Inheritance and Expression of Adult Plant Resistance to Leaf Rust in Era Wheat

B. EZZAHIRI, Department of Plant Pathology, Institut Agronomique et Veterinaire Hassan II, B.P. 6202, Rabat-Instituts, Morocco, and A. P. ROELFS, Cereal Rust Laboratory, Agricultural Research Service, U.S. Department of Agriculture, University of Minnesota, St. Paul 55108

ABSTRACT

Ezzahiri, B., and Roelfs, A. P. 1989. Inheritance and expression of adult plant resistance to leaf rust in Era wheat. Plant Disease 73:549-551.

The inheritance of adult plant resistance to leaf rust (*Puccinia recondita* f. sp. *tritici*) was studied in the bread wheat (*Triticum aestivum*) cultivar Era in Morocco and the United States. Adult plant resistance was shown to be conferred by two complementary genes, *Lr*13 and *Lr*34. The magnitude of the effect resulting from the gene interaction was influenced by environment. *Lr*10 and an unknown gene for seedling resistance were also present in Era.

Era wheat (*Triticum aestivum* L.), CI 13986, an awned, semidwarf spring wheat (5), has been widely grown since its release in 1972 in Minnesota (7–9). Leaf rust caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* is a major disease of wheat. Resistance genes are known but most are quickly overcome by the pathogen (8). The leaf rust resistance provided by Era has given adequate, durable resistance in its area of cultivation. The pedigree (6) of Era is: Thatcher/Supreza//Frontana/3/Kenya 58/Newthatch/7/Frontana/6/Frontana/Thatcher//Pembina/5/Frontana/Thatcher/2/Mida/Kenya 117A/3/Norin 10/Brevor//unknown line/4/Kenya 58/Newthatch/2/Lee. Leaf rust resistance in Era comes from Supreza and Frontana, which probably have identical resistance. Supreza (leaf-rust resistant) was crossed with Mentana (susceptible) to obtain Frontana. Dyck and Samborski (3) postulated that Frontana possesses the genes *Lr*T2, *Lr*T3, and *Lr*13. *Lr*13 was described in Frontana by Dyck et al (4), and *Lr*T2 has been designated *Lr*34 (R. A. McIntosh, *personal communication*). Our objectives were to determine for the cultivar Era: 1) the inheritance of resistance, 2) the identity of the genes involved, and 3) the expression of the resistance under two environments, Minnesota and Morocco.

MATERIALS AND METHODS

Two single plant selections, Era-1 and Era-3, were crossed with the susceptible cultivar Baart (CI 1697). Even though wheat is self-pollinated, and therefore plants are homozygous for most traits, cultivars are often heterogeneous for many characters. Two plants of Era were used to reduce the probability that an atypical Era plant would be studied. The F_1 plants were grown in the greenhouse, and 13 F_2 populations were obtained. Seeds with F_3 embryos were randomly selected and grown in the greenhouse in the winter of 1981. Two spikes were harvested separately from each F_3 plant, and seeds from each spike were planted as F_4 lines in the field at Rosemount, Minnesota, in 1982 and in Mograne, Morocco, in 1985.

A total of 473 and 367 F_3 derived lines in the F_4 generation were planted in Minnesota and Morocco, respectively. Each entry was planted in a 50-cm row within a longer nursery row consisting of 50 entries. Nursery rows and entries within a row were separated by 50 cm. The parents were included between each five progeny entries.

A bulk urediospore collection from the area was sprayed on the plants at the boot stage using a lightweight mineral oil as a carrier to supplement natural infection at Rosemount. Three rows of a susceptible local cultivar (Fertas) were planted along both sides of the trial to enhance inoculum production and distribution in Morocco. Two rows, each 1 m long, of Frontana (CI 12470) and CT263 (a Thatcher backcross line near-isogenic for *Lr*13) were included as checks. Lines 920 and 922, possessing *Lr*34 and *Lr*T3, respectively (3), were added in the Morocco tests.

Crosses with Era were made with cultivars and lines carrying the genes *Lr*13, *Lr*34, and *Lr*T3 to test Era for its postulated genotype for leaf rust resistance. A total of 351 F_2 adult plants from the crosses Era/Frontana, Era-1/Line 920 (*Lr*34), Era-1/Line 922 (*Lr*T3), Era-3/Line 920, Era-3/Line 922, CT263 (*Lr*13)/Line 920, CT263/Line 922, and Era/CT263 were evaluated for their reaction to the culture UN13 (MO-X) of *P. recondita*. This culture was typical of the Moroccan cultures and is virulent on seedlings of Era. Plants were inoculated (1) at heading with a spore suspension in mineral oil. The inoculated plants were then incubated for 20 hr at high humidity. Rust reactions were recorded 14 days after inoculation according to the system described by Stakman et al (10). Genetic ratios were tested for goodness of fit by a chi-square test.

