The Role of *Lr10, Lr13,* and *Lr34* in the Expression of Adult-Plant Resistance to Leaf Rust in the Wheat Cultivar Era

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ABSTRACT

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Elucidation of the genetic basis of the highly effective resistance in Era wheat to *Puccinia recondita* f. sp. *tritici* could assist breeders in reconstructing similar *Lr* gene combinations in other cultivars. Attempts to relate the presence of *Lr10, Lr13,* and *Lr34* with the expression of adult-plant resistance showed that a combination of these genes did not necessarily confer high levels of resistance to pathotype UVPrt8 of *P. r.* f. sp. *tritici*. The most resistant adult F_2 plant derived from a cross between Era and line RL6058 was homozygous for *Lr10, Lr13,* and *Lr34*, but other F_2 plants exhibiting intermediate levels of adult-plant resistance also appeared homozygous for all three genes. In the leaf rust–susceptible background of Line E, no clear relationship between *Lr13* and expression of adult-plant resistance derived from Era was observed. Limited evidence was obtained that *Lr10* in association with an unknown gene or *Lr13* interacted with *Lr34* to confer an improved level of resistance to leaf rust in certain plants. Mostly results indicated a lack of interaction among *Lr10, Lr13,* and *Lr34*. It seems unlikely that wheat breeders will be able to reconstruct a similar Era-type of leaf rust resistance by combining *Lr10, Lr13,* and *Lr34*.

In 1970, the semidwarf wheat (*Triticum aestivum* L.) cultivar Era (CI 13986), with resistance to several important diseases, was released in Minnesota (10). Following its release, Era was widely grown in the hard red spring wheat region of the United States (13) and proved to have adequate, long-lasting resistance to leaf rust caused by *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* (8). It is believed that the Era-type leaf rust resistance is also present in the wheat cultivars Wheaton (3) and Marshall (4).

According to the pedigree of Era, infection type data, and genetic studies, the cultivar contains the *Lr10, Lr13,* and *Lr34* genes for resistance to leaf rust (2,8,15, 19,20,24). Era may also have an additional, unidentified gene for seedling resistance (8). The nature of adult-plant resistance in Era appears more intricate. Ezzahiri and Roelfs (8) demonstrated that adult-plant resistance could be attributed to *Lr13, Lr34,* and a third, unknown gene. In combination with the other two genes, *Lr34* interacted in a complementary way to enhance resistance.

If *Lr10* and *Lr13* interact with *Lr34* to provide durable resistance, wheat breeders could combine these genes in future cultivars to maintain a level of resistance similar to that of Era. The objective of our study was to investigate the role of *Lr10* and *Lr13* in the expression of adult-plant resistance in Era.

MATERIALS AND METHODS

All experimental work was conducted at the Department of Plant Pathology, University of the Orange Free State, Bloemfontein, South Africa.

Adult-plant resistance. A leaf rust–resistant single plant selection of Era was crossed with RL6058 (Thatcher*6 × PI 58548 [*Lr34*] [7]) and with the susceptible cultivar Line E (W2691 × Indian H [12]). F_2 plants from the crosses Era × Line E and Era × RL6058, the parents, and Thatcher (Tc) backcross lines RL6004 (Tc*Lr10*) and CT263 (Tc*Lr13*) were grown (three per pot) in plastic pots containing 4 kg of soil in a greenhouse at 18 to 25°C. Three weeks after planting, and weekly thereafter for the duration of the experiment, a water-soluble fertilizer (6.5-2.7-13.0 N-P-K) was applied (0.5 g per pot) as a soil drench. Flag leaves of 441 Era × Line E and 292 Era × RL6058 F_2 plants, and of the check lines, were inoculated (1) with fresh urediniospores of pathotype UVPrt8 (Table 1) of *P. r.* f. sp. *tritici.* Pathotype UVPrt8, which occurs commonly in South Africa (17), is virulent to Era seedlings but avirulent to adult plants in the field (16). At the time of inoculation, the growth stage of F_2, parent, and check plants varied from 49 (first awns visible) to 69 (flowering complete) on the decimal scale (25).

