Characterization of Adult-Plant Resistance to Leaf Rust of Wheat Conferred by the Gene *Lr22a*

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ABSTRACT

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Inoculation of adult-plant resistant wheat line RL6044 with *Puccinia recondita* f. sp. *tritici* established that resistance gene *Lr22a* could be detected by infection types produced on the third and fourth leaves of 30-day-old plants but not on the third leaf of 23-day-old plants. With six isolates of the pathogen from the Cereal Rust Laboratory, the mean latent period of RL6044 was 40 hr greater than that of line E, a susceptible line. Density of uredinia was not reduced, but their mean size on flag leaves of RL6044 was about 70% less than on line E. With four South African isolates on flag leaves, the mean difference in latent period between RL6044 and line E was 134 hr. Urediniospore production 19 days after inoculation was about 89% lower on RL6044 than on the susceptible cultivar Morocco. The absence of an interaction between individual resistance components of *Lr22a* and different races of the wheat leaf rust pathogen suggest that this gene may be useful for managing epidemics of *P. recondita* f. sp. *tritici*.

The search for stable and durable sources of resistance to the rusts of wheat (*Triticum aestivum* L.) has been made among resistant species of the Gramineae related to bread wheat (19). There have been several successful transfers of genes for resistance to stem rust (*Puccinia graminis* Pers. f. sp. *tritici*) and leaf rust (*P. recondita* Rob. ex Desm. f. sp. *tritici*) (*P. r.* f. sp. *tritici*) from species related to wheat (4,8,13,14,19). Although some of these resistance genes have limited value in cultivar development because of undesirable linkages (14), new resistance genes should continue to enhance our potential to manage the rust pathogens of wheat.

Kerber and Dyck (12) and Dyck and Kerber (7) reported the development of two synthetic hexaploid wheat lines (2n = 42 = AABBDD) with different leaf rust resistance genes derived from *Aegilops squarrosa* (2n = 14 = DD). In the first study, Tetra Canthatch (the extracted AABB tetraploid component of the common wheat cultivar Canthatch), was combined with *A. squarrosa* var. *meyeri* (accession RL5289) and a gene for seedling resistance, *Lr21*, was transferred from the wild species (16). In the second study, Tetra Canthatch was crossed with *A. squarrosa* var. *strangulata* (accession RL5271) to produce another synthetic hexaploid line that possessed gene *Lr22*, a gene for adult-plant resistance to leaf rust (16). After the development of a Thatcher backcross line, RL6044 (Thatcher*7//Tetra Canthatch/*A. squarrosa* var. *strangulata* RL5271), the gene *Lr22* was designated *Lr22a* (6). *Lr22a* is at the same locus as *Lr22b*, another gene for adult-plant resistance in Thatcher, but *Lr22b* was not retained in developing RL6044 (6).

Previous studies on *Lr22a* indicated that the gene produced an intermediate host response (7,9). Pathogen races highly virulent to *Lr22a* may exist or may come into existence, but the fact that the gene does not completely suppress the pathogen suggests it may condition a stable type of resistance. Such stability could confer an increased level of durability (10).

The objective of our work was to characterize the expression of resistance conditioned by gene *Lr22a* as influenced by plant growth stage and age of leaf tissue and to determine the effects of different races of *P. r.* f. sp. *tritici* on latent period, numbers of uredinia on leaves, uredinial size, and urediniospore production.

MATERIALS AND METHODS

Infection types, numbers of uredinia, latent period, and uredinial size were studied on leaves of the following spring wheats: line RL6044 (a Thatcher backcross line with leaf rust resistance gene *Lr22a*) and line E W3498 (Gabo*3/Charter//Little Club/Indian H, a susceptible check line). Seeds of both lines were obtained from the Cereal Rust Laboratory (CRL), St. Paul, MN. The production of urediniospores on flag leaves of RL6044 was compared with production on the susceptible cultivar Morocco, seed of which was obtained from CIMMYT in Mexico. Experiment 1 was done at the CRL, and experiments 2 and 3 were done at the Small Grain Centre, Bethlehem, South Africa.

