Major Gene Controls of Field Resistance to Spot Blotch in Wheat Genotypes ‘Milan/Shanghai #7’ and ‘Chirya.3’

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ABSTRACT

Neupane, R. B., Sharma, R. C., Duveiller, E., Ortiz-Ferrara, G., Ojha, B. R., Rosyara, U. R., Bhandari, D., and Bhatta, M. R. 2007. Major gene controls of field resistance to spot blotch in wheat genotypes ‘Milan/Shanghai #7’ and ‘Chirya.3.’ *Plant Dis.* 91:692-697.

A number of exotic wheat (*Triticum aestivum*) genotypes resistant to spot blotch caused by *Cochliobolus sativus* are being used to improve the resistance of commercial cultivars in the warm regions of South Asia. The objective of the present study was to determine the inheritance of field resistance to spot blotch in two resistant (R) wheat genotypes, ‘Chirya.3’ and ‘Milan/Shanghai #7’ (MS#7), which were crossed to a susceptible (S) commercial cultivar, ‘BL1473.’ The two resistant genotypes also were crossed to determine allelic relationships for resistance between them. Spot blotch severity was recorded on the parents and on F₁, F₂, and F₃ progenies. The F₁ plants from the two crosses between susceptible and resistant genotypes had low disease severity like the resistant parents, indicating that resistance in Chirya.3 and MS#7 is conditioned by dominant gene action. The F₂ plants segregated in 3R:1S ratios, and the F_{2,3} families showed the ratio of 1R:1S:2S, segregating for R and S, suggesting that resistance in the two resistant parents is conditioned by a single, dominant gene. The F₁ plants from the cross between the two resistant genotypes were resistant, whereas their F₂ progenies segregated in 15R:1S, suggesting that the resistance genes in MS#7 and Chirya.3 are nonallelic. These simply inherited sources of resistance could be useful for improving spot blotch resistance in the warm regions of South Asia and also may offer useful diversity to breeding programs for developing spot-blotch-resistant wheat cultivars in other regions.

Spot blotch caused by *Cochliobolus sativus* (Ito & Kuribayashi) Drechs. ex Das-tur (anamorph *Bipolaris sorokiniana* (Sacc.) Shoemaker)—also reported in South Asia as helminthosporium leaf blight or foliar blight—has been an important disease of wheat (*Triticum aestivum* L.) in warmer wheat-growing regions in the last two decades (2,6,9,12,17,18,30). The disease has been a particularly serious biotic constraint in eastern regions of South Asia (5,7,27), affecting the livelihood of millions of small farmers depending on wheat cultivation (8). Losses between 20 and 52% have been reported on susceptible cultivars (20,26,27) in farmers’ fields. Although important progress has been made in recent years by wheat breeding programs targeting materials suitable for the Gangetic Plains (11,24,31), recently released cultivars still show substantial

reductions in grain yield under resource-constrained farming conditions (27). In an early study in Nepal, India, and Bangladesh, Dubin et al. (4) identified several wheat genotypes exotic to the region that possessed better resistance than the local commercial cultivars. Recently, Duveiller and Sharma (11) reported several wheat genotypes with high levels of resistance to spot blotch in the eastern Gangetic Plains of South Asia.

Despite the necessary time commitment, the most economically sound and ecologically friendly strategy to address the spot blotch problem is to develop resistant cultivars. To do so efficiently requires an understanding of the genetics of resistance in improved genotypes. The limited genetic studies so far published have reported inconclusive and contrasting results. Both qualitative and quantitative inheritance of spot blotch resistance are suggested (14). Dominant and recessive genes are reported to control inheritance of resistance and, in certain cases, epistasis also has been found. Adlakha et al. (1) reported that spot blotch resistance in the seedling stage was conditioned by one or two dominant genes. Srivastava et al. (34) indicated that seedling resistance to spot blotch was controlled by two dominant epistatic genes. Similarly, Sharma and Bhatta (22) found that three dominant epistatic genes were

involved in the genetic control of spot blotch. In a field study in Mexico, Velazquez (36) reported that spot blotch resistance was partially dominant, with two to three genes conditioning adult plant resistance. In contrast, others have reported that one to three complementary recessive genes confer resistance to wheat foliar blight (19,32,33). Likewise, Bhushan et al. (3) reported that two recessive genes with additive effect controlled leaf blight resistance in Punjab, India. Joshi et al. (16) reported that three additive genes controlled spot blotch resistance in the eastern Gangetic Plains of India. Sharma et al. (25) reported that spot blotch resistance in wheat was quantitatively inherited, with intermediate to high estimates of heritability.