Inoculated plants were kept in a dark dew chamber for 19 h before being transferred to an air-conditioned greenhouse compartment where the ambient temperature was maintained at 12 to 18°C (15°C). This environment was selected because a previous study indicated that adult-plant resistance in Era in a greenhouse is best expressed at low temperatures (18). Duplicate sets of the check and parental cultivars, and 70 Era × RL6058 F_2 plants, were placed at 24 to 28°C (26 C). Illumination of 120 $\mu E \cdot m^{-2} \cdot s^{-1}$ was provided by cool-white fluorescent tubes for 12 h each day to supplement daylight. F_2 plants at 15°C were classified according to infection type (IT) 16 days after inoculation, whereas those at 26°C were scored after 13 days. ITs were scored according to the descriptions of Roelfs (21): resistance to susceptibility ranged from 0, indicating no macroscopic sign of infection, to 4, describing large uredinia without chlorosis (c) or necrosis (n). Chlorotic flecks are indicated by a semicolon (;), and plus or minus signs denote pustules that are larger or smaller than the normal range for a given IT.

Relationship between *Lr10, Lr13,* and adult-plant resistance. Seed was harvested from 41 Era × Line E and 23 Era × RL6058 F_2 plants, each of which had been characterized for flag leaf reaction to pathotype UVPrt8. These selections represented the complete range of observed flag leaf ITs (1 to 4 for Era × Line E and ; to 3$^+$ for Era × RL6058) and were at the same

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Table 1. Avirulence/virulence formulae of South African pathotypes of *Puccinia recondita* f. sp *tritici* used to evaluate seedling and adult-plant resistance in Era wheat and its progenies

Pathotype	*Lr* genes[a]
UVPrt2	1,2a,2b,3ka,11,13,15,17,20,24,26,30/2c,3a,3bg,10,14a,16
UVPrt8	3a,3bg,3ka,11,16,20,26,30/1,2a,2b,2c,10,13,14a,15,17,24
UVPrt10	3a,3bg,3ka,10,11,16,20,24,26,30/1,2a,2b,2c,13,14a,15,17

[a] Avirulence/virulence formulae based on seedling data at 20°C, except for *Lr13,* which was tested at 26°C.

growth stage at the time of evaluation. To relate the presence or absence of genes assumed to be *Lr10* or *Lr13* with the adult-plant reaction observed in the F_2, seed of each Era × RL6058 F_3 family was divided, providing two groups for testing. Seedlings were inoculated with either pathotype UVPrt2 or UVPrt10 (Table 1) to detect which adult F_2 plants, all homozygous for *Lr34*, were also homozygous for *Lr13* or *Lr10*. Tests for *Lr13* were conducted at 26°C, and those for *Lr10* at 20°C. Era × Line E F_3 families were tested in the seedling stage for *Lr13* with pathotype UVPrt2 at 26°C. Unexpectedly, UVPrt10 was avirulent to Line E and thus confounded confirmation of *Lr10* in Era × Line E progeny. The identity of the resistance gene in Line E is not known.

Progeny from three Era × RL6058 F_3 families (ER6, ER10, and ER16), which displayed different seedling reactions to UVPrt2 and UVPrt10, were tested for *Lr10* and *Lr13*. To confirm the presence or absence of these genes, single F_4 plants (ER6/2, ER10/1, and ER16/1) were selected from each of these families on a basis of IT and test-crossed with RL6004 and CT263. F_2 populations from these crosses were tested in the greenhouse with the appropriate pathotype–temperature combination for *Lr10* and *Lr13*.

Parental and control genotypes were included in all seedling tests. ITs produced on plants at 20 and 26°C were scored 12 and 9 days after inoculation, respectively. At the time of evaluation in all tests, pustule development appeared maximal on the susceptible cultivars.

