Influence of Genetic Background on the Expression of Wheat Leaf Rust Resistance Gene *Lr*22a

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ABSTRACT

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F_4 families homozygous for *Lr*22a, derived from crosses between the wheat genotypes RL6044 (Thatcher:*Lr*22a) and Zaragoza or SST33 (leaf rust-susceptible) were developed. Quantitative assessment of latent period of *Puccinia recondita* f. sp. *tritici* and number of uredinia per centimeter of square leaf surface of these families indicated significantly different levels of resistance. Although infection types, resulting from inoculations with different isolates of known virulence, denoted the presence of *Lr*22a, certain F_4 families exhibited a latent period statistically equal to that of the susceptible control. Other F_4 families showed resistance superior to that of RL6044. Selected F_5 families indicated that levels of adult-plant resistance superior to that of the parent could be maintained in a selection program. Enhanced levels of resistance were apparently not caused by the combination of *Lr*22a with other known, but ineffective genes for hypersensitive seedling resistance in the susceptible parents, or by the growth stage of plants in families segregating for maturity. It is hypothesized that modifying genes, which cannot be detected qualitatively, interacted with *Lr*22a to produce different levels of resistance. These modifying genes were not associated entirely with *Lr*22a since F_4 families without the gene also varied for latent period and the number of uredinia.

Additional keywords: genetics, *Puccinia recondita, Triticum aestivum.*

The degree of resistance conferred by the genes *Lr*21, *Lr*22a, and *Lr*32 to leaf rust (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*) decreased progressively during their transfer from diploid *Triticum tauschii* (Coss.) Schmal. to hexaploid common wheat *T. aestivum* L. em. Thell (6,13,18). Valkoun et al (30) also reported a stepwise dilution of seedling resistance transferred from diploid *T. monococcum* L. to the hexaploid level. Similarly, resistance conditioned to wheat stem rust (*P. graminis* Pers. f. sp. *tritici* Eriks. & Henn.) by the genes *Sr*21, *Sr*22, and *Sr*33 was diluted when the genes were transferred from the diploid to hexaploid level (18).

However, resistance need not necessarily be less effective when genes are transferred from a lower to higher level of ploidy. The high degree of stem rust resistance mediated by *Sr*35 was maintained during transfer of the gene from *T. monococcum* to common wheat (18). In transferring leaf rust resistance from five accessions of *Aegilops speltoides*, Dvorak (5) found that resistance was diluted only in progeny from one hybrid.

The above-mentioned reports of variation in levels of resistance, conferred by genes originally transferred from the wild relatives of common wheat, were based on the qualitative comparison of infection types. The objective of our study was to quantify some aspects of the sensitivity of a wheat leaf rust resistance gene to its genetic background. *Lr*22a in wheat line RL6044 confers an increased latent period, small uredinia (infection type 1^+), and reduced sporulation. The gene is, however, not associated with a reduction in the number of pustules per unit of leaf area (22). Thus, due to its characteristic expression, and previous reports of sensitivity to its genetic environment (6,24), *Lr*22a was selected for quantitative assessments of disease in segregating progeny.

MATERIALS AND METHODS

First F_4 assessment. Latent period. *Lr*22a was inherited as a partially recessive gene in crosses of the Thatcher backcross line RL6044 with the South African spring wheat cultivars Zaragoza and SST33 (24). In the latter study, several F_2 plants from both crosses, displaying the *Lr*22a low reaction, were harvested for progeny testing. No susceptible F_3 plants were observed among those selections, thus confirming homozygosity for *Lr*22a. These F_3 plants were advanced and 20 F_4 families from the Zaragoza × RL6044 cross and 18 families from the SST33 × RL6044 cross were randomly selected. Five plants per family were grown per pot containing 5 kg of soil, in a greenhouse with a 12-hr day/night temperature regime of 20–22/12–14 C. Plant nutrition was as described elsewhere (23). In order to assess several families from both crosses and to remain within the sample size for which quantitative measurements can timeously be performed in the available research infrastructure, five plants of each family and parental genotype were evaluated. Forty-three days after planting, the fourth leaf of each plant was inoculated with fresh urediniospores of *P. r. tritici*, using the Andres and Wilcoxson inoculation device (2). Plants from the RL6044 × Zaragoza cross were inoculated with isolate 3SA57 and those from the RL6044 × SST33 cross with isolate 3SA86. Isolates 3SA57 and 3SA86 are virulent to Zaragoza and SST33, respectively, but avirulent to RL6044 (Table 1). Before inoculation, single pustule isolates from each of the Zaragoza and SST33 virulent races were established and confirmed for purity on a differential *Lr* gene set (Table 1). Isolates 3SA57 and 3SA86 were then increased in isolation on mutually exclusive host lines and the remaining urediniospores were stored in liquid nitrogen for future use.