In recent years, efforts have been made to identify spot-blotch-resistant wheat genotypes derived from crosses involving new, alien resistance sources such as *Thinopyrum curvifolium* (Lange) D. R. Dewey or synthetic hexaploid wheats derived from so-called “wide” crosses between a *Triticum turgidum* var. *durum* (Desf.) Husnot and *Triticum tauschii* (Coss.) Schmal. Duveiller and Sharma (11) identified a number of wheat genotypes that possessed high levels of resistance to spot blotch along with acceptable grain yield and maturity. The most resistant and highest-yielding genotype was Milan/Shanghai #7. Other studies have confirmed that Milan/Shanghai #7 and Chirya.3 are highly resistant to spot blotch (10,16,19). The present study was conducted to determine the inheritance of field resistance to spot blotch in Milan/Shanghai #7 and Chirya.3 under natural disease epidemics in two hot spot locations where plant type and spot blotch expression are excellent.

MATERIALS AND METHODS

The crosses were made in the 2003–04 wheat-growing season (November to March) and the F₁ plants were grown in an off-season, high-altitude field nursery in 2004 (June to October) at Marpha (28°43’N and 83°15’E, 2,900 masl, in the Himalayas), Nepal, to produce the F₂ seed. Because there was limited seed for F₁s but enough for F₂ populations and the parents, two field trials were conducted simultaneously with the remaining F₁ seed and F₂ populations in 2005. Both trials were

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Accepted for publication 21 December 2006.

doi:10.1094/PDIS-91-6-0692
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conducted side-by-side at Rampur (27°40'N and 84°19'E at 228 meters above sea level [masl]) and Bhairahawa (27°06'N and 82°04'E at 105 masl), Nepal. These are environmentally contrasting lowland sites 130 km from each other where spot blotch is a serious, endemic problem of wheat (28). Relative humidity in Rampur is usually higher than elsewhere in the Nepal lowlands, known as the *tarai*. This favors the early onset of spot blotch epidemics, with the first lesions (1 to 2 mm) already visible about 4 weeks after sowing. However, spot blotch has been severe on the wheat crop for the past several years at both sites. Rampur soils are a medium-textured loam, compared with heavy clay soil at Bhairahawa. The two study sites are a part of the vast eastern Gangetic Plains of South Asia, characterized by high temperatures and humidity and classified

as mega-environment 5 in CIMMYT's system for describing wheat target environments (35).

Three wheat parents, 'BL1473,' 'Chirya.3,' and 'Milan/Shanghai #7,' were used in the study. BL1473 (Nepal 297/NL531; CIMMYT, CID 166468) is an early-maturing, spot-blotch-susceptible commercial cultivar in Nepal (29). Chirya.3 (CS/Th cul/Vee/3/Ald/Pvn/4/Ningmai No.4/Oleson//Ald/Yangmai No. 4; CIMMYT, CID 54384) and Milan/Shanghai #7 (CIMMYT, CID 20026) are genotypes of intermediate maturity derived from wide crosses at CIMMYT. They have shown high levels of spot blotch resistance in South Asia, including Nepal (11,28). BL1473 was crossed with Milan/Shanghai #7 and Chirya.3 to study the inheritance of spot blotch resistance. Chirya.3 was crossed with Milan/Shanghai #7 to

determine allelic relationships of resistance genes between the two.