Effects of pathogen isolates from CRL. Seeds of RL6044 and line E were planted in methyl bromide-treated soil in 10-cm plastic pots. After emergence, plants were thinned to one per pot and kept in a greenhouse at 18–25 C. Daylight was supplemented for 12 hr/day with light from cool-white fluorescent lamps emitting 1,100 μE m^{-2} s^{-1}. A water-soluble fertilizer (23:19:17, NPK) was applied three times during the experiment at a rate of 0.4 g/pot.

Plants were inoculated with an Andres inoculation device (2) 55 days after planting when flag leaves of main tillers were fully extended and heads had just emerged (Romig growth stage 12 [5]). Extra tillers were removed the day before inoculation. Plants were inoculated with fresh urediniospores of *P. r.* f. sp. *tritici* suspended in lightweight mineral oil (Soltrol 170, Phillips Chemical Company, Borger, TX) at a concentration of 0.2 mg of spores per milliliter of oil. The inoculation device was set to spray the urediniospore suspension onto the adaxial surfaces of leaves for 1 sec. The discharge nozzle of the inoculator was 160 mm from the surfaces of the leaves. Six isolates of the pathogen were studied that possessed differential virulence to the following wheat leaf rust resistance genes: *Lr1, Lr2a, Lr2c, Lr3, Lr3ka, Lr9, Lr10, Lr16, Lr17, Lr18,* and *Lr24*. Avirulence/virulence characteristics of the isolates are given in Table 1.

After inoculation, paper clips were attached to tips of the leaves to uniformly position their adaxial surfaces for even dew formation in a dew chamber. Plants were kept in the chamber for 19 hr in darkness at 22 C; during the last 3 hr, leaves were allowed to dry off gradually. Plants were then transferred to a growth

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chamber programmed to maintain 21 C during the day and 19 C at night. A 14-hr day length of 860 μE m^{-2} s^{-1} light intensity was provided by fluorescent lamps.

On each flag leaf, an area covering about two-thirds of the leaf and extending a minimum of 20 mm from the terminal and proximal end of the leaf was marked with a water-resistant marker. These areas were inspected daily and when uredinia became visible; those within the marked area were counted at 0800 and 2000 hours each day until the logarithmic phase of uredinium eruption had passed. A final count of uredinia was made 24 hr later. Latent period was calculated by linear regression as the number of hours after inoculation when 40% of the uredinia were visible (1).

Infection types (20) were recorded 15 days after inoculation. Flag leaves were then 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-3000, Lambda Instruments Corporation, Lincoln, NE). The number of uredinia per square centimeter of flag leaf surface was calculated. Twelve leaves, representing six replicates, were studied for each wheat line and leaf rust isolate combination in determining latent period and density of uredinia.

The size of uredinia was estimated by measuring two diameters of five randomly selected uredinia per leaf. For each wheat line/rust isolate combination, measurements were taken from images of four leaves that had been photographed at a known magnification. From these measurements, the size of a uredinium was calculated using this formula: area = $AB/4$, where A = length and B = width.

Effects of plant age on resistance due to *Lr22a*. Seeds of RL6044 were planted in soil in 10-cm plastic pots and grown (four plants per pot) in a greenhouse at 19–23 C. Daylight was supplemented with light from cool-white fluorescent lamps at 900 μE m^{-2} s^{-1} for 12 hr/day. Three consecutive plantings were made at 7-day intervals. Each planting consisted of three replicates. Plants were inoculated on the same day (when they were 16, 23, and 30 days old) when the fourth leaf on the 30-day-old plants was well developed. Plants 30 days old displayed the fourth, third, and second leaves. Plants 23 days old had the third, second, and first leaves. Plants 16 days old displayed only the second and first leaves.