All leaves were inoculated with a suspension of 0.2 mg of urediniospores per milliliter of light mineral oil. After inoculation, oil on the leaves was allowed to evaporate for 2 hr before plants were placed in a dew chamber where they were kept in darkness at 18–20 C for 19 hr. During the last 3 hr in the chamber, dew formation was terminated and leaves dried off gradually. Plants

were then placed at 18–20 C in a greenhouse where daylight was supplemented with 900 μE m^{-2} sec^{-1} provided by cool-white fluorescent tubes for 12 hr each day.

On each inoculated leaf a 5-cm-long portion, never closer than 2 cm to either the base or tip of the leaf, was marked. These areas were inspected daily, and, when uredinia became visible, those within the marked area were counted. Counting continued until no more primary uredinia appeared. The log number of uredinia visible at each inspection, until 80% of the primary number had formed, was regressed against time. Latent period was then calculated for each plant as the number of hours after initiation of the dew chamber cycle when 40% of the final number of primary uredinia were visible as erumpent structures (1).

Infection types and number of uredinia. After infection types (0–4 scale) (26) had been determined 15 days postinoculation, leaves were detached and the area of the portion of the leaf on which uredinia had been counted was determined with a leaf area meter (model LI-3100, Lambda Instruments Corporation, Lincoln, NE). The number of uredinia per square centimeter of leaf surface was calculated. According to the 0–4 cereal rust infection type scale (26), a "0" indicates an immune host response without any macroscopic sign of infection. A susceptible response, characterized by large uredinia without chlorosis (c) or necrosis (n), is denoted by a "4". Chlorotic flecks are shown by ";" and plus or minus signs indicate pustules that are larger or smaller than the normal size limit. When the larger uredinia are distributed predominantly towards the base of the leaf, the infection type is described by "Z".

Detection of ineffective genes. Zaragoza carries the gene *Lr*3a derived from one of its parents, Mengavi (25), and SST33 has a gene, most probably *Lr*13, for hypersensitive resistance to *P. r. tritici*. In crosses with a susceptible cultivar both genes behaved partially dominant and, furthermore, a test cross of SST33 with Manitou (*Lr*13) yielded no susceptible F_2 segregates (Z. A. Pretorius, *unpublished*). Twenty days after the quantitative inoculation described above, regrowth of plants in families of the Zaragoza cross, that did not exhibit within-family variation for the *Lr*22a infection type, was inoculated with isolate 3SA86 according to the method of Browder (4). Families of the SST33 cross were inoculated with isolate 3SA57. These isolates are avirulent to Zaragoza and SST33, respectively (Table 1), and inoculations were conducted to determine in which plants *Lr*3a and the gene assumed to be *Lr*13 had been retained.

Growth period. To assess the relationship between growth period and expression of *Lr*22a resistance, we recorded the number of days to heading for each F_4 plant.

Second F_4 assessment. A second experiment, but with different sets of adult-plant-resistant F_4 families derived from the same F_3 populations, was carried out as described above. The fifth leaf on each of five plants of 11 F_4 families per cross were inoculated with urediniospores of either isolates 3SA57 or 3SA86 45 days after planting. Spores were retrieved from the inoculum supply previously stored in liquid nitrogen. Latent period, number of uredinia, infection type, and number of days to heading were determined. Inoculations also were made to indicate the presence of the ineffective genes *Lr*3a and *Lr*13. The leaf rust-susceptible wheat cultivar, Morocco, was inoculated along with the parental cultivars.

Third F_4 assessment. F_4 families, selected for susceptibility in the F_2 (24), and again for the absence of *Lr*22a in the F_3 were developed. Six plants from each of five families of the Zaragoza cross and of six families of the SST33 cross were evaluated as before for latent period, number of uredinia, and infection type. Assessments were made on the fourth leaves of F_4 plants as well as of the parental cultivars.

