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Characterization of variability and relationships among components of partial resistance to leaf rust in CIMMYT bread wheats

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Summary. A study of spring bread wheat (*Triticum aestivum*) germ plasm developed at the International Maize and Wheat Improvement Center (CIMMYT) showed highly significant phenotypic variability for each component of partial resistance (namely, uredial appearance period, latency period, uredial number and uredial size) to *Puccinia recondita* f. sp. *tritici*. All of the wheat genotypes displayed longer uredial appearance and latency periods and decreased uredial number and uredial size when compared to the susceptible check cultivar 'Morocco'. Positive correlations between uredial appearance period and latency period, and uredial number and uredial size, and negative correlations between uredial appearance and latency periods and uredial number and uredial size, inclusive, suggested that the components of partial resistance were either tightly linked or under pleiotropic genetic control. Compared to 'Morocco', all entries had slow disease progress in the field and variation occurred in the germ plasm for the area under the leaf rust progress curve. Disease progress was negatively correlated with uredial appearance and latency periods, whereas a positive correlation was observed with uredial number and uredial size. Certain genotypes displayed high levels of partial resistance resulting in low disease incidence in the field.

Key words: *Puccinia recondita tritici* – *Triticum aestivum* – Rust resistance

Introduction

Partial resistance, or slow rusting, to leaf rust (caused by *Puccinia recondita* f. sp. *tritici*) has been reported in some bread wheat (*Triticum aestivum* L.) cultivars (Kuhn et al. 1978; Shaner and Finney 1980; Bjarko and Line 1988a, b; Broers 1989). In the spring wheat germ plasm developed by the international Maize and Wheat Improvement Center (CIMMYT) however, there is only limited information available on this type of resistance even though this germ plasm is grown on more than 50 million hectares worldwide (Dalrymple 1986). Because this germ plasm is meant to be grown in diverse environments, and with the intention of avoiding a narrow genetic basis of resistance over an extended area, the wheat breeding philosophy of CIMMYT has been to maintain and enhance the diversity of pathogen resistance in the germ plasm. One avenue by which these goals are being reached with respect to wheat leaf rust is via the utilization of partial resistance mechanisms, which have been hypothesized to be durable (Kuhn et al. 1978).

Partial resistance is characterized by depressed epiphytotic development despite the ultimate expression of a high infection type (Parlevliet 1975, 1979, 1988). The rate of epiphytotic development is delayed as a result of lengthened latency period, decreased uredial number, smaller uredia or reduced sporulation (Ohm and Shaner 1976; Parlevliet 1979, 1988).

Because initial studies indicated that partial resistance to leaf rust was present in CIMMYT bread wheat germ plasm (Rajaram et al. 1988), a more detailed analysis of the components of partial resistance was undertaken.

Materials and methods

Twenty-six genotypes (Table 1) developed at CIMMYT and selected for their various degrees of partial resistance to leaf rust, which had been observed over numerous location/years, were chosen for greenhouse experiment 1. Because they were selected

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Table 1. Wheat genotypes with their seedling and adult plant reactions when tested with *P. recondita tritici* pathotype TCB/TD, experiment 1