Table 2. Flag leaf infection types of wheat cultivar Era, Line E and Thatcher (Tc) backcross lines at two temperatures to pathotype UVPrt8 of *Puccinia recondita* f. sp. *tritici*

	Infection type at temperature	
Cultivar or line	**12 to 18°C**	**24 to 28°C**
Era	1^+	2^-
Line E	3^+	4
RL6058 (Tc*Lr34*)	1^{++}	3
RL6004 (Tc*Lr10*)	3	$3^=$
CT263 (Tc*Lr13*)	3^+	3^c
Thatcher	3^+	3^+

RESULTS

Adult-plant resistance. Era was resistant, whereas Line E, RL6004 (Tc*Lr10*) and CT263 (Tc*Lr13*) plants were susceptible at 15 and 26°C to pathotype UVPrt8 (Table 2). RL6058 (Tc*Lr34*) produced a flag leaf IT very similar to Era at 15°C but was susceptible at 26°C. Both RL6004 and CT263 exhibited slightly lower ITs at 26°C than at 15°C.

A ratio of 122 resistant (IT range of 1 to 2) to 319 susceptible (IT 3 or 4) among the Era × Line E F_2 plants suggested the segregation of a single recessive gene ($\chi^2_{1:3}$ = 1.67) to pathotype UVPrt8 at 15°C. No susceptible Era × RL6058 segregates were observed among the 222 F_2 plants tested at 15°C. At a greenhouse temperature of 26°C, however, eight derivatives from this cross were susceptible and 62 resistant.

Relationship between *Lr10*, *Lr13*, and adult-plant resistance. *Lr13* (IT ;$1^{=cn}$ to X^{cn}) was present in 38 of the 41 Era × Line E F_3 families tested (Table 3). ITs on flag leaves of F_2 plants not containing *Lr13* were 1^+, 2, and 3^{++}. Of the 38 families in which *Lr13* was confirmed on the basis of IT, six were homozygous for this gene. *Lr13* was, furthermore, present in 15 of the 16 F_3 families derived from susceptible F_2 plants (flag leaf ITs 3, 3^{++}, and 4).

The relationship between the flag leaf reaction of Era × RL6058 F_3 plants and the presence of *Lr10* and *Lr13* is shown in Table 4. *Lr10* occurred in 10 and *Lr13* in eight of the 12 Era × RL6058 F_3 families derived from F_2 plants tested at 15°C. Flag leaf ITs of F_2 plants without *Lr10* were ;1 and 1^+, and of plants without *Lr13* were ;1, 1, and 1^+. A 1^+ IT was recorded for the F_2 plant whose F_3 progeny did not reveal *Lr10* or *Lr13*. Reactions of Era × RL6058 F_2 plants containing *Lr10*, *Lr13*, and *Lr34* ranged from ; to 2^+. All Era × RL6058 F_2 plants selected at 26°C possessed *Lr13*. All but two of these F_3 families also possessed *Lr10*. In this material, ITs of F_2 plants postulated to contain *Lr10*, *Lr13*, and *Lr34* varied from ; to 3^+.

In the F_3, family ER6 was homozygous for *Lr10* (IT ; to ;1 to UVPrt10), but the 2^{++} IT displayed by seedlings in this family to UVPrt2 deviated from the typical *Lr13* seedling reaction (X^{cn}) at 26°C (Table 5). The 2^{++} IT was allocated on a basis of medium-sized uredinia associated with the characteristic green islands and chlorotic borders (21). Evaluation of

Table 3. The relationship between the adult-plant reaction of Era × Line E F_2 plants to *Puccinia recondita* f. sp. *tritici* and the presence of *Lr13*, based on 41 F_3 family progeny tests

		F_2 parent plants[c] with genotype			
F_3 family numbers[a]	**F_2 flag leaf IT[b]**	***Lr13Lr13***	***Lr13lr13***	***lr13lr13***	**Total**
EE1 to 6	1	0	6	0	6
EE7 to 9	1^+	0	2	1	3
EE10 to 14	1^{++}	2	3	0	5
EE15 to 25	2	2	8	1	11
EE26 to 28	3	1	2	0	3
EE29 to 40	3^{++}	0	11	1	12
EE41	4	1	0	0	1
Total		6	32	3	41

[a] F_3 families were grouped according to F_2 flag leaf infection types.
[b] Infection types (ITs) produced by pathotype UVPrt8 on flag leaves.
[c] The presence of *Lr13* was determined by inoculating F_3 seedlings with pathotype UVPrt2.