F_5 assessment. To test the feasibility of selecting for duration of latent period in plants with *Lr*22a, eight plants derived from each of four F_4 families per cross were evaluated. These families had differed in latent period in the previous F_4 experiments. Four plants, each from a different F_5 family, were grown per pot containing 5 kg of soil in a greenhouse at 19–25 C. The fifth leaf of each plant was inoculated with fresh urediniospores of isolates 3SA57 or 3SA86 46 days after planting. Parental cultivars were also included. Inoculation, incubation, and resistance assessment were as described for F_4 families.

Data analyses. Data for latent period and number of uredinia were analyzed for variance on the basis of complete randomization. For each cross and experiment, F_4 families, that did not exhibit phenotypic variation among plants for *Lr*22a infection types were analyzed together with the parental genotypes. Tukey's procedure (29) was applied to reveal statistical differences ($P < 0.05$) among means for latent period and number of uredinia.

TABLE 1. Flag leaf infection types of parental cultivars and lines following inoculation with isolates 3SA57 and 3SA86 of *Puccinia recondita* f. sp. *tritici*

Cultivar or line	Infection type[a] produced by isolate	
	3SA57[b]	3SA86[c]
SST33	2cn	4
Zaragoza	4	;
RL6044 (*Lr*22a)[d]	1^+	1^+

[a] Infection types are according to the 0–4 scale described by Roelfs (26). A chlorotic or necrotic fleck without erupting uredinia, is indicated by ;. Small uredinia, usually associated with a chlorotic or necrotic border are denoted by 1. A 2 is similar to the previous class except that uredinia are larger. Susceptibility is indicated by a 4, where uredinia are large and without any chlorotic or necrotic borders. Infection types are further refined by plus or minus signs to indicate that uredinia within a specific class are slightly larger or smaller than normal. More chlorosis or necrosis than normal is shown by c or n.

[b] Avirulence/virulence combination: *Lr*1, 2a, 2b, 3ka, 9, 11, 13, 15, 17, 20, 21, 24, 26, 29, 30/2c, 3a, 3bg, 10, 14a, 14b, 16, 25.

[c] Avirulence/virulence combination: *Lr*3a, 3bg, 3ka, 9, 11, 16, 20, 21, 26, 29, 30/1, 2a, 2b, 2c, 10, 13, 14a, 14b, 15, 17, 24, 25.

[d] RL6044 is a Thatcher backcross line containing *Lr*22a.

RESULTS

F_4 assessments. Tables 2 and 3 show the mean latent period, number of uredinia per square centimeter, infection type, number of days to heading, as well as the presence of *Lr*3a or *Lr*13 in F_4 families that did not exhibit within-family variation for low infection type to *Lr*22a. In the cross between Zaragoza and RL6044, means from the first F_4 assessment indicated that between families, latent period varied from 170 to 233 hr, despite all plants being homozygous for *Lr*22a (Table 2). Latent period in line RL6044 and Zaragoza were 197 and 150 hr, respectively. Number of uredinia varied from 2.9 to 9.6 per square centimeter of leaf surface. Infection types of *Lr*22a lines ranged from ;1 to 2. Seven families appeared homozygous for *Lr*3a in addition to *Lr*22a. The presence of *Lr*3a was indicated by a 0; to ; adult-plant infection type to isolate 3SA86. Plants that did not possess *Lr*3a showed typical *Lr*22a reactions. Segregation for maturity resulted in heading of plants from 65 to 96 days after planting.

In the second F_4 assessment with Zaragoza × RL6044 families, mean latent period ranged from 182 to 226 hr (Table 2) and infection types varied from 1 to 1^+. The latent period in RL6044 was 206 hr and that in Zaragoza and Morocco 163 and 169 hr, respectively. Number of uredinia varied between 2.3 and 6.3 per square centimeter of leaf area. Eight families possessed *Lr*3a and heading was completed 62–97 days after planting.