The parental cultivars and lines utilized in this study also were tested in the seedling stage with several leaf rust isolates; 7-day-old seedlings were inoculated (1) and incubated at high humidity for 20 hr. Infection types were recorded 10 days after inoculation according to the system described by Stakman et al (10).

RESULTS AND DISCUSSION

The lines were grouped into highly resistant, moderately resistant, segregating, and susceptible classes according to their reactions in the Minnesota field tests. All lines showing a 0;12 infection type (IT) were placed in the moderately resistant class. Lines segregating for highly and moderately resistant reactions were also put in this category. Thus, the segregating category included only the lines containing plants with high and low infection types.

The proportion of susceptible lines was consistently smaller in the cross involving Era-3 than in that involving Era-1 (Table 1). Therefore, the two crosses were analyzed separately. Results from the derived F_3 lines in the F_4 generation from Baart/Era-1 and Baart/Era-3 are given in Table 1. The hypothesis of two complementary genes (Table 2) was tested. Because CT263, which possesses *Lr*13, showed a moderately resistant reaction in Minnesota and a resistant reaction in Morocco (Table 3), one gene (A) in Era that conditions a moderately resistant reaction is probably *Lr*13. Another gene (B) is not detectable by itself but interacts with gene A to confer a highly resistant reaction. A chi-square test of the pooled data fit the hypothesis

Scientific Journal Series Paper 15,588, Minnesota Agricultural Experiment Station, University of Minnesota, St. Paul.

Accepted for publication 13 December 1988 (submitted for electronic processing).

Table 1. Field response to *Puccinia recondita* of F_3 derived lines in the F_4 generation of the crosses Baart/Era-1 and Baart/Era-3 at Rosemount, Minnesota, in 1984

F_2 line	Number of F_3 lines	Host response class: Resistant Obs.[a]	Resistant Exp.[a]	Moderately resistant Obs.	Moderately resistant Exp.	Susceptible Obs.	Susceptible Exp.	Segregating Obs.	Segregating Exp.
				Baart/Era-1[b]					
1-1	37	3	5.2	9	8.7	16	14.0	9	9.2
1-2	37	4	5.2	11	8.7	15	14.0	7	9.2
1-3	33	3	4.5	11	7.7	13	12.3	6	8.2
1-4	31	2	4.3	8	7.3	14	11.6	7	7.7
1-5	30	5	4.2	10	7.0	10	11.2	5	7.5
Total	168	17	23.4	49	39.4	68	63.1	34	41.8
				Baart/Era-3[c]					
3-1	67	8	9.4	27	21.6	16	15.2	16	18.7
3-2	45	5	6.3	18	14.5	8	10.2	14	12.6
3-3	40	7	5.6	16	12.9	8	9.0	9	11.2
3-4	30	6	4.2	12	9.6	6	6.8	6	8.4
3-5	29	2	4.0	8	9.3	7	6.6	12	8.0
3-6	34	3	4.7	12	10.9	8	7.7	11	9.5
3-7	32	3	4.5	11	10.3	9	7.3	9	9.0
3-8	28	2	3.9	12	9.0	7	6.4	7	7.8
Total	305	36	42.6	116	98.1	69	69.2	84	85.2

[a] Number of observed (obs.) and expected (exp.) individuals.
[b] Hypothesis: Two complementary genes (resistant = 14%, moderately resistant = 23.5%, susceptible = 37.5%, segregating = 25%). χ^2 pooled = 4.80 ($0.1<P<0.5$), χ^2 heterogeneity = 5.59 (not significant).
[c] Hypothesis: Three genes (resistant = 14%, moderately resistant = 32.2%, susceptible = 22.8%, segregating = 28%). χ^2 pooled = 4.37 ($0.1<P<0.5$), χ^2 heterogeneity = 10.02 (not significant).

Table 2. Postulated gentotypes for adult plant resistance to *Puccinia recondita* in Era wheat and response of lines with the specific *Lr* genes

Gene(s)[a]	Minnesota	Morocco
	Response of Era-1 (postulated resistance AABB)	
A	Moderately resistant	Resistant
B	Susceptible	Susceptible
A + B	Resistant	Immune
F_2 ratio	9R:3MR:4S	12R:4S
	Response of Era-3 (postulated resistance AABBCC)	
A	Moderately resistant	Resistant
B	Susceptible	Susceptible
C	Susceptible	Susceptible
A + B	Resistant	Immune
A + C	Moderately resistant	Resistant
B + C	Moderately resistant	Moderately resistant
A + B + C	Resistant	Immune
F_2 ratio	36R:21MR:7S	50R:7MR:7S

[a] A = *Lr*13, B = *Lr*34, and *Lr*C = previously undescribed gene.