Entry no	Cultivar or cross and pedigree	Reaction[a]	
		Seedling	Adult plant
1	Kt/Bage//Fn/U/3/Bza/4/Trm/5/Aldan/6/Seri CM84833-3M-0Y-0M-9Y-0M	3	3
2	Kvz//Bb/Cha/3/Trm/4/Mon/Ald CM80748-7Y-02M-0Y-5M-2Y-0M	3c3+	3c
3	Bow/Crow//Buc/Pvn CM75966-E-4M-3Y-03M-2Y-0B	3	3
4	Lfn/II58.57//Glen/3/Celaya CM78971-B-2M-01Y-06M-2Y-1B-0Y	3+	3+
5	Cno/Son//Cno/Inia/3/Pvn/4/Cnr CM83734-2M-0Y-0M-3Y-0M	3+	3
6	CI14227/Trm//Mad/3/Thb CM83693-6Y-0M-0Y-5M-0Y	3	3+
7	Bow*2/Prl CM90319-A-4B-4Y-1B-0Y	3	3
8	Seri/Thb CM83304-10Y-0M-0Y-1M-0Y	3+	3
9	Vee#5/Pvn CM74542-5M-2Y-02M-3Y-0B-41M-0Y	3	3
10	Genaro 81	3	3
11	Vee#5/Thb CM83347-17M-0Y-0M-9Y-0M	3+	3
12	Glen/Prl CM83273-17Y-1B-1Y-1B-0Y	3	3c
13	Eraf/Yr/3/Pato/On//Maya/4/Kea CM76260-40Y-08M-04Y-1B-1Y-0B	3	3
14	Gimpel CM64849-7M-1Y-3M-1Y-0M-52B-0Y-43M-0Y	3+	3
15	Kauz CM67458-4Y-1M-3Y-1M-2Y-0B-1Y	3	3c
16	PF72640/PF7326/PF7065/Ald/3/Vee CM81131-26Y-03M-0Y-4M-1Y-0M	3+	3
17	Vee/Bow CM67394-11Y-1M-2Y-1M-3Y-0B-43M-0Y	3	3
18	Cook/Vee//Dove/Seri CM69279-C-2Y-1M-5Y-1M-0Y-2Y	3	3+
19	Garuda CM64224-5Y-1M-1Y-2M-0Y-1Y	3+	3
20	Peacock CM74539-1M-3Y-1M-2Y-2M-0Y	3+	3
21	Seri 82	3	3
22	Huar/Cj/6*Huar/3/H570.71/5*Era CMH81A.519-3B-4Y-2B-2Y-3B-1Y-1B-0Y	3	3
23	F12.71/Coc//Gen CM76689-9Y-03M-012Y-1B-2Y-0B	3	3
24	Klat/Tan//Gen CM82585-03TOPM-1Y-02M-0Y-2M-1Y-0M	3+	4
25	Frontana	3	3+
26	Fct/Sara CM80976-40Y-025H-0Y-4M-2Y-0M	3+	3+
27	Siete Cerros	3+	4
28	Morocco	4	4

[a] Reactions 3 and 4, based on a 0–4 scale, indicate susceptible responses, the only difference is the relative uredial size (4 larger than 3) as observed visually. Reaction followed by "c" indicates chlorotic tissue surrounding the uredia

Table 2. Wheat genotypes with their seedling and adult plant reactions when tested with *P. recondita tritici* pathotype TBD/TM, experiment 2

Entry no.	Cultivar or cross and pedigree	Reaction[a]	
		Seedling	Adult plant
1	Flycatcher CM43598-II-8Y-1M-3Y-1M-3Y-0B	3+	3c
2	Opata 85	3+	3c
3	Pavon 76	3+	3
4	Myna SWM4589-7Y-18M-1Y-0M-56B-0Y-1B	3+	3
5	Klat/Tan//Gen CM82585-03TOPM-1Y-02M-0Y-2M-1Y-0M	3+	3+
6	Siete Cerros	3+	3+
7	Morocco	4	4

[a] Reactions 3 and 4, based on a 0–4 scale, indicate susceptible responses, the only difference is the relative uredial size (4 larger than 3) as observed visually. Reaction followed by "c" indicates chlorotic tissue surrounding the uredia

from different parental combinations, there was an increased possibility that they possessed unique genes or gene combinations for partial resistance to *P. r. tritici*. 'Frontana' was included in the study because it is considered to possess durable partial resistance (Roelfs 1988). 'Morocco' was included as a susceptible cultivar.