In the F_4 assessments with families derived from the cross between SST33 and RL6044, means indicated that latent period varied from 188 to 233 hr (Table 3). In both inoculations the latent period in RL6044 was intermediate between these extremes and uredinia developed most rapidly on SST33. The number of uredinia ranged from 5.8 to 13.0 per square centimeter of leaf surface and infection types 1^+, 1^{++}, and 2 were observed. Six families additionally expressed the *Lr*13 hypersensitive resistance (infection type 2cn) of SST33. In the first inoculation, heading was completed between 64 and 100 days after planting and between 66 and 96 days in the second inoculation.

Different infection types for *Lr*22a were produced among plants

TABLE 2. Latent period, number of uredinia, infection type, growth period, and indication of the defeated *Lr*3a gene assessed on F_4 families from the cross Zaragoza × RL6044[a] following inoculation with *Puccinia recondita* f. sp. *tritici*

Cultivar or line	Latent period (hr)	Uredinia/ cm^2 leaf surface	Infection type[b]	Presence of *Lr*3a[c]	Days to heading[d]
First F_4 assessment[e]					
A21R	233 a	6.8 abc	1^+	*	65–87
A34R	232 a	6.3 abc	1	*	75–96
A14R	212 ab	2.9 a	1^+	—	87
A28R	206 abc	3.6 ab	1^+	—	89
A17R	206 abc	8.4 c	1^+	*	65–75
A10R	201 bcd	5.3 abc	1^+	*	65–75
RL6044	197 bcde	7.3 bc	1^+	—	85
A18R	193 bcde	7.8 bc	1^+	*	84–95
A5R	190 bcde	7.3 bc	;1	—	70–88
A37R	183 cde	9.6 c	1^+	*	89
A8R	176 def	7.8 bc	1^+	—	93
A39R	174 def	5.3 abc	2	*	77–82
A36R	170 ef	9.0 c	1^{++}	—	73–87
Zaragoza	150 f	5.8 abc	4	*	77
Second F_4 assessment					
A29R	226 a	4.4 ab	1	*	65–79
A3R	222 ab	2.3 a	1	*	72–74
A15R	218 ab	4.8 ab	1	—	83
A27R	217 ab	2.9 a	1	*	65–73
RL6044	206 ab	4.8 ab	1^+	—	84
A11R	204 abc	4.0 ab	1	*	62–65
A16R	203 abc	4.0 ab	1^+	*	73–92
A19R	202 bc	4.8 ab	1^+	*	77–95
A23R	202 bc	3.6 ab	1^+	*	77–95
A30R	202 bc	4.8 ab	1^+	—	74–79
A32R	182 cd	6.3 b	1^+	*	91–97
Morocco	169 d	5.8 b	4	—	68
Zaragoza	163 d	2.9 a	4	*	76

[a] RL6044 is a Thatcher backcross line with gene *Lr*22a. All F_4 families were homozygous for *Lr*22a.
[b] Infection types on 0–4 scale (26). Plus signs indicate pustules that are larger than the normal size limit; ";" indicates chlorotic or necrotic flecks without erupting uredinia.
[c] * indicates presence of the ineffective *Lr*3a gene for low reaction to *P. recondita* f. sp. *tritici* in a family. — indicates absence of *Lr*3a.
[d] Range indicates within-family variation for number of days to heading.
[e] Values followed by different letters in a column differed significantly at $P < 0.05$ according to Tukey's procedure (29).

TABLE 3. Latent period, number of uredinia, infection type, growth period, and indication of the defeated *Lr*13 gene assessed on F_4 families from the cross SST33 × RL6044[a] following inoculation with *Puccinia recondita* f. sp. *tritici*

Cultivar or line	Latent period (hr)	Uredinia/ cm^2 leaf surface	Infection type[b]	Presence of *Lr*13[c]	Days to heading[d]
First F_4 assessment[e]					
D12R	223 a	5.8 a	1^+	*	64–106
D20R	231 a	10.9 ab	1^+	—	88
D34R	226 ab	11.0 ab	1^+	*	86
D6R	224 ab	10.8 ab	1^+	—	87
D16R	209 abc	11.1 ab	1^+	—	83–92
D15R	204 bc	10.9 ab	1^+	—	89
D7R	203 bc	10.2 ab	1^+	—	88
RL6044	190 cd	8.4 ab	1^+	—	85
D17R	188 cd	13.0 b	1^+	*	85
D39R	188 cd	11.6 b	1^{++}	—	93–100
D3R	188 cd	10.9 ab	2	—	90
SST33	169 d	8.4 ab	4	*	66
Second F_4 assessment[e]					
D31R	233 a	11.6	1	—	85
D28R	222 ab	10.9	1	—	90
D29R	220 ab	9.6	1^+	*	88
D5R	212 bc	10.8	1^+	—	86–96
D26R	207 bc	11.0	1^+	*	88
RL6044	205 bc	10.9	1^+	—	85
D32R	198 c	11.6	1^+	*	75
Morocco	166 d	13.0	4	—	66
SST33	142 e	9.0	4	*	66