Table 3. Adult plant reactions (anthesis) to *Puccinia recondita* of Era, Frontana, Baart, and lines with specific *Lr* genes in Minnesota (1981 and 1982) and Morocco (1984 and 1985)

Cultivar or line	Minnesota Severity	Minnesota Response	Morocco Severity	Morocco Response
Baart (*Lr*10)	60	S[a]	60	S
CT263 (*Lr*13)	60	MR	Trace	R
Line 920 (*Lr*34)	···[b]	···	40	MS-S
Line 922 (*Lr*T3)	···	···	60	S
Era (*Lr*10, 13, 34, C, D)	Trace	R	0	I
Frontana (*Lr*13, 34, T3)	0	I	0	I

[a] I = immune, R = resistant, MR = moderately resistant, MS = moderately susceptible, S = susceptible.
[b] Not evaluated.

Table 4. Field response to *Puccinia recondita* of F_3 derived lines in the F_4 generation of the crosses Baart/Era-1 and Baart/Era-3 in Morocco in 1985

F_2 line	Number of F_3 lines	Host response class: Immune, resistant Obs.[a]	Immune, resistant Exp.[a]	Moderately resistant Obs.	Moderately resistant Exp.	Susceptible Obs.	Susceptible Exp.	Segregating Obs.	Segregating Exp.
				Baart/Era-1[b]					
1-1	37	15	13.8	···	···	10	13.8	12	9.3
1-2	38	13	14.2	···	···	12	14.2	13	9.5
1-3	32	14	12.0	···	···	9	12.0	9	8.0
1-4	30	13	11.2	···	···	8	11.2	9	7.5
1-5	30	9	11.2	···	···	10	11.2	11	7.5
Total	167	64	62.4	···	···	49	62.4	54	41.8
				Baart/Era-3[c]					
3-1	66	20	24.7	5	7.2	18	15.0	23	18.8
3-2	42	16	15.8	3	4.6	10	9.6	13	12.0
3-3	37	11	14.0	3	4.1	11	8.4	12	10.5
3-4	29	11	10.9	2	3.2	7	6.6	9	8.3
3-5	26	8	9.8	1	2.9	8	5.9	9	7.4
Total	200	66	75.2	14	22.0	54	45.5	66	57.0

[a] Number of observed (obs.) and expected (exp.) individuals.
[b] Hypothesis: Two complementary genes (resistant = 37.5%, susceptible = 37.4%, segregating = 25%). χ^2 pooled = 0.87 ($0.5<P<0.9$), χ^2 heterogeneity = 4.97 (not significant).
[c] Hypothesis: Three genes (resistant = 37.5%, moderately resistant = 11.0%, susceptible = 22.8%, segregating = 28.5%). χ^2 pooled = 7.18 ($0.5<P<0.1$), χ^2 heterogeneity = 1.95 (not significant).

Table 5. Segregation for adult plant resistance to culture UN13 (MO-X) of *Puccinia recondita* in F_2 populations of crosses in greenhouse tests

Cross[a]	No. of F_2 plants evaluated	No. of plants per infection type: 0;1c–0;12	12–c	3–4	Ratio	*P* value
Era/CT263	18	18	···	···	···	···
Era/Frontana	24	24	···	···	···	···
Era-1/Line 922	41	27	6	8	9:3:4	0.5–0.1
Era-1/Line 920	37	23	···	14	3:1	0.5–0.1
Era-3/Line 922	43	29	5	9	9:3:4	0.5–0.1
Era-3/Line 920	56	45	···	11	3:1	0.5–0.1
CT263/Line 922	40	13	20	7	1:2:1	0.5–0.1
CT263/Line 920	59	30	11	18	9:3:4	0.9–0.5

[a] Parental infection types: CT263 (*Lr*13) = 0;12. Era (*Lr*10, 13, 34, C, D postulated) = 0;1c. Frontana (*Lr*13, 34, T3) = 0;1-c. Line 920 (*Lr*34) = 3. Line 922 (*Lr*T3) = 4.