Greenhouse experiment 2 consisted of seven spring bread wheat genotypes (Table 2). The common genotypes in the two experiments were 'Siete Cerros', 'Morocco', and 'Klat/Tan/Gen'. The detailed cross and pedigree or full name for the genotype abbreviations are described by Villareal and Rajaram (1988).

The pathogen materials used for Experiment 1 and 2, respectively, consisted of two Mexican *P. r. tritici* pathotypes, TCB/TD and TBD/TM. The designations are based on Long and Kolmer (1989) and Singh (1991). The avirulence/virulence formulas for these pathotypes on known *Lr* genes are:

TCB/TD = *Lr*3ka, 9, 10, 11, 16, 17, 19, 21, 24, 25, 27+31, 29, 30, 32, 33 / 1, 2a, 2b, 2c, 3, 3bg, 13, 14a, 14b, 15, 18, 20, 23, 26, 28.

TBD/TM = *Lr*3ka, 9, 11, 16, 19, 21, 23, 24, 25, 26, 29, 30, 32, 33 / 1, 2a, 2b, 2c, 3, 3bg, 10, 13, 14a, 14b, 15, 17, 18, 20, 27+31, 28.

When inoculated with pathotypes TCB/TD or TBD/TM (experiment 1 and 2, respectively), all genotypes displayed high seedling infection types (ranging from "3c" to "4", based on the "0–4" infection type scale described by Stakman et al. 1962; Tables 1 and 2), indicating that none of the known major leaf rust resistance genes was functional in these genotypes with their respective pathotypes. Hence, both host and pathogen materials were suitable for the present studies. Two pathotypes were used because some of the wheat genotypes listed in Table 1 possess known major leaf rust resistance genes for which pathotype TBD/TM was avirulent. Similarly, certain entries in Table 2 displayed low seedling reactions with pathotype TCB/TD.

The greenhouse experiments consisted of two planting dates at a 7-day interval with three replicates per planting date. Genotypes and replicate combinations were planted in 2.5-l plastic pots filled with a soil/compost mixture. Two planting dates were necessary to subsequently choose sufficient tillers of the growth stage "anthesis" so that the entire experiment could be inoculated on the same day. Standard greenhouse growing procedures were followed between seeding and anthesis. The greenhouse was maintained at 18 °C night and 22 °C day temperatures. Plants from the two planting dates were brought together, and tillers of similar growth stage (i.e., anthesis) were chosen for inoculation on the same day. Thinning was performed to achieve four tillers per genotype per replicate. Although the inoculum suspension density was not quantified, each flag leaf was uniformly sprayed for 5 s with the same urediospore-Soltrol 250 suspension. After 18 h in a mist chamber, the pots were dispersed on greenhouse benches in a randomized complete block design.

Flag leaves were individually evaluated for uredial appearance period (visually assessed in days from inoculation to the appearance of the first uredia), latency period (visually assessed in days from inoculation to the rupture of leaf epidermis by 50% of the uredia) and uredial number (measured as the number of uredia per unit area). All of the uredia on each flag leaf were counted, and flag leaf area was determined with a LICOR Model LI-3100 area meter (LICOR Corp, Lincoln, Neb.). Uredial size (measured as length × width of uredia) was determined with a metered magnifying lens on the day coinciding with the end of the latency period: four flag leaves were randomly chosen from the 12 inoculated plants in the three replications, with up to ten of the ruptured uredia per leaf measured. On flag leaves where fewer than ten ruptured uredia were present, the sizes of all of the available ruptured uredia were measured. Analysis of variance was carried out using Statistical Analysis Systems (1985) procedures and programs. Correlations were calculated on means using Pearson Correlations.