[a] RL6044 is a Thatcher backcross line with gene *Lr*22a. All F_4 families were homozygous for *Lr*22a.
[b] Infection types on 0–4 scale (26). Plus signs indicate pustules that are larger than the normal size limit.
[c] * indicates presence of the ineffective *Lr*13 gene for low reaction to *P. recondita* f. sp. *tritici* in a family. — indicates absence of *Lr*13.
[d] Range indicates within-family variation for number of days to heading.
[e] Values followed by different letters in a column differed significantly at $P < 0.05$ according to Tukey's procedure (29). In the second assessment, numbers of uredinia did not vary significantly.

within certain F_4 families. The range of infection types, and latent period and numbers of uredinia associated with these extreme infection types recorded per family, are presented in Table 4. Infection types observed among families listed in Table 4 often were of the Z type. Some plants in three families of the SST33 × RL6044 cross produced no or a negligible number of uredinia, thus precluding calculation of the latent period. In Zaragoza derivatives without the *Lr*22a gene, but not for those from SST33, latent period varied significantly (Table 5). The number of pustules on leaves differed among SST33 derivatives, however, while those on Zaragoza progeny ranked similar (Table 5). All F_4 families produced 3^{++} infection types.

F_5 assessment. Mean latent period, number of uredinia, and range of infection types determined on eight plants per F_5 family, derived from resistant and moderately resistant F_4 plants, are shown in Table 6. Variable infection types occurred within all families, except D12R. Considering the infection types of the F_4 parent plants, only family D17R gave rise to F_5 plants with lower reactions. While only a limited number of plants could be evaluated, no D4R plants with fleck reactions only, as observed in the F_4 (Table 4), were detected. On a basis of means for latent period, families A21R, A34R, and D12R showed the expected higher levels of resistance in the F_5 generation. The F_5 families D17R and D3R exhibited latent periods statistically similar to that of D12R, although they were statistically distinguishable in the F_4. Latent period in all respective families differed significantly from Zaragoza or SST33. Latent period in families A36R and A32R was statistically shorter than in RL6044. Within each cross, a statistically similar number of uredinia developed on the four *Lr*22a families. RL6044 supported more uredinia than Zaragoza or SST33 (Table 6).

TABLE 4. Range of latent period and number of uredinia per square centimeter of leaf surface determined on single plants with *Lr*22a from F_4 families of the crosses Zaragoza × RL6044 and SST33 × RL6044, but segregating for expression of infection type

Family/ cross	Infection type range[a]	Latent period (hr)[b]/ range	Range for no. of uredinia/cm^2
First assessment			
Zaragoza × RL6044			
A4R	z;1 z1 ;1 1^+	216–177	6.6–10.3
A6R	z1$^+$ 1^{++}	230–174	6.6–10.5
A9R	1^+ 1^{++}	228–194	7.9–16.6
A13R	;1n ;1^+ 1^+	217–205	1.9–10.9
A25R	;1 1^+	212–182	5.7–10.6
A33R	z;1 1^+	203–172	4.4–12.3
A35R	1n 1 1^+	202–150	3.4–6.8
A38R	;1n 1^+	199–177	2.5–6.4
SST33 × RL6044			
D1R	;1 1^+	222–202	1.9–14.8
D4R[c]	;n ;1n 1^+	···–227	0–10.4
D9R	z;1 z;1^+ z2 1 1^+	236–144	3.6–9.0
D11R[c]	; ;1= 1^+	···–208	0.8–7.2
D14R[c]	;1= ;1 1^{++}	···–208	0.9–7.9
D19R	z;1 1^+	283–193	3.9–11.8
D22R	;1 1 1^+	239–209	8.1–10.4
D35R	1^{++} 2	212–161	10.7–12.5
Second assessment			
Zaragoza × RL6044			
A7R	;1 1	253–227	3.1–2.9
SST33 × RL6044			
D24R	1 1^+	229–217	7.5–10.0
D25R	1 1^{++}	219–201	7.8–14.8
D27R	;1 1^+	238–201	11.2–9.8
D33R	1^+ 2^+	233–166	13.7–11.9
D38R	1 1^+	230–210	7.3–14.1