Plants were inoculated with a South African (SA) isolate of *P. r.* f. sp. *tritici* (isolate 3SA78, Table 1). Fresh urediniospores (about 0.5 mg/ml) were suspended in lightweight mineral oil (Soltrol 130) and atomized onto leaves according to procedures outlined by Browder (3). Plants were placed in a dew chamber in darkness at 19 C for 19 hr, and during the last 3 hr, they were allowed to dry off. They were then transferred to a greenhouse set at 19–23 C with a 12-hr cycle of 900 μE m^{-2} s^{-1} light intensity. Twelve days after plants were placed in the greenhouse, infection types were recorded on the second, third, and fourth leaves of 30-day-old plants; on the third, second, and first leaves of 23-day-old plants; and on the second and first leaves of 16-day-old plants.

Effects of SA isolates of *P. r.* f. sp. *tritici*. Plants of RL6044, line E, and the leaf rust-susceptible wheat cultivar Morocco were grown in soil in 15-cm pots in a plastic greenhouse in which temperatures ranged from 20 to 30 C. Three weeks after planting and weekly thereafter for the duration of the experiment, a water-soluble fertilizer (6.5:2.7:13.0, NPK) was applied as a soil drench at a rate of 0.5 g/pot.

Flag leaves of RL6044 and line E that were of similar age and appearance were inoculated with the Andres device 104 days after planting when plants were at growth stage 15 based on the Romig scale (5). Four SA isolates of *P. r.* f. sp. *tritici* (isolates 3SA57, 3SA58, 3SA60, and 3SA62) were selected for their differential virulence to the following wheat leaf rust resistance genes: *Lr1, Lr2a, Lr3, Lr3ka, Lr3bg, Lr11, Lr15, Lr16, Lr17, Lr20, Lr24,* and *Lr30* (Table 1).

Each isolate was sprayed onto four flag leaves of RL6044 and line E at a concentration of 0.2 mg of urediniospores per milliliter of Soltrol 130 oil. The inoculation device was set to spray the urediniospore suspension onto the adaxial surfaces of leaves for 1 sec. The discharge nozzle of the inoculator was 160 mm from the surfaces of the leaves. Twenty additional flag leaves each of RL6044 and Morocco were similarly inoculated with isolate 3SA62. Inoculated plants were incubated in a dew chamber at 19 C for 19 hr; during the last 3 hr, they were allowed to dry off. They were then placed in a greenhouse at 19–23 C with daylight supplemented with 900 μE m^{-2} s^{-1} from fluorescent lamps for 12 hr/day.

Leaves were inspected daily at 0800 hours, and uredinia within designated areas were counted. The latent period for RL6044 and line E infected with the different isolates was calculated as described in the first experiment. Infection types were recorded 14 days after plants were inoculated.

Urediniospores were collected from upper surfaces of leaves of Morocco and RL6044 infected with isolate 3SA62, using a laboratory pump with fixed vacuum capacity connected to a cyclone collector (3) to which gelatine capsules of known weight were attached. The capsules were left open for 1 hr after collection to air-dry the spores, then the capsules and spores were weighed. Collection from Morocco began 7 days after inoculation and continued until secondary sporulating uredinia formed (19 days after inoculation). Collection from RL6044 was on days 13, 16, and 19 after inoculation because sporulation was slight. Primary uredinia were counted and urediniospore yield was expressed as milliligrams of spores produced per uredinium for each collection. The mass of spores collected from 20 leaves represented 10 replicates in data analyses.

The first two experiments were arranged as randomized complete block designs, and the data were analyzed for variance. Tukey's procedure for comparison of means was applied where analysis of variance indicated significant differences (21).