The genotypes represented in the greenhouse experiments were planted in the field at Ciudad Obregon, Sonora, Mexico during the 1987–1988 crop cycle in a three replicate, randomized complete block design to compare the greenhouse observations with the field response where disease increase is multicyclical. Plots consisted of two 3-m rows seeded 15 cm apart with 70 cm between plots. An epiphytotic was created by inoculating spreader rows (composed of 'Morocco' plus other leaf rust-susceptible cultivars) planted at 20-plot intervals with an inoculum consisting of an equal mixture of the TCB/TD and TBD/TM

Table 3. Analysis of variance for components of partial resistance and Area Under Leaf Rust Progress Curve (AULRPC) for lines in experiments 1 and 2

Source of variation	Greenhouse Mean squares				Field Mean squares	Greenhouse Mean squares	
	df	Uredial appearance period	Latency period	Uredial number	AULRPC	*df*	Uredial size
Experiment 1							
Replication	2	0.898**	0.019	10.9	944	–	–
Entry	27	2.141**	1.401**	1,111.5**	324,799**	27	0.0086**
Error	54	0.171	0.278	21.3	2,453	84	0.0009
Experiment 2							
Replication	2	0.082	0.027	27.0	1,061	–	–
Entry	6	2.011**	2.258**	2,305.6**	1,052,139**	6	0.0611**
Error	12	0.235	0.090	174.5	2,969	21	0.0010

** $P<0.01$

pathotypes. Upon the appearance of the first symptoms of infection on the highly susceptible cv 'Morocco', the genotypes were evaluated for leaf rust severity and reaction using the "Modified Cobb" scale (Peterson et al. 1948) at 10-day intervals for a total of three recordings. The area under the leaf rust progress curve (AULRPC) was calculated from these disease observations using a computer program developed at CIMMYT.

Results and discussion

The adult plant infection types (based on a 0–4 scale, Tables 1 and 2) assessed in the greenhouse for all genotypes were recorded to be high (ranging from "3c" to "4"), indicating that there were no hypersensitive reactions involved due to gene(s) effective only in the adult-plant growth stage. Analyses of variance (Table 3) indicated that all of the components studied were highly variable ($P<0.01$). The mean responses of genotypes in rank order for all variables for experiments 1 and 2 are given in Tables 4 and 5, respectively.

The fast-rusting cv 'Morocco' had the shortest uredial appearance and latency periods, the highest uredial number and the largest uredial size in both experiments. Furthermore, 'Morocco' displayed the most susceptible field response with the largest AULRPC (Tables 4 and 5).

When expressed as a percentage of the value recorded for 'Morocco', experiment 1 genotypic ranges (Tables 4) were 108–179% for uredial appearance period, 114–149% for latency period, 2–58% for uredial number, 22–66% for uredial size and 1–50% for AULRPC. Similar changes were noted for the genotypes represented in experiment 2 (Table 5). In both experiments the genotypes exhibited diverse responses to the traits measured, indicating that the CIMMYT bread wheat germ plasm included in this study was variable for the components of partial resistance and in field response. Similar observations of longer latency period, lower uredial number and smaller uredia were associated with partial resistance, or slow rusting, to leaf rust by Ohm and Shaner (1976) and Broers (1989).

Correlation coefficients between the components of partial resistance and AULRPC (Table 6) were moderately high in both experiments. Uredial appearance period was positively correlated with latency period in both experiments ($r=0.843$ and 0.951, respectively). Thus, observation of uredial appearance period could be substituted for latency period when large numbers of plants are to be screened for partial resistance to leaf rust. However, the relationship of these two components with uredial number, uredial size and AULRPC indicated that latency period per se was a more inclusive criterion (because of higher respective correlation coefficients) for the selection of partial resistance. Furthermore, a significant variation between replicates for uredial appearance period in experiment 1 (Table 3) also indicated that for genotypic description purposes latency period must be used.

Negative correlations between uredial appearance period, latency period and uredial number and uredial size were observed (Table 6). The determination of uredial size and uredial number on the ultimate day of latency period was intended to reduce possible variation resulting from the continued growth of uredia after epidermal rupture (Kuhn et al. 1978). For this reason, a fixed day after inoculation for the measurement of uredial size would tend to result in smaller uredia in genotypes with longer latency periods.