[a] Infection types on 0–4 scale (26). Z indicates predominant distribution of larger uredinia towards the leaf base; n indicates necrosis and "+" indicates gradation above an established infection type class; "=" indicates uredia at lower size limit for infection type; and ";" indicates chlorotic or necrotic flecks without erupting uredinia.

[b] Extreme latent period values correspond with lowest and highest infection types.

[c] No uredinia or too few developed to determine latent period.

DISCUSSION

The modification of phenotype resulting from interactions between avirulence genes in a pathogen and resistance genes in a host, by unknown genes in both and by environmental effects, is well documented (7–11,16,17,21,28). Furthermore, transgressive segregation for resistance is not an uncommon phenomenon in host-pathogen systems (12,15). In the wheat leaf rust system for example, Lee and Shaner (15) found transgressive segregation for length of latent period when they intercrossed slow-rusting cultivars. In their study, enhanced levels of resistance were ascribed to additive effects of different genes mediating slow-rusting.

Variation in the expression of *Lr*22a has previously been reported. Dyck and Kerber (6) found that plants of segregating F_3 lines, from a cross between Thatcher and a synthetic hexaploid with *Lr*22a, showed a gradation of infection types. They assumed that plants with intermediate reactions were heterozygous for

TABLE 5. Latent period and number of uredinia per square centimeter of leaf area of F_4 plants, without *Lr*22a, derived from crosses of Zaragoza and SST33 with RL6044

Cultivar or line per cross	Latent period (hr)[a]	No. of uredinia/cm^2[a]
RL6044 × Zaragoza		
RL6044	214 a	15.6
AS12	161 b	15.0
AS8	153 b	17.9
Zaragoza	136 bc	15.3
AS9	134 bc	13.4
AS4	122 c	14.0
AS7	113 c	14.5
RL6044 × SST33		
RL6044	224 a	14.2 bc
DS5	149 b	17.7 ab
DS11	148 b	15.2 bc
DS3	140 b	12.0 c
SST33	138 b	11.6 c
DS4	135 b	13.5 bc
DS1	132 b	20.6 a
DS12	132 b	16.9 abc

[a] Column values within a cross followed by different letters differed significantly at $P < 0.05$ according to Tukey's procedure (29). In the RL6044 × Zaragoza cross, numbers of uredinia did not vary significantly.

TABLE 6. Latent period, number of uredinia, and infection types determined on F_5 families[a] selected from the crosses Zaragoza × RL6044 and SST33 × RL6044

Cultivar or line/ cross	Latent period (hr)	No. of uredinia/cm^2 leaf surface	Infection type range[b]
Zaragoza × RL6044			
A34R (1)	239 a	15.2 ab	1 1^+
A21R (1^+)	235 a	15.1 ab	1 1^+ 1^{++} 2
RL6044	225 a	19.4 b	1^+
A36R (1^{++})	187 b	16.8 ab	1^+ 1^{++}
A32R (1^+)	183 b	16.0 ab	1^+ 1^{++} 2
Zaragoza	144 c	12.3 a	4
SST33 × RL6044			
D12R (1^+)	241 a	14.4 ab	1^+
D17R (1^+)	239 a	14.3 ab	;1 ;1^+ 1^+ 2
RL6044	230 a	21.2 b	1^+
D4R (;1n)	228 a	14.4 ab	1^+ 2
D3R (2)	219 a	18.5 ab	1^{++} 2 2^+
SST33	178 b	12.2 a	4

[a] Single plant selections evaluated in the F_4 generation (Tables 2–4) were advanced and tested in the F_5. The infection type displayed by each selected F_4 plant is indicated in brackets after the family designations.

[b] Variation for infection type observed among eight plants per F_5 family.