Table 6. Infection types of selected wheat lines to selected cultures of *Puccinia recondita*

Host lines (*Lr* gene)	Unified numeration race and culture: 3 MN-FQD	3 MN-TBB	1 MO-11	13 MO-X
Era (*Lr*10, 13, 34, C?, D)[a]	12c	0;1+c	0;1c	3–
Frontana (*Lr*13, 34, T3)	0;	4	3	4
Baart (*Lr*10)	4	0;1c	4	4
Tc*Lr*10 (*Lr*10)	3	0;1	4	4
CT263 (*Lr*13)	3+	3+	3+	4
Line 920 (*Lr*34)	···[b]	···	4	4
Line 922 (*Lr*T3)	···	···	3+	4
RL 6050 (*Lr*34, T3)	···	···	3–	4

[a] Commercial seed lot.
[b] Not evaluated.

Table 7. Infection types of seven isolates of *Puccinia recondita* on a series of single gene resistances

Lr gene	Unified numeration race and culture						
	3 MN-FQD	13 MN-TBB	17 MN-KGB	1 MO-11	3 MO-40	13 MO-32	13 MO-X
1	0;	3	0;	0	0	4	4
2a	0;	4	4	0;	0;	4	4
2c	3	4	4	0;	4	4	4
3	3	4	3+	0;1c	4	4	4
3ka	3	2	2	0;	0;	0;1-c	0;
9	4	0;	0;	0;	0;	0;	0;
10	3	0;	4	4	4	4	4
11	...[a]	...	...	3	3	3	3
16	3	1n	1+n	4	4	4	4
17	...	...	...	12	12	12c	3
18	3	3	1+	3	3	3	4
19	0;	0;	0;	0;	0;	0;	0;
24	0;	0;	0;	0;	0;1n	0;	0;1n

[a] Not evaluated.

of two complementary genes (Table 1). The combined data of eight families from Baart/Era-3 fit a three-gene ratio (Table 1). One gene was postulated to be *Lr*13. The second gene apparently is identical to gene B postulated in Era-1, and a third gene not present in Era-1 and ineffective by itself interacted with gene B to condition a moderately resistant reaction. Because of the difference in resistance of Era-1 and Era-3, neither population could be used to confirm the results of the other cross.

The crosses involving Era-1 and Era-3 showed different proportions of susceptible and moderately resistant lines in Morocco (Table 4). For Baart/Era-1, only three categories were distinguishable: immune to highly resistant, susceptible, and segregating. Some of the segregating lines showed individual plants with 0;1+ IT. This reaction was not shown by the nonsegregating lines and may be due to *Lr*13 in the heterozygous state. *Lr*13 confers a highly resistant reaction in Morocco (Table 3). Because the pooled data of 167 F_4 lines fit a two-gene ratio (Table 4), one gene, highly resistant, was postulated to be *Lr*13 in the homozygous state. The second gene, B, was not detected by itself but complemented *Lr*13 to confer an immune reaction, as postulated in Table 2. The analysis of the data from Baart/Era-3 fit a three-gene ratio (Table 4). In this cross, some lines showed a moderate resistance (12+c), indicating they probably possessed B and C genes (Table 4).

Thus, Era-1 and Era-3 segregated for the same genes in two different environments. *Lr*13 was so effective against cultures in Morocco, however, that the complementary effect of *Lr*13 and gene B was less evident than in Minnesota. Differences in the environment between the locations may be partly responsible for the variation in the expression of *Lr*13. This gene has been reported to be temperature-sensitive (2).

Adult plants of Era and Frontana were immune to highly resistant under field conditions in both Minnesota and Morocco (Table 3). All plants in the F_2 population resulting from Era/Frontana were highly resistant to culture UN13 (MO-X) of *P. recondita* (Table 5). Era and Frontana appear to possess the same gene(s) conditioning resistance in adult plants. Thus, gene *Lr*13, present in Frontana (4), is postulated to correspond to gene A in our study. This is substantiated by our obtaining no segregation when Era is crossed to CT263, the line possessing *Lr*13 (Table 5). The F_2 populations resulting from Era-1/Line 920 (*Lr*34) and Era-3/Line 920 segregated for one gene when tested with *P. recondita* culture UN13 (MO-X), indicating that Era-1 and Era-3 also have *Lr*34 in common (Table 5). The line with *Lr*34 is moderately susceptible to culture UN13 (MO-X) but is complementary with *Lr*13, as shown by the F_2 segregating ratio of CT263/Line 920.