Table 4. The relationship between the adult-plant reaction of Era × RL6058 F_2 plants to *Puccinia recondita* f. sp. *tritici* and the presence of *Lr10* and *Lr13*, based on 23 F_3 family progeny tests

			Number of F_2 parent plants[c] with genotype									
			Lr10Lr10			***Lr10lr10***			***lr10lr10***			
F_3 family numbers[a]	**F_2 flag leaf IT[b]**	**Temp. (F_2 plants)**	***Lr13Lr13***	***Lr13lr13***	***lr13lr13***	***Lr13Lr13***	***Lr13lr13***	***lr13lr13***	***Lr13Lr13***	***Lr13lr13***	***lr13lr13***	**Total**
ER1	;	15°C	1	0	0	0	0	0	0	0	0	1
ER2 to 5	;1	15°C	1	0	0	0	1	1	0	1	0	4
ER6 to 8	1 to 1^{++}	15°C	0	0	1	0	1	0	0	0	1	3
ER9 to 12	$2^=$ to 2^+	15°C	1	0	0	0	2	1	0	0	0	4
ER13 to 14	;	26°C	1	0	0	0	1	0	0	0	0	2
ER15 to 17	;1	26°C	0	0	0	0	2	0	0	1	0	3
ER18 to 19	$2^=$	26°C	0	0	0	0	1	0	0	1	0	2
ER20 to 23	3^- to 3^+	26°C	0	0	0	0	4	0	0	0	0	4
Total			4	0	1	0	12	2	0	3	1	23

[a] F_3 families were grouped according to F_2 flag leaf infection types.
[b] Infection types (ITs) produced by pathotype UVPrt8 on flag leaves.
[c] The presence of *Lr10* and *Lr13* was determined by inoculating F_3 seedlings with either pathotype UVPrt10 or UVPrt2.

RL6004 × ER6/2 and CT263 × ER6/2 F_2 progeny provided genetic evidence that ER6 contained *Lr10* but not *Lr13* (Table 6). The 15:1 (χ^2 = 0.06) ratio indicated segregation of *Lr13* and a second dominant gene for resistance to UVPrt2. Based on seedling ITs, family ER16 was homozygous for *Lr13* but expressed an IT 2, which deviated from the typical *Lr10* low reaction to UVPrt10. Here, progeny from the RL6004 × ER16/1 cross revealed the absence of *Lr10* or other genes effective to UVPrt10 in ER16 (Table 6). No susceptible segregates were found in the CT263 × ER16/1 F_2, indicating that these two lines have a gene in common. Confirmation of *Lr13* in ER16 thus suggested that *Lr13* and *Lr34* may have interacted to produce improved resistance to UVPrt10 in this family. According to the seedling ITs, family ER10 was homozygous for both *Lr10* and *Lr13*. This was confirmed by the absence of susceptible F_2 segregates when tested with UVPrt2 or UVPrt10 (Table 6).

DISCUSSION

The genetic nature of leaf rust resistance in Era appears complex. Similar to the observations of Ezzahiri and Roelfs (8), the IT of Era was consistently lower than what is conditioned by any of the *Lr* genes known to reside in this cultivar (Fig. 1). This indicated additional *Lr* genes, as was proposed (8), or perhaps gene interaction. Complementary interaction occurs between *Lr27* and *Lr31* (23), whereas resistance enhancement has been attributed to several *Lr* gene pairs (9,11,22).

Genetic studies aimed at identifying leaf rust resistance genes other than *Lr10*, *Lr13*, and *Lr34* in Era have mostly been unsuccessful (Z. A. Pretorius, *unpublished*). It appears that the full complement of major and modifying genes, which all contribute to the leaf rust resistance of Era, cannot be easily analyzed. This implies that it would be extremely difficult to reconstruct Era resistance by pyramiding the essential genes. If these additional modifying genes are important in the optimum expression of certain resistance gene combinations, the deliberate combining of *Lr10*, *Lr13*, and *Lr34* would not necessarily result in improved resistance. However, by using Era as a crossing parent in a breeding program, and through selection for the desired leaf rust response in ensuing generations, it has been shown that Era resistance can successfully be retained (3,4).