*Lr*22a. In an inheritance study with *Lr*22a (24), similar variation in reaction to *P. r. tritici* was commonly observed in the F_2, and within and between F_3 families. Here, the variable expression of infection types was regarded as the result of modifying genes influencing gene expression, rather than gene dosage in heterozygotes (24). The results of the present study support this contention. We hypothesize that several modifier genes are involved in the expression of *Lr*22a and that certain resistance gene combinations are necessary to confer a low infection type, increased latent period, and reduced uredinium density. Our hypothesis is based on our observations that neither the defeated *Lr* genes in Zaragoza or SST33, nor the growth rate of plants appeared to be responsible for the variation in *Lr*22a resistance. Residual effects of defeated wheat stem rust (3,14) and powdery mildew (19) resistance genes have been reported. Knott and Weller (14) stated that in the same genotype, one or two ineffective genes could alter the resistance controlled by an effective gene. In our study, enhanced or reduced levels of resistance were apparently not associated with the combination of *Lr*22a with either *Lr*3a or *Lr*13. Previously, the value of *Lr*13 in gene combinations was emphasized in the Canadian cultivar Columbus, where it interacted with *Lr*16 to produce resistance superior to that conferred by either gene alone (27). Admittedly, our tests indicated the presence of only one defeated gene in each cross. Other unknown, ineffective major genes could also be involved in the modification of *Lr*22a resistance.

In previous studies (23), the long latent period conditioned by *Lr*22a was not dramatically influenced by differences in host growth stage. Similarly, the growth rate of plants, as reflected by the number of days to heading, did not appear responsible for the variation observed in the present quantitative assessments of resistance. Early maturing plants were not necessarily the most resistant, nor were late maturing plants the most susceptible, although the fourth leaf of early maturing plants would have been physiologically older at the time of inoculation. Generally, the latent period of *P. r. tritici*, as well as slow-rusting, is best displayed in adult plants (31). Our studies were conducted at relatively early stages of plant development. Greater differences in latent period could have been expected if more mature plants had been used.

It is presently not known whether the genes modifying *Lr*22a were transferred from RL6044 or whether genes in Zaragoza and SST33 influenced the expression of *Lr*22a. However, similar variation was noted when the gene was transferred into these two genetically different backgrounds. The postulated modifier genes are apparently not strictly associated with *Lr*22a, since background effects were evident in Zaragoza and SST33 derivatives without *Lr*22a. The retention of background genes other than the target gene occurs in developing near-isogenic lines by backcrossing (32,33), thus implying that RL6044 could have contributed modifying genes. However, on a basis of morphological characters and reaction to several diseases, little variation was noted between RL6044 and the recurrent parent Thatcher (33). In the barley leaf rust system, Parlevliet and Kuiper (20) found that the cultivar Cebada Capa possessed genes, mediating long latent period, apart from the *Pa*7 gene for hypersensitive resistance to *P. hordei*. In the presence of genes for hypersensitive resistance, the involvement of unknown, minor genes would most probably not be readily detectable in qualitatve assessments of resistance.

In our study it appeared that the higher 1^{++} and 2 infection types, denoting larger uredinia and thus less effective *Lr*22a resistance, were always associated with a shorter latent period. The data presented in Table 4 also strongly suggest that the lowest infection type was related to fewer uredinia that erupted over a longer period of time. Because the determination of latent period is time consuming, selection for higher levels of resistance, on the basis of infection type alone, could be advantageous in breeding programs. However, many families displayed similar lower infection types and the longest latent period would thus not necessarily be selected. Furthermore, exceptions such as family A5R (Table 2), where the lower ;1 infection type was not associated with a longer latent period, did occur. Wilson and Shaner (31) similarly found that the factors for long latent period in the triticale line PI429155 were not retained in one of its derivatives selected for hypersensitive resistance to *P. r. tritici*. They concluded that selection for low infection type alone, without considering latent period, would fail to maximally exploit leaf rust resistance in PI429155. We also suggest that the development of wheat cultivars with *Lr*22a resistance should not be based entirely on infection types. Numbers of uredinia were more variable and not as sensitive to illustrate genetic background effects. Variation, which could be exploited in searching for the highest levels of *Lr*22a resistance did, however, occur. In progeny tests, selected families generally reacted as expected and, therefore, confirmed that breeding lines with superior levels of *Lr*22a resistance could be developed.

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