Although the relative ranking of most of the genotypes for the measured components did not change significantly, several genotypes exhibited ranking fluctuations. For example, in experiment 1; entry 7 (Bow*2/Prl) was ranked 7th for latency period and 8th for uredial size, but 25th for uredial number. Entry 20 ('Peacock') was

Table 4. Ranking and mean response of the 28 wheat genotypes included in experiment 1 for components of partial resistance and AULRPC to *P. recondita tritici* pathotype TCB/TD

Greenhouse test												Field test		
Uredial appearance period			Latency period			Uredial number			Uredial size			AULRPC		
Entry no.	Days	% of Morocco	Entry no.	Days	% of Morocco	Entry no.	Uredia/10 cm^2	% of Morocco	Entry no.	mm^2	% of Morocco	Entry no.	Units	% of Morocco
1	10.0	179	1	11.9	149	1	2	2	6	0.067	22	1	8	1
3	8.7	155	2	11.2	140	5	7	8	12	0.081	27	3	15	1
4	8.0	142	3	11.0	138	26	8	8	1	0.082	27	6	22	1
2	7.8	139	4	10.3	129	9	9	10	25	0.096	32	5	35	2
6	7.7	138	5	10.3	129	3	10	10	3	0.097	32	22	44	3
11	7.6	136	6	10.3	129	6	12	12	4	0.100	33	13	51	3
15	7.4	132	7	10.3	129	4	13	13	2	0.101	33	2	77	5
14	7.3	131	8	10.2	128	20	13	14	7	0.108	36	12	83	5
16	7.2	130	9	10.2	127	23	14	15	5	0.110	36	18	91	6
17	7.2	129	10	10.2	127	13	16	17	19	0.111	37	17	98	6
9	7.1	127	11	10.2	127	15	17	17	16	0.112	37	26	106	7
25	7.0	126	12	10.1	126	11	18	19	8	0.114	38	14	106	7
8	7.0	126	13	10.1	126	12	18	19	11	0.115	38	15	121	7
23	7.0	126	14	10.0	125	8	22	23	9	0.120	40	7	131	8
10	6.9	124	15	9.9	124	2	23	24	14	0.120	40	9	138	8
26	6.9	124	16	9.9	124	22	24	25	10	0.121	40	8	174	11
18	6.9	124	17	9.9	124	21	25	26	21	0.126	42	25	181	11
5	6.8	122	18	9.8	123	16	25	26	17	0.127	42	11	190	12
12	6.8	122	19	9.8	123	18	26	27	22	0.130	43	20	192	12
20	6.8	121	20	9.8	123	10	29	31	15	0.131	43	10	211	13
7	6.7	119	21	9.8	122	14	33	35	26	0.135	44	19	284	17
19	6.6	118	22	9.7	121	17	37	39	13	0.139	46	24	322	20
21	6.5	117	23	9.6	120	25	40	42	23	0.156	51	23	357	22
22	6.4	115	24	9.6	120	19	44	46	20	0.171	56	16	371	23
13	6.3	113	25	9.5	118	7	45	48	27	0.177	58	21	386	24
24	6.1	109	26	9.4	118	24	49	52	18	0.191	63	4	576	35
27	6.0	108	27	9.1	114	27	55	58	24	0.200	66	27	826	50
28	5.6	100	28	8.0	100	28	95	100	28	0.304	100	28	1,640	100
LSD (0.05)	0.7	12		0.9	11		8	8		0.042	14		81	5

Table 5. Ranking and mean response of the 7 wheat genotypes included in experiment 2 for components of partial resistance and AULRPC to *P. recondita tritici* pathotype TBD/TM

