted on the basis of plot means. For analysis of phenotypic correlations among plant height, heading date, and susceptibility to *S. tritici*, the total of individual plant values was used.

Results and discussion

Table 1. Percent coverage by symptoms (PCS), *Septoria* progress coefficient (SPC), plant height, and heading date for five winter wheat parents grown at the Hyslop Agronomy Farm, Corvallis OR, 1985–1986

Winter wheat parents	Means				
	(PCS) %	(SPC)	Plant height (cm)	Heading date (days)	Maturity date (days)
rht_1rht_2	21.6^{cd}	0.37^{d}	131.4^{a}	145.3^{b}	186.6^{b}
rht_1Rht_2	14.2^{d}	0.18^{e}	90.2^{c}	145.6^{b}	186.7^{b}
Rht_1rht_2	27.4^{bc}	0.46^{c}	111.7^{b}	147.4^{a}	188.6^{a}
Rht_1Rht_2	32.7^{b}	0.69^{b}	83.3^{c}	146.6^{ab}	187.9^{ab}
Tibet Dwarf	55.6^{a}	0.94^{a}	34.7^{d}	122.4^{c}	150.6^{c}

Genotypes denoted by the same letter in the same column are not significantly different at the 0.05 level using LSD

Variability in the mean disease expression was observed between the tall, semidwarf, and dwarf near-isogenic lines, despite their common genetic background (Table 1). Lowest disease severity mean values were found for the semidwarf rht_1Rht_2. The highest disease reactions were observed for the dwarf Rht_1Rht_2. The near-isogenic line, rht_1rht_2, was the tallest and the double-dwarf, Rht_1Rht_2, the shortest. Differences for heading dates among the isogenic lines were small. Tibet Dwarf had higher disease mean values than the four isogenic lines. It was also 50 cm shorter than the double-dwarf, Rht_1Rht_2. Heading date for Tibet Dwarf was approximately 25 days earlier than for the four isogenic lines.

Frequency distributions, ranges, means, and standard deviations of the percent coverage of disease in the four uppermost leaves were calculated for the parents, F_1, and F_2 populations (Table 2). The F_2 mean for percent coverage of disease was intermediate between the two parents for the four crosses. The frequency distribution of the F_2 between the tall isogenic line, rht_1rht_2 × Tibet Dwarf, suggests that individual plant types were recovered with reactions similar to both the susceptible and resistant parents. In this cross, the range of the F_2 also indicates that transgressive segregation toward resistance was present.

Similar F_2 mean values for disease reaction were observed between rht_1Rht_2, and Rht_1Rht_2 × Tibet Dwarf. Transgressive segregation toward resistance was observed in the F_2 population between rht_1Rht_2 × Tibet Dwarf. Resistant F_2 plants with 1% levels of infection were present.

Data for the cross between Rht_1Rht_2 × Tibet Dwarf are not easily interpreted. The mean value for susceptibility was lower for the F_2 population than it was for the F_2. Although the frequency distribution of the F_2 indicated that a great number of plants were susceptible to the disease, it seems probable that the Rht_2 dwarfing gene conferred some resistance. F_2 plants with disease severity of less than 15% were present in this population.

Table 2. Frequency distributions, ranges, means, and standard deviations of percent coverage by symptoms of winter wheat parents, F_1, and F_2 progeny populations

Parents, F_1s and F_2s	Classes (PCS)								
	A	B	C	D	E				
	5–15	16–25	26–35	36–45	>45	*N*	Range	Mean	SD
$rht_1 rht_2$	17	6	21	0	0	44	11–34	21.6	9.6
F_1	0	13	5	1	0	19	22–34	28.0	6.8
F_2	14	58	29	48	31	180	1–58	31.5	12.9
$rht_1 Rht_2$	15	26	0	0	0	41	8–20	14.2	4.9
F_1	0	5	3	0	0	8	21–30	24.2	3.05
F_2	3	34	42	38	56	173	1–56	34.6	11.4
$Rht_1 rht_2$	0	7	30	8	0	45	25–32	28.5	3.2
F_1	0	0	1	9	28	38	35–55	44.3	3.3
F_2	0	12	12	35	113	185	16–59	41.6	10.4
$Rht_1 Rht_2$	0	0	45	0	0	45	25–32	32.7	3.2
F_1	0	0	1	13	5	19	31–48	41.5	4.5
F_2	4	30	28	55	58	175	10–55	36.4	11.1
Tibet Dwarf (common parent)	0	0	0	0	169	169	51–63	55.3	2.8