Temperature is important in the expression of Era resistance. This can at least partly be attributed to the environment-specific expression of all three major *Lr* genes. Browder (2) characterized *Lr10* as moderately sensitive to environmental influences. This study and others (5,6,19) have shown that the optimum expressions of *Lr13* and *Lr34* are strongly influenced by temperature. The low-temperature adult-plant resistance of Era previously recognized in greenhouse studies (18) can be attributed to *Lr34*. The strong phenotypic resemblance in the small-uredinium reaction between segregates and RL6058 suggested the involvement of *Lr34*. Of the 222 Era × RL6058 F_2 plants evaluated at 15°C, only 20 had ITs slightly higher than the characteristic 1^+ of RL6058.

The testing of F_3 progenies of F_2 plants exhibiting different adult-plant reactions clearly showed that the presence or absence of *Lr10* or *Lr13* was not correlated with the F_2 adult-plant reaction. A highly resistant Era × Line E F_2 plant (IT 1^+) did not contain *Lr13*, whereas several susceptible F_2 plants (ITs 3^{++} to 4) contained *Lr13*. In the Era × RL6058 cross, the most resistant F_2 plant at 15°C (IT ;) was homozygous for *Lr10*, *Lr13*, and *Lr34*. Conversely, an F_2 plant displaying a $2^=$ flag leaf reaction also appeared homozygous for the three genes. All families in which *Lr13* was postulated contained plants showing either a mesothetic reaction or severe chlorosis and necrosis in association with pustules (ITs $;1^{cn}$ to X^{cn}). In the Era × RL6058 F_3 family ER6, *Lr13* could not unequivocally be identified on a basis of IT. The 2^{++} IT exhibited by all plants in this family was distinctly different from the typical *Lr13* low reaction. Homozygosity for *Lr10* in ER6 raised the question whether *Lr10* in combination with *Lr34* could have conferred resistance to pathotype UVPrt2. The data obtained in the test crosses confirmed the absence of *Lr13* in ER6 but indicated segregation of a gene not previously detected. *Lr10* in ER6 was confirmed by the absence of susceptible segregates in the RL6004 × ER6/2 cross. This suggested that *Lr10*, *Lr34*, and an unknown gene combined to produce an improved resistance to UVPrt2. In ER16, genetic evidence was obtained that *Lr13* was present alongside *Lr34*. We assume that the resistance displayed to UVPrt10 by ER16, which lacks *Lr10*, resulted from interaction between *Lr13* and *Lr34*.

All Era × RL6058 F_2 adult plants that were susceptible at 26°C segregated for *Lr10* and *Lr13* in the F_3. The F_2 adult-plant reactions could thus have been influenced by heterozygosity for *Lr10* or *Lr13*, the absence or suppression of essential modifying genes, or by the fact that *Lr34* is less effective at high temperatures (5).

Table 5. Seedling infection types of parental and check wheat cultivars and lines at two temperatures to pathotypes UVPrt2 and UVPrt10 of *Puccinia recondita* f. sp. *tritici*

	Infection type produced to pathotype			
	UVPrt2		UVPrt10	
Cultivar or line	20°C	26°C	20°C	26°C
Era	$;1^{cn}$	;	;	$;1^{=c}$
Line E	3^{++}	3^+	2^+3	2^+3
RL6004 (Tc*Lr10*)	3	3	$;1^-$	$;1^c$
CT263 (Tc*Lr13*)	3^{++}	X^{cn}	3^{++}	3^+
RL6058 (Tc*Lr34*)	3^{++}	3^{++}	3^{++}	3^{++}
Thatcher (Tc)	3^{++}	3^{++}	3^{++}	3^{++}
ER6/2[a]	2	2^{++}	;	$;^c$
ER10/1[b]	$;^{cn}$	$;^{cn}$	;	$;^c$
ER16/1[c]	X^{cn}	$X^{=cn}$	2	2

[a] Era × RL6058 F_4 line with *Lr10*, *Lr34*, plus an unknown gene.
[b] Era × RL6058 F_4 line with *Lr10*, *Lr13*, and *Lr34*.
[c] Era × RL6058 F_4 line with *Lr13* and *Lr34*.

