Effects of Growth Stage and Temperature on Components of Resistance to Leaf Rust in Wheat Genotypes with *Lr*26

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ABSTRACT

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In a qualitative assessment of the reactions of seedlings of wheat cultivars Kavkaz (*Lr*26+) and Veery (*Lr*26+) to an isolate of *Puccinia recondita* f. sp. *tritici* virulent to *Lr*26, only Kavkaz exhibited a lower infection type at increased temperatures. Quantitative evaluations indicated that seedlings with and without *Lr*26 responded similarly to leaf rust infection. The latent period in flag leaves of Kavkaz, Gamtoos (Veery 3), and RL6078 (Thatcher:*Lr*26) was longer than in the leaf rust-susceptible cultivar Thatcher. These differences were more pronounced at 12–18 C than at 24–28 C. Fewer and smaller uredinia developed on flag leaves of certain *Lr*26 carriers than on susceptible cultivars. On the basis of uredinium size, a postanthesis loss of adult-plant resistance occurred in Gamtoos. Temperature did not influence the density of uredinia on wheat genotypes with *Lr*26, but higher temperatures restricted the size