Greenhouse test												Field test		
Uredial appearance period			Latency period			Uredial number			Uredial size			AULRPC		
Entry no.	Days	% of Morocco	Entry no.	Days	% of Morocco	Entry no.	Uredia/10 cm^2	% of Morocco	Entry no.	mm^2	% of Morocco	Entry no.	Units	% of Morocco
1	7.7	138	1	10.6	132	3	3	3	2	0.094	22	1	15	1
3	7.5	135	2	10.3	128	5	7	8	3	0.095	22	4	50	3
2	7.5	134	3	10.1	126	4	9	10	4	0.105	24	2	61	4
4	7.2	129	4	10.1	126	1	16	18	1	0.112	26	3	274	17
5	7.1	127	5	10.0	125	2	21	25	6	0.133	30	5	322	20
6	6.0	108	6	9.3	116	6	27	31	5	0.184	42	6	826	50
7	5.6	100	7	8.0	100	7	86	100	7	0.437	100	7	1,640	100
LSD (0.05)	0.9	17		0.6	7		7	8		0.046	11		115	7

Table 6. Correlation coefficients (based on means) between various components of partial resistance and AULRPC for lines in experiment 1 (above diagonal, $n=28$) and experiment 2 (below diagonal, $n=7$)

	Uredial appearance period	Latency period	Uredial number	Uredial size	AULRPC (field)
Uredial appearance period		+0.843**	−0.617**	−0.616**	−0.467**
Latency period	+0.951**		−0.695**	−0.750**	−0.697**
Uredial number	−0.805*	−0.906**		+0.692**	+0.767**
Uredial size	−0.774*	−0.899**	+0.917**		+0.752**
AULRPC (field)	−0.937**	−0.987**	+0.900**	+0.901**	

*, ** $P<0.05$ and 0.01, respectively

ranked 20th for latency period and 24th for uredial size, but 8th for uredial number. Entry 25 ('Frontana') ranked 25th for latency period and 23rd for uredial number, but 4th for uredial size.

With the germ plasm studied, linkage between genic loci or pleiotropism by one genic locus could result in the phenotypic associations noted above since all entries displayed longer uredial appearance and latency periods, lower uredial numbers and smaller uredia. The results can be better explained if it is assumed that there are no separate genes controlling the components of partial resistance, but only genes for partial resistance per se (Parlevliet 1986), which results in a pleiotropic basis for the components of partial resistance. The deviations noted in relative rankings may indicate variability for genes or gene combinations for partial resistance in the germ plasm. Furthermore, these genes must have differential efficiencies in their control of the components of partial resistance, which would result in ranking fluctuations.

If pleiotropism or tight linkage determines partial resistance, and hence its components, wheat pathologists and geneticists must question the number of such genes in the complex that are ncesssary to achieve a high level of partial resistance. Knott and Padidam (1988) indicated that for stem rust (caused by *Puccinia graminis* f. sp. *tritici*) resistance in wheat, relatively few genes (three to four) with small individual effects could result in larger effects when brought together, i.e., the interaction between the genes was not merely additive, but multiplicative. Similar results have been obtained by Kuhn et al. (1980), Bjarko and Line (1988 a, b) and the senior author of this article (Singh, unpublished) with regard to leaf rust resistance, indicating that effective partial resistance could be achieved through the accumulation of only a few such genes.

The significant ($P<0.01$) correlations in both experiments between the components of partial resistance and AULRPC indicate that selection for longer latency period, uredial number or smaller uredia would result in genotypes with lower AULRPC. However, genotypic exceptions were observed with experiment 1, entry 4 (Lfn/II58.57//Glen/3/Celaya) ranked 4th for latency period, 7th for uredial number and 6th for uredial size, but 24th for AULRPC. Since the greenhouse environment, in particular the temperature range (18–22 °C), was distinct from that of the field, it is possible that differential genic sensitivity to temperature/environment may have occurred. Because a greenhouse environment may be less than representative of possible field conditions, selection for low AULRPC, or low final rust severity, would simplify selection for the accumulation of multiple genes for partial resistance.

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