Table 6. Response classes of F_2 wheat seedlings derived from crosses between Era × RL6058 lines and RL6004 (Tc*Lr10*) or CT263 (Tc*Lr13*) to *Puccinia recondita* f. sp. *tritici*

			Number of plants				
Cross	Pathotype[a]	Temp.	Resistant	Susceptible	Low IT range	Ratio	χ^2
CT263 × ER6/2	UVPrt2	26°C	441	31	; to 2	15:1[b]	0.062
RL6004 × ER6/2	UVPrt10	20°C	498	0	; to $;1^{=c}$	15:1	–
CT263 × ER10/1	UVPrt2	26°C	423	0	$;^c$ to X^{+c}	15:1	–
RL6004 × ER10/1	UVPrt10	20°C	402	0	; to $;1^{=c}$	15:1	–
CT263 × ER16/1	UVPrt2	26°C	398	0	$;^{cn}$ to X^{+c}	15:1	–
RL6004 × ER16/1	UVPrt10	20°C	250	84	$;^c$ to 2	3:1	0.004

[a] Pathotype UVPrt2 is virulent to *Lr10* and avirulent to *Lr13*, whereas UVPrt10 is avirulent to *Lr10* and virulent to *Lr13*.
[b] Assuming that family ER6/2 does not contain *Lr13*, a 3:1 ratio (χ^2 = 85.53) was expected. The observed ratio suggested segregation of two dominant genes for resistance to UVPrt2.

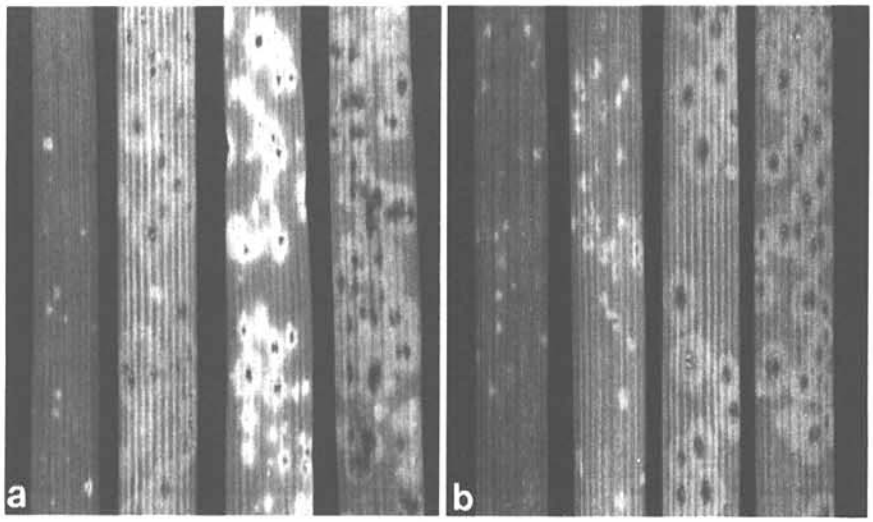

Fig. 1. Infection types (ITs) produced **(A)** at 26°C by pathotype UVPrt2 of *Puccinia recondita* f. sp. *tritici* on the adaxial surface of primary leaves of, from left to right, Era (IT ;), RL6004 (Tc*Lr10*, [IT 3]), CT263 (Tc*Lr13*, [IT X^{cn}]), and RL6058 (Tc*Lr34*, [IT 3^{++}]), and **(B)** at 20°C by pathotype UVPrt10 on Era (IT ;), RL6004 (IT ;1^{-}), CT263 (IT 3^{++}), and RL6058 (IT 3^{++}).

Until the nature of the Era resistance genotype has been characterized more fully, it appears unlikely that similar adult-plant resistance can be reconstructed by combining *Lr10*, *Lr13*, and *Lr34*. Considering the urgent need for effective genetic resistance to leaf rust other than the almost exhausted monogenic *Lr* sources in wheat (13), the unraveling of genotypes such as Era should prove useful.