Thus, the adult plant resistance in Era is controlled by the interaction of genes *Lr*13 and *Lr*34. The expression of *Lr*13, a gene for adult plant resistance, is enhanced by the presence of another gene, *Lr*34, which was undetected by itself (Table 3). These results support Dyck et al (4), who reported that the expression of *Lr*13 is enhanced by modifiers. In this study, *Lr*34 interacted with a third gene (C) in Era-3 to give a moderately resistant reaction under field conditions. It was not possible to confirm the identity of gene C when using culture UN13 (MO-X). Both Era-1/Line 922 (*Lr*T3) and Era-3/Line 922 segregated for two genes, probably *Lr*13 and *Lr*34 (Table 5). Dyck and Samborski (3) described the interacting genes *Lr*34 and *Lr*T3 in Frontana but did not report an interaction with *Lr*13.

Tests were conducted to evaluate the relationship of low infection types obtained in seedling plants of Era with some cultures of *P. recondita* to the genes postulated to confer resistance in Era (Table 6). The seven cultures of *P. recondita* used in this study were characterized by their virulence to a series of single gene lines of the host (Table 7).

The low infection types obtained on seedlings of Era, Baart, and the line possessing *Lr*10 when using the culture UN13 (MN-TBB) (Table 6) suggest the presence of *Lr*10 in Era and Baart. Browder (2) postulated from pedigree analysis and infection type data that Era possessed *Lr*10. Era possesses an additional seedling resistance gene (*Lr*D) that is detected by culture UN1 (MO-11) of *P. recondita* (Table 6). The low infection type obtained on seedlings of Era-3 when inoculated with this culture is not due to *Lr*10, *Lr*34, or *Lr*T3 (Table 6). The genes *Lr*34 and *Lr*T3 interacted to give a low IT when tested by Dyck and Samborski (3), but they are both ineffective when used singly. However, RL 6050 possessing *Lr*34 and *Lr*T3 was susceptible to the isolate UN1 (MO-11) (Table 6), indicating that the low IT obtained on Era with this culture was not due to the combination of *Lr*34 and *Lr*T3, but to another gene or genes.

Era's resistance to leaf rust is conditioned by two seedling resistance genes (*Lr*10 and a previously undesignated gene, *Lr*D). The adult plant resistance in Minnesota and Morocco was due to *Lr*13 and *Lr*34 and in a portion of the plants, to an undescribed adult plant resistance gene (*Lr*C). *Lr*13, *Lr*34, and *Lr*C seem to enhance and complement the expression of resistance.

ACKNOWLEDGMENT

We thank D. V. McVey, USDA-ARS, Cereal Rust Laboratory, St. Paul, MN, for providing the seed of the Baart/Era crosses.

LITERATURE CITED

1. Browder, L. E. 1971. Pathogenic specialization in cereal rust fungi, especially *Puccinia recondita* f. sp. *tritici*: Concepts, methods of study and application. U.S. Dep. Agric. Tech. Bull. 1432. 51 pp.
2. Browder, L. E. 1980. A compendium of information about named genes for low reaction to *Puccinia recondita* in wheat. Crop Sci. 20:775-779.
3. Dyck, P. L., and Samborski, D. J. 1982. The inheritance of resistance to *Puccinia recondita* in a group of common wheat cultivars. Can. J. Genet. Cytol. 24:273-283.
4. Dyck, P. L., Samborski, D. J., and Anderson, R. G. 1966. Inheritance of adult plant leaf rust resistance derived from the common wheat varieties Exchange and Frontana. Can. J. Genet. Cytol. 8:665-671.
5. Heiner, R. E., and McVey, D. V. 1971. Registration of Era wheat. Crop Sci. 11:604.
6. Purdy, L. H., Loegering, W. Q., Konzak, C. F., Peterson, C. J., and Allan, R. E. 1968. A proposed standard method for illustrating pedigrees of small grain varieties. Crop. Sci. 8:405-406.
7. Reitz, L. P., and Hamlin, W. G. 1978. Distribution of the varieties and classes of wheat in the United States in 1974. U.S. Dep. Agric. Stat. Bull. 604. 98 pp.
8. Samborski, D. J. 1985. Wheat leaf rust. Pages 39-59 in: The Cereal Rusts. Vol. 2. Diseases, Distribution, Epidemiology, and Control. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando, FL.
9. Siegenthaler, V. L., Stepanich, J. E., and Briggle, L. W. 1986. Distribution of the varieties and classes of wheat in the United States, 1984. U.S. Dep. Agric. Stat. Bull. 739. 106 pp.
10. Stakman, E. C., Stewart, D. M., and Loegering, W. Q. 1962. Identification of physiologic races of *Puccinia graminis* var. *tritici*. U.S. Dep. Agric. ARS-E6/7. 53 pp.