The three F₁ populations along with the three parents were planted in single, 1-m rows with 0.25-m row spacing and replicated three times in a randomized complete block arrangement. Individual rows were planted with 20 seed and thinned after emergence to maintain 10 plants per row. The three F₂ populations and the three parents were planted using the same experimental design and plant density, but plots consisted of three 5-m rows with 50 to 60 plants per replication. Fertilizer was applied prior to seeding as recommended for the experimental site, using N, P₂O₅, and K₂O at 120, 60, and 40 kg ha⁻¹, respectively. Plots were kept free of weeds by hand weeding. The trial was seeded on 26 November 2004 at Rampur and 3 December 2004 at Bhairahawa. The optimum

Table 1. Mean spot blotch severity with standard deviation recorded on the three wheat parents and their F₁ and F₂ progeny at three growth stages (ZGS59, ZGS71, and ZGS77) in the inheritance study

Generation ^b	Spot blotch severity (%) ^a								
	Rampur, 2005			Bhairahawa, 2005			Rampur, 2006		
	ZGS59	ZGS71	ZGS77	ZGS59	ZGS71	ZGS77	ZGS59	ZGS71	ZGS77
BL1473	29 ± 0.6	47 ± 1.2	76 ± 2.3	27 ± 0.5	44 ± 1.0	73 ± 1.6	31 ± 0.6	48 ± 1.2	78 ± 1.8
Chirya.3	0	4 ± 0.1	13 ± 0.6	0	5 ± 0.1	12 ± 0.7	0	5 ± 0.1	10 ± 0.6
MS#7	0	6 ± 0.1	12 ± 1.3	0	4 ± 0.1	13 ± 1.1	0	4 ± 0.1	11 ± 1.0
BL1473 × Chirya.3 F ₁	0	6 ± 0.1	17 ± 1.0	0	7 ± 0.2	15 ± 0.8	...	...	...
BL1473 × Chirya.3 F ₂ (R)	0	8 ± 0.1	16 ± 1.3	0	9 ± 0.2	17 ± 1.4	...	...	...
BL1473 × Chirya.3 F ₂ (S)	24 ± 0.5	41 ± 1.1	69 ± 1.6	27 ± 0.5	42 ± 0.6	68 ± 1.7	...	...	...
BL1473 × MS#7 F ₁	0	4 ± 0.1	15 ± 0.7	0	7 ± 0.1	16 ± 0.8	...	...	...
BL1473 × MS#7 F ₂ (R)	0	6 ± 0.1	15 ± 0.4	0	7 ± 0.1	17 ± 0.2	...	...	...
BL1473 × MS#7 F ₂ (S)	26 ± 0.4	45 ± 1.3	66 ± 1.4	23 ± 0.5	39 ± 0.7	67 ± 1.6	...	...	...
Chirya.3 × MS#7 F ₁	0	3 ± 0.1	12 ± 0.8	0	4 ± 0.1	12 ± 1.0	...	...	...
Chirya.3 × MS#7 F ₂ (R)	0	6 ± 0.1	13 ± 0.3	0	7 ± 0.2	13 ± 0.2	...	...	...
Chirya.3 × MS#7 F ₂ (S)	23 ± 0.4	38 ± 0.6	71 ± 1.8	22 ± 0.3	37 ± 0.5	66 ± 1.5	...	...	...

^a Data shown ± standard deviation.

^b MS#7 = Milan/Shanghai #7. R = resistant and S = susceptible plants.

Table 2. χ^2 Goodness-of-fit test for spot blotch resistance involving three resistant and one susceptible wheat genotypes studied at two sites in Nepal in 2005 and 2006^a