RESULTS

Effects of pathogen isolates from CRL. Latent periods were shorter on line E than on RL6044 with each pathogen isolate (Table 2). Latent period also appeared to vary with the pathogen isolate studied, especially on susceptible line E, but the differences were not large. The interaction of pathogen isolates and wheat genotypes was statistically significant ($P = 0.05$) for latent period as indicated by the shorter latent periods produced by isolates CRL 82-CGB-OV and CRL 82-TBL-MX on line E without a corresponding reduction on RL6044.

The variation in mean numbers of uredinia on flag leaves (Table 2) was due

Table 1. Virulence characteristics of Cereal Rust Laboratory (CRL) and South African (SA) isolates of *Puccinia recondita* f. sp. *tritici* used in experiments measuring the resistance components of the adult-plant resistance gene *Lr*22a

Isolate[a]	Avirulence/virulence combination
CRL 82-PHD-IV	*Lr*2a, 9, 16, 18, 24/1, 2c, 3, 3ka, 10, 17
CRL 82-FLD-DZ	*Lr*1, 2a, 10, 16, 17, 18, 24/2c, 3, 3ka, 9
CRL 82-CGB-OV	*Lr*1, 2a, 2c, 3ka, 9, 16, 17, 18, 24/3, 10
CRL 82-TBL-MX	*Lr*3ka, 9, 10, 16, 17, 24/1, 2a, 2c, 3, 18
CRL 82-MJB-MCV	*Lr*2a, 2c, 3ka, 9, 17, 18, 24/1, 3, 10, 16
CRL 80-KGB-DJ	*Lr*1, 3ka, 9, 16, 17, 18, 24/2a, 2c, 3, 10
3SA57	*Lr*1, 2a, 3ka, 11, 15, 17, 20, 24, 30/3, 3ka, 16
3SA58	*Lr*3, 3ka, 3bg, 11, 16, 20, 30/1, 2a, 15, 17, 24
3SA60	*Lr*2a, 3bg, 15, 16, 17/1, 3, 3ka, 11, 20, 24, 30
3SA62	*Lr*3, 3ka, 3bg, 11, 16, 20, 24, 30/1, 2a, 15, 17
3SA78	*Lr*3, 3ka, 3bg, 11, 16, 17, 20, 24, 30/1, 2a, 15

[a]Different differential sets were used to characterize CRL and SA isolates of wheat leaf rust.

Table 2. Mean latent period, uredinium density, and uredinial size on flag leaves of RL6044 (*Lr22a*) and line E (susceptible check) after inoculation at Romig growth stage 12 with different Cereal Rust Laboratory (CRL) isolates of *Puccinia recondita* f. sp. *tritici*[x]

CRL isolates	Latent period (hr)[y]			Uredinia/cm² of flag leaves[y]			Uredinial size (mm²)[z]		
	RL6044	Line E	Isolate mean	RL6044	Line E	Isolate mean	RL6044	Line E	Isolate mean
82-PHD-IV	192 a	149 b	171	9.8 b	10.9 ab	10.4	0.116	0.440	0.278
82-FLD-DZ	181 a	145 bcd	163	14.1 ab	10.6 ab	12.4	0.141	0.391	0.266
82-CGB-OV	181 a	135 cd	158	11.2 ab	12.5 ab	11.9	0.132	0.547	0.340
82-TBL-MX	181 a	134 d	158	14.9 ab	13.3 ab	14.1	0.151	0.409	0.280
82-MJB-MCV	181 a	148 bc	165	11.6 ab	15.4 a	13.5	0.131	0.484	0.308
80-KGB-KJ	181 a	146 bcd	164	10.5 ab	11.6 ab	11.1	0.150	0.530	0.340
Line mean[z]	183	143		12.0	12.4		0.137 a	0.467 b	

[x] Tukey's procedure (21) was used for comparison of means. Isolate × line, isolate, and line means should be compared for each resistance component individually and not with each other.
[y] Interaction of line × isolate was significant at $P = 0.05$.
[z] Only line means were significant at $P = 0.05$.