Classification of parents, F_1, and F_2 populations to severity classes (A–E) based on leaf covered by pycnidia of *S. tritici*

Mean values of the F_1 and F_2, from the cross between $Rht_1 rht_2$ × Tibet Dwarf, were more closely related to the susceptible parent than to the resistant parent. The frequency distribution of the F_2 indicated that plants in class A (5–15), considered as resistant in this study, were not recovered. A large number of F_2 plants with PCS higher than 45% was observed. It should be noted, however, that the range of the resistant parent fell between classes B and D. Results in this cross suggest that the Rht_1 dwarfing gene is not associated with resistance. This conclusion is supported by the high population PCS mean values for the F_1 (44.3%) and F_2 (41.6%).

In an effort to determine whether plant height, heading, maturity dates, and susceptibility to *Septoria tritici* blotch are associated, phenotypic correlations were determined.

Both percent coverage of symptoms (PCS) and *Septoria* progress coefficient (SPC) gave similar results, when phenotypic associations among plant height, heading, maturity date, and susceptibility to *Septoria tritici* blotch were measured (Tables 3 and 4). There was also close agreement between the phenotypic and genetic correlation coefficients for the F_2 population.

Phenotypic correlations between plant height, PCS, and SPC were high and negative. There was clear evidence of linkage between genes controlling plant height and resistance to *Septoria tritici* blotch. It was also found that a tendency for susceptibility to *Septoria tritici* blotch was negatively associated with maturity date.

Our evidence did not clearly show a negative association when determining the phenotypic associations between *Septoria tritici* blotch and heading date. The same response was expected when determining the associations between *Septoria tritici* blotch, maturity date, and heading date, as heading date has been used to predict early maturity.

Establishing appropriate breeding objectives is essential for success in the development of short, stiff-strawed, early maturing wheat cultivars. Early maturing wheat cultivars are important in a multiple cropping system and in low-rainfall regions to escape drought and other abiotic and biotic stresses. Under irrigated or higher rainfall conditions, higher fertility rates can be employed with short, stiff-strawed cultivars, thereby increasing yield levels by avoiding the lodging that frequently occurs with taller cultivars.

The difficulties in combining short plant stature and earliness with resistance to *Septoria tritici* blotch (Rosielle and Brown 1979) and *Septoria nodorum* blotch (Scott et al. 1982) have led some researchers to conclude that pleiotropy or tight linkage might have interfered with incorporation efforts. Small negative correlations reported in other studies do not support this hypothesis (Danon et al. 1982). The use of different sources of resistant winter wheat germ plasm had led breeders from the International Maize and Wheat Improvement Center (CIMMYT) to develop a considerable number of semidwarf, high-yielding lines, having a degree of resistance to *Septoria tritici* blotch (Mann et al. 1985; Rajaram and Dubin 1977). These findings might also suggest that the semidwarf character is not closely linked to susceptibility to *Septoria tritici* blotch.

Our data indicate that differences do exist for response to *Septoria tritici* blotch between the Norin

Table 3. Correlations between percent coverage by symptoms (PCS), plant height, heading, and maturity date in F_1s and F_2s of specified crosses

Cross	Characters	Phenotypic correlations			
		N	F_1	*N*	F_2
CB23-77268	(PCS) vs				
CI 17864 (rht_1 rht_2)	Plant height	19	−0.268	180	−0.606 **
	Heading date	19	−0.351	180	0.036
	Maturity date	19	−0.731 **	180	−0.241 **
CB22-77267	(PCS) vs				
CI 17873 (rht_1 Rht_2)	Plant height	8	0.166	173	−0.570 **
	Heading date	8	0.048	173	0.100
	Maturity date	8	−0.431	173	−0.232 **
CB18-77262	(PCS) vs				
CI 17869 (Rht_1 rht_2)	Plant height	38	−0.098	185	−0.614 **
	Heading date	38	0.066	185	0.065
	Maturity date	38	0.207	185	−0.213 **
CB11-77253	(PCS) vs				
CI 17862 (Rht_1 Rht_2)	Plant height	19	−0.261	175	−0.517 **
	Heading date	19	0.226	175	−0.162
	Maturity date	19	−0.379	175	−0.415 **