Generation ^b	Location	Early-maturity group				Late-maturity group				Both maturity groups				
		No. of plants		R:S	χ^2	No. of plants		R:S	χ^2	No. of plants		R:S:Sg	χ^2	
		R	S			R	S			R	S			
BL1473	Rampur	...	60	...	...	...	...	...	...	...	...	...	...	...
	Bhairahawa	...	60	...	...	...	...	...	...	...	...	...	...	...
Chirya.3	Rampur	...	...	...	...	60	...	...	...	...	...	...	...	...
	Bhairahawa	...	...	...	...	60	...	...	...	...	...	...	...	...
MS#7	Rampur	...	...	...	...	60	...	...	...	...	...	...	...	...
	Bhairahawa	...	...	...	...	60	...	...	...	...	...	...	...	...
BL1473 × Chirya.3) F ₁	Rampur	30	0	...	...	...	...	...	...	...	...	...	...	...
BL1473 × Chirya.3) F ₂	Rampur	81	26	3:1	0.87	45	15	3:1	1.00	126	41	...	3:1:0	0.89
BL1473 × Chirya.3) F ₁	Bhairahawa	30	0	...	...	...	...	...	...	...	...	...	...	...
BL1473 × Chirya.3) F ₂	Bhairahawa	41	14	3:1	0.94	27	9	3:1	1.00	68	23	...	3:1:0	0.95
BL1473 × Chirya.3) F ₃	Rampur	...	...	...	...	...	...	...	...	43	39	80	1:1:2	0.89
BL1473 × MS#7 F ₁	Rampur	30	0	...	...	...	...	...	...	...	...	...	...	...
BL1473 × MS#7 F ₂	Rampur	74	25	3:1	0.95	43	14	3:1	0.94	117	39	...	3:1:0	1.00
BL1473 × MS#7 F ₁	Bhairahawa	30	0	...	...	...	...	...	...	...	...	...	...	...
BL1473 × MS#7 F ₂	Bhairahawa	61	20	3:1	0.95	35	11	3:1	0.86	96	31	...	3:1:0	0.88
BL1473 × MS#7 F ₃	Rampur	...	...	...	...	...	...	...	...	41	36	74	1:1:2	0.82
Chirya.3 × MS#7 F ₁	Rampur	...	...	...	...	30	0	...	...	...	...	...	...	...
Chirya.3 × MS#7 F ₂	Rampur	...	...	...	...	87	6	15:1	0.94	...	...	...	...	...
Chirya.3 × MS#7 F ₁	Bhairahawa	...	...	...	...	30	0	...	...	...	...	...	...	...
Chirya.3 × MS#7 F ₂	Bhairahawa	...	...	...	...	110	7	15:1	0.90	...	...	...	...	...

^a R = resistant, S = susceptible, R:S = ratio tested, and Sg = segregating for R and S.

^b MS#7 = Milan/Shanghai #7.

wheat-seeding period in the region is between 20 November and 10 December.

The trials were managed under natural disease infection. The experimental field had no residue from the previous wheat crop. The field remained submerged in floodwater for several weeks in August and September 2004, as is the case in most years in the lowlands of Nepal grown to rice. Disease spreader rows of a mixture of foliar blight-susceptible wheat genotypes were seeded at both ends of each experimental plot.

Disease severity was recorded at several growth stages up to Zadoks' stage ZGS77 (37). After this stage, natural senescence also started and diseased leaf area could not always be clearly separated from natural senescence. Disease severity data at ZGS59, ZGS71, and ZGS77 have been presented (Table 1). The F₂ plants were classified as early or late, in comparison with the early-maturing parent BL1473. When the main tiller of a plant had headed by the time all main tillers in a BL1473 plot had spikes completely emerged, the plant was tagged as early maturing. Plants

heading later than BL1473 were classified as late maturing. Disease data were recorded at different growth stages, but we used the score at ZGS77 for the analyses. Spot blotch severity was scored visually for each row at weekly intervals using a double-digit (00 to 99), modified version of Saari and Prescott's scale (13,21) for wheat foliar diseases. The first digit (D₁) indicates disease progress in height and the second digit (D₂) refers to severity measured as the diseased leaf area. For each score, percentage of disease severity was estimated based on the following formula:

$$\% \text{ severity} = (D_1/9) \times (D_2/9) \times 100$$

The F₂ plants were harvested individually and threshed to sow F_{2,3} progeny rows.

The F₃ progeny rows were grown as 1-m rows with 20 seed per row in three replications at Rampur only. The two crosses between susceptible and resistant parents were evaluated in the F₃ generation. A row of the susceptible and resistant parents was sown after every 10 progeny rows. We seeded disease spreader rows with a mixture of foliar blight-susceptible genotypes

at both ends of each experimental plot. The trial was planted on 26 November 2005 and managed according to the procedure described earlier for the F₂ generation. An F₃ progeny row was classified as "susceptible" when all plants in the family were susceptible, "resistant" when all plants were resistant, and "segregating" when plants were both susceptible and resistant.