LITERATURE CITED

1. Browder, L. E. 1965. An atomizer for inoculating plants with spore-oil suspension. Plant Dis. Rep. 49:455.
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. Busch, R., McVey, D., Rauch, T., Baumer, J., and Elsayed, F. 1984. Registration of Wheaton wheat. Crop Sci. 24:622.
4. Busch, R., McVey, D., Youngs, V., Heiner, R., and Elsayed, F. 1983. Registration of Marshall wheat. Crop Sci. 23:187.
5. Drijepondt, S. C., and Pretorius, Z. A. 1989. Greenhouse evaluation of adult-plant resistance conferred by the gene *Lr34* to leaf rust of wheat. Plant Dis. 73:669-671.
6. Drijepondt, S. C., Pretorius, Z. A., and Rijkenberg, F. H. J. 1991. Expression of two wheat leaf rust resistance gene combinations involving *Lr34*. Plant Dis. 75:526-528.
7. Dyck, P. L. 1977. Genetics of leaf rust reaction in three introductions of common wheat. Can. J. Genet. Cytol. 19:711-716.
8. Ezzahiri, B., and Roelfs, A. P. 1989. Inheritance and expression of adult plant resistance to leaf rust in Era wheat. Plant Dis. 73:549-551.
9. German, S. E., and Kolmer, J. A. 1992. Effect of *Lr34* in the enhancement of resistance to leaf rust of wheat. Theor. Appl. Genet. 84:97-105.
10. Heiner, R. E., and McVey, D. V. 1971. Registration of Era wheat. Crop Sci. 11:604.
11. Kolmer, J. A. 1992. Enhanced leaf rust resistance in wheat conditioned by resistance gene pairs with *Lr13*. Euphytica 62:123-130.
12. Luig, N. H. 1983. A Survey of Virulence Genes in Wheat Stem Rust, *Puccinia graminis* f. sp. *tritici*. Verlag Paul Parey, Berlin.
13. Martens, J. W., and Dyck, P. L. 1989. Genetics of resistance to rust in cereals from a Canadian perspective. Can. J. Plant Pathol. 11:78-85.
14. Martinez-Gonzales, J. M. S., Wilcoxson, R. D., Stuthmann, D. D., McVey, D. V., and Busch, R. H. 1983. Genetic factors conditioning slow rusting in Era wheat. Phytopathology 73: 247-249.
15. McVey, D. V. 1989. Verification of infection-type data for identification of genes for resistance to leaf rust in some hard red spring wheat. Crop Sci. 29:304-307.
16. Pretorius, Z. A., and Kemp, G. H. J. 1988. Effect of adult-plant resistance on leaf rust development and grain yield in wheat. Phytophylactica 20:341-343.
17. Pretorius, Z. A., and Le Roux, J. 1988. Occurrence and pathogenicity of *Puccinia recondita* f. sp. *tritici* on wheat in South Africa during 1986 and 1987. Phytophylactica 20:349-352.
18. Pretorius, Z. A., Rijkenberg, F. H. J., and Wilcoxson, R. D. 1988. Effects of growth stage, leaf position and temperature on adult-plant resistance of wheat infected by *Puccinia recondita* f. sp. *tritici*. Plant Pathol. 37:36-44.
19. Pretorius, Z. A., Wilcoxson, R. D., Long, D. L., and Schafer, J. F. 1984. Detecting wheat leaf rust resistance gene *Lr* 13 in seedlings. Plant Dis. 68:585-586.
20. Rizvi, S. S. A., and Statler, G. D. 1982. Probable genotypes of hard red spring wheats for resistance to *Puccinia recondita* f. sp. *tritici*. Crop Sci. 22:1167-1170.
21. Roelfs, A. P. 1988. Genetic control of phenotypes in wheat stem rust. Annu. Rev. Phytopathol. 26:351-367.
22. Samborski, D. J., and Dyck, P. L. 1982. Enhancement of resistance to *Puccinia recondita* by interactions in wheat. Can. J. Plant Pathol. 4:152-156.
23. Singh, R. P., and McIntosh, R. A. 1984. Complementary genes for reaction to *Puccinia recondita tritici* in *Triticum aestivum*. I. Genetic and linkage studies. Can. J. Genet. Cytol. 26:723-735.
24. Statler, G. D. 1984. Probable genes for leaf rust resistance in several hard red spring wheats. Crop Sci. 24:883-886.
25. Tottman, D. R. 1987. The decimal code for the growth stages of cereals, with illustrations. Ann. Appl. Biol. 110:441-454.