Table 3. Effects of plant age on infection types[a] on different leaves of wheat line RL6044 infected with *Puccinia recondiat* f. sp. *tritici*[b]

Age of plants at inoculation (days)	Infection type (leaf)			
	First	Second	Third	Fourth
16[c]	4	4	···	
23[d]	4	3+	3	···
30[e]	···	2+3	2+	1+

[a] Infection types according to a scale of 0–4 (20).
[b] Isolate 3SA78.
[c] Third and fourth leaves not yet developed at inoculation.
[d] Fourth leaf not yet developed at inoculation.
[e] First leaf became chlorotic before infection types could be determined.

Table 4. Duration of latent period (hr) measured on flag leaves of RL6044 (*Lr22a*) and line E (susceptible check) inoculated at Romig growth stage 15 with four South African (SA) isolates of *Puccinia recondita* f. sp. *tritici*

SA isolates	Latent period (line)[y]		Isolate mean
	RL6044	Line E	
3SA57	299	147	223
3SA58	304	167	236
3SA60	298	174	236
3SA62	280	155	218
Line mean[z]	295	161	

[y] Isolate × line and isolate means did not differ significantly according to analysis of variance.
[z] Line means were significantly different at $P = 0.01$ according to Tukey's procedure (21).

to the interaction of wheat lines with isolates ($P = 0.05$) and, slightly, due to pathogen isolates and wheat lines (Table 2). The significant interaction appeared to be due to the effects of isolates CRL 82-FLD-DZ and CRL 82-MJB-MCV on the two lines.

The mean size of uredinia (Table 2) produced by the six CRL isolates was significantly less on RL6044 than on line E ($P = 0.01$). Uredinia on RL6044 were 70.7% smaller than those on line E. Isolate means indicated that the isolates produced uredinia of about equal size.

Effects of plant age on resistance attributed to *Lr22a*. Infection types produced on leaves of line RL6044 when plants were of different ages are shown in Table 3. Resistance to *P. r.* f. sp. *tritici* attributed to gene *Lr22a* was evident on the fourth leaves of plants that were 30 days old at inoculation as well as on the older leaves of these 30-day-old plants. Resistance was not obvious on plants that were 23 or 16 days old at inoculation, but there was some indication of the resistance gene on second and third leaves of 23-day-old plants. Resistance was not detectable in 16-day-old plants or on the first leaves of 23-day-old plants.

Throughout all other experiments with CRL and SA isolates of the pathogen, RL6044 showed a 1+ infection type on flag leaves. This infection type was characterized by small uredinia associated with a slight amount of chlorosis.

Effects of SA isolates of *P. r.* f. sp. *tritici*. Mean latent period was 134 hr longer in RL6044 than in line E (Table 4). The lengths of the latent periods did not differ significantly among pathogen isolates, and there was no isolate × line interaction.

Urediniospore production on RL6044 and Morocco was estimated by collecting spores at different time intervals after inoculation (Fig. 1). Urediniospores were collected from a mean of 162 ± 31 uredinia per flag leaf of RL6044 and 149 ± 24 uredinia per flag leaf of Morocco. Spore yield on RL6044 began 13 days after inoculation, whereas that on Morocco began after 7 days. Nineteen days after inoculation, Morocco yielded a mean of 0.0269 mg of spores per uredinium and RL6044 yielded a mean of 0.0028 mg of spores per uredinium.

DISCUSSION

According to Dyck and Samborski (9), gene *Lr22a* has not yet been incorporated into a commercial wheat cultivar. Characterization of the resistance components in our experiments suggests that the gene has great potential as a source of resistance to leaf rust of wheat, particularly because it is effective against different races and isolates of the pathogen. The partially dominant mode of inheritance of *Lr22a* (7) and the distinctive infection type provide evidence that the gene could easily be incorporated into adapted wheat genotypes. If the gene continues to condition slow rusting, it will be desirable because selection of slow-rusting progeny is more rapid with this type of monogenically inherited resistance than with quantitatively inherited resistance. Most likely, the high uredinial density on leaves of line RL6044 has tended to mask the potential effectiveness of the gene during routine screening done in the past.