** Significantly different at the 0.01 level

Table 4. Correlations between *Septoria* progress coefficient (SPC) and plant height, heading, and maturity date for F_1s and F_2s of specified crosses

Cross	Characters	Phenotypic correlations			
		N	F_1	*N*	F_2
CB23-77268	(SPC)				
CI 17874 (rht_1 rht_2)	Plant height	19	−0.328	180	−0.646 **
	Heading date	19	−0.331	180	0.089
	Maturity date	19	−0.765 **	180	−0.219 **
CB22-77267	(SPC) vs				
CI 17873 (rht_1 Rht_2)	Plant height	8	−0.214	173	−0.519 **
	Heading date	8	0.355	173	0.073
	Maturity date	8	−0.082	173	−0.263 **
CB18-77262	(SPC) vs				
CI 17869 (Rht_1 rht_2)	Plant height	38	−0.251	185	−0.533 **
	Heading date	38	0.033	185	0.019
	Maturity date	38	−0.324 *	185	−0.194 *
CB11-77253	(SPC) vs				
CI 17862 (Rht_1 Rht_2)	Plant height	19	0.373	175	−0.456 **
	Heading date	19	−0.373	175	−0.174 *
	Maturity date	19	−0.142	175	−0.430 **

*,** Significantly different at the 0.01 and 0.05 level, respectively

10 Rht_1 and Rht_2 dwarfing genes. Thus, to select short, early maturing cultivars with acceptable levels of resistance, it will be important to use the most resistant dwarfing source available for parental material. In our experiment, the Rht_2 dwarfing gene was generally associated with a higher level of resistance than the Rht_1 gene. This resistance was transmitted to the F_1 and F_2 generations. Therefore, these results indicate that improvement would appear to be possible for *Septoria tritici* blotch resistance via crosses with the Rht_2 gene (Tables 1 and 2). These results support preliminary studies carried out by Scott and Benedikz (1985), where plants possessing the Rht_2 dwarfing gene had higher levels of resistance regardless of plant height. However, later studies have suggested that the Rht_2 gene might not be closely associated with resistance to *Septoria tritici* blotch (Eyal et al. 1987).

In this study, shorter wheats had generally higher *Septoria tritici* blotch susceptibility, which might be a manifestation of the ladder effect by which the inoculum reaches the upper canopy (Bahat et al. 1980). Nevertheless, tall-susceptible, and short-resistant plants were recovered in the F_2 populations, as has been previously suggested (Danon et al. 1982). Note, however, that in progeny of crosses where the Rht_2 dwarfing gene was present, a higher frequency of short-resistant plants was recovered within each particular class than in progeny of crosses involving Rht_1 (Table 2).

The phenotypic correlations supported the hypothesis that late maturity was associated with taller plants and lower *Septoria tritici* blotch reactions. However, the evidence is not clear as to the association between early heading and susceptibility, since the phenotypic correlation values were low. This might indicate that the longer the plants are exposed to the infection periods, the greater the chances of being attacked by the pathogen.

The high negative phenotypic correlation coefficients found between *Septoria tritici* blotch and short stature in the F_2 generations suggest that these traits are associated and that genetic linkages may be involved. The presence of dwarf and semidwarf resistant wheats observed in the F_2 generations favors linkages rather than pleiotropism, as previous reports have suggested (Danon et al. 1982; Rosielle and Brown 1979; Rossielle and Boyd 1985).

We conclude that it should be possible to select shorter, earlier maturing wheat cultivars with acceptable levels of resistance to *Septoria tritici* blotch. It is important that the emphasis be placed on the source of the Rht_2 dwarfing gene and that large F_2 populations be grown to obtain the desired plant types. This procedure would also avoid possible linkages between short stature, earliness, and susceptibility to *Septoria tritici* blotch.

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