For F₂ plants, we analyzed the results for individual locations as well as for plants separated into early- and late-maturity groups. Frequency distributions for spot blotch severity of the three F₂ populations at two sites were accomplished. A χ^2 analysis was used to test goodness of fit to hypothetical ratios and to verify that observed deviations were within statistically acceptable limits ($P \geq 0.05$).

RESULTS

High spot blotch severity occurred in the experimental plots, as reflected by the high disease severity of the susceptible cv. BL1473 at growth stage ZGS77 in both years (Table 1). No other foliar disease was present. In particular, the level of leaf

Fig. 1. Frequency distribution for wheat spot blotch severity in the field at three growth stages in the F₂ generation of the BL1473 × Chirya.3 cross of wheat grown at Rampur and Bhairahawa, Nepal, in the 2004–05 growing season; spot blotch severity on the parents and on F₁.

rust (*Puccinia tritricina* Eriks.) remained negligible throughout the growing season. The typical symptoms of spot blotch—lesions >1 to 2 cm long—were clearly noticeable on the spreader rows and the susceptible parent as early as the fourth week of January, before the crop headed, and were uniformly visible on all plants in a plot. The presence of *B. sorokiniana* conidia could be observed under the microscope on all of the 150 diseased leaves randomly sampled from the experimental plots at each site in each year, after 24 to 48 h of incubation on moist blotting paper, and isolates from representative samples confirmed the high incidence of *C. sativus*. Weather conditions were optimal for wheat cultivation in 2005; however, a long dry spell occurred during the 2006 spring wheat season.

At growth stage ZGS77, BL1473 showed >70% disease severity, whereas the resistant parents had <15% severity (Table 1), confirming previous reports

(11,29). Toward maturity, disease severity on the susceptible parents reached 100% but was below 20% on the resistant parents. Severity on the flag and penultimate leaves of the susceptible parents reached 100%, but was <10% on the resistant parents on the two uppermost leaves.

All F₁ plants of a cross between early-maturing susceptible and late-maturing resistant plants headed early. On the other hand, all F₁ plants from the cross between two late-maturing resistant parents headed late. All F₁ plants showed the same, low disease severity as the resistant parent in all three crosses, indicating dominant gene control of resistance (Table 2). Frequency distribution patterns in the F₂ generation were bimodal in all three populations at three growth stages at both locations (Figs. 1 to 3). The F₂ plants that were resistant at ZGS59 remained resistant at the later growth stages as well. The F₂ plants from the two crosses between susceptible (S) and resistant (R) parents segregated at a

ratio of 3R:1S, suggesting that resistance was conditioned by a single dominant gene (Table 2). This was further confirmed by the segregation pattern (1R:1S:2S, segregating for R and S) of the F₃ progeny rows. Plants rated as susceptible from the F₂ generation also were susceptible in the F₃ generation. On the other hand, plants considered resistant in the F₂ generation produced progenies that were either homozygous resistant or segregated as resistant and susceptible. No resistant F₂ plant produced a homozygous susceptible F₃ progeny. The segregating F₃ families showed more resistant and fewer susceptible progenies, as expected when resistance is dominant over susceptibility.

The F₂ plants from the cross between the two resistant parents segregated at 15R:1S, indicating that the spot-blotch-resistant genes in the two parents were nonallelic. This was expected, given that the resistant parents come from different genetic backgrounds: Milan/Shanghai #7

Fig. 2. Frequency distribution for spot blotch severity in the field at three growth stages in the F₂ generation of the BL1473 × Milan/Shanghai #7 cross of wheat grown at Rampur and Bhairahawa, Nepal, in the 2004–05 growing season; spot blotch severity on the parents and on F₁.

was developed by CIMMYT from a cross between tan-spot-resistant Milan and spot-blotch-resistant Shanghai #7; Chirya.3 is derived from a wide cross.