It is possible that a race of *P. r.* f. sp. *tritici* virulent to *Lr22a* could evolve; however, the expression of gene *Lr22a* suggests that selection pressure to produce such a race would not be strong. Unfortunately, evidence for durability of the gene and for the amount of protection that gene *Lr22a* can provide in the field is not available because of limited exploitation of the gene. Greenhouse evaluation of the gene in our study, suggests that it would be valuable in breeding programs.

Epidemiologically, *Lr22a* may be useful in reducing the rate of rust development because it conditions a long latent period, small uredinia, and reduced spore production. Despite the fact that *Lr22a* is associated with high numbers of uredinia, the other components would retard the progress of epidemics by restricting the logarithmic increase of inoculum and disease.

Other studies have indicated that slow rusting in wheat or barley genotypes is

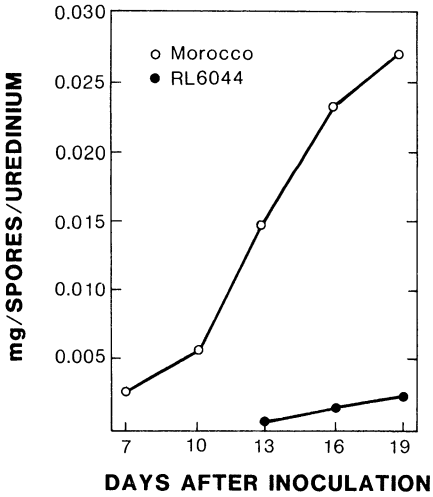

Fig. 1. Mean urediniospore yield rate (milligrams per uredinium) on wheats RL6044 (*Lr22a*) and Morocco (susceptible check) 7–19 days after inoculation with isolate 3SA62 of *Puccinia recondita* f. sp. *tritici*. Tukey's procedure (21) indicated significant differences at $P = 0.01$ between total spore yield of RL6044 and Morocco 19 days after inoculation.

associated with low numbers of uredinia produced on leaf surfaces (11,15,17,18). This was not the case in this study, clearly indicating that the relationship between resistance components in a particular host-pathogen interaction should be established before using one component for screening purposes. In this study, latent period appeared to be a useful stable component, regardless of differences in aggressiveness in different races. The effectiveness of resistance, as expressed in duration of latent period, appeared to be enhanced in plants as they grew older. More information is needed to quantify this effect, however.

The fact that *Lr22a* confers resistance only in postseedling growth stages classifies this gene as an "adult-plant resistance" gene. Other genes, such as *Lr12* and *Lr13*, also mediate adult-plant resistance to wheat leaf rust, but their associated low infection types indicate that hypersensitivity is involved, and differential infection with races has been reported (9). Another gene for adult-plant resistance in the wheat line PI 250413 was considered to condition horizontal resistance because it was resistant to all races tested and the presence of uredinia indicated that resistance was incomplete (9). From these studies and the work presented here, it is clear that resistance mechanisms and their expression are often unique and that a convenient classification of resistance categories should be avoided without detailed studies of the interactions involved. In the adult-plant resistance category, similarities in expression of resistance exist, but the phenotypic characterization and stability of resistance components to different races of the pathogen undoubtedly vary in wheat genotypes.

When gene *Lr22a* was originally transferred from the diploid donor parent (*A. squarrosa* line RL5271) to the synthetic hexaploid (line RL5404), the level of resistance was reduced somewhat (7). The infection type in adult plants of line RL5271 was 0, whereas in line RL5404, it was 1+. According to Dyck and Kerber (7), the gene was slightly less effective in the synthetic hexaploid line because it was sensitive to its genetic background. Consequently, the exploitation of *Lr22a* in a breeding program may require a careful evaluation of progenies to select those with superior degrees of resistance.

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