Segregation ratios in the F_2 generation were consistent for both early- and late-maturity groups at both locations, suggesting an absence of genetic association between wheat maturity and spot blotch resistance, a finding in agreement with the previous results of Sharma and Bhatta (23) and Joshi et al. (15).

DISCUSSION

Duveiller and Sharma (11) recently reported that Milan/Shanghai #7 showed the most stable spot blotch resistance among a number of resistant genotypes, in a study across 35 environments in the plains of eastern India, Nepal, and Bangladesh. Milan/Shanghai #7 also showed the highest grain yields and was the most stable among leading spot-blotch-resistant genotypes, including the region's most recently released commercial cultivars.

The results of our study, conducted under field conditions, also shows that Chirya.3 possesses a single dominant gene for spot blotch resistance, which is different from the previous findings (16,19). Ragiba et al. (19) reported that spot blotch resistance in Chirya.3 was conditioned by two recessive genes, whereas Joshi et al. (16) found that resistance in Chirya.3 was conditioned by two additive genes. The study of Ragiba et al. (19) was performed in a controlled growth chamber and did not report disease scoring based on growth stage. In other studies involving 12 experiments conducted on plants grown in pots under strictly controlled conditions, Duveiller et al. (12) found very high variability in results from inoculation by *C. sativus* and, given the difficulties of correlating the observations with field results, recommended screening in the field to factor in plant expression. Recent field results by Duveiller et al. (10) confirmed the importance of growth stage in disease development: spot blotch appears to be

highly modulated by crop physiological stage and, probably, sink-sources relations affecting leaf senescence and susceptibility to the pathogen. Joshi et al. (16) conducted a field study but used inoculation with a single isolate, which also suggests that conditions in their experiment were not conducive to the early onset of epidemics. Disease severity was recorded on the two uppermost leaves only, which may not properly reflect the natural progress of the disease, in contrast to when the double-digit scale is used (13). In our study, we evaluated the whole plant, considering that average severity spread vertically in the canopy, and segregated data by growth stage, which may have considerable effect in spot blotch assessment (4,5). An epidemiological study of spot blotch in South Asia also showed that growth stage plays a critical role in expression of host reaction to *C. sativus* (10). In the present study, the pathogen was present from seedling to advanced crop growth stages, exposing plants continuously to a severe natural

Fig. 3. Frequency distribution for wheat spot blotch severity in the field at three growth stages in the F_2 generation of the Chirya.3 $\times$ Milan/Shanghai #7 cross of wheat grown at Rampur and Bhairahawa, Nepal, in the 2004–05 growing season; spot blotch severity on the parents and on F_1 .

inoculum pressure. The susceptible cultivar and spreader rows had disease symptoms on the flag leaf even prior to heading. Finally, we classified the maturity into early and late, and scored disease severity separately for the two groups, not accomplished in the previous studies by Joshi et al. (16) and Ragiba et al. (19).

Milan/Shanghai #7 possesses a single dominant gene for spot blotch resistance, a new finding that should be valuable to wheat-breeding programs in South Asia, where the disease substantially reduces the grain yields of recently developed wheat cultivars (11,27). The results of our study also show that Chirya.3 possesses a single dominant gene for spot blotch resistance. Milan/Shanghai #7 already has been proven to be a useful source of resistance in 35 different environments in South Asia (E. Duveiller, unpublished data). Several studies have reported the high level of spot blotch resistance inherent in Chirya.3 (10,16,19). The present findings will help wheat geneticists and breeders to employ these resistance sources in future breeding research and offer diversity to international programs targeted at developing spot-blotch-resistant wheat lines.

ACKNOWLEDGMENTS

Financial support for this CIMMYT/IAAS collaborative study was made available by CIMMYT and Directorate General for Cooperation and Development (Belgium Government) funding to UCL-CIMMYT project on "Evaluation of Cropping Systems: The Nonspecific Pathogens," Phase II in South Asia. We thank S. Pradhan for assistance in preparing figures and tables and M. Listman for revising the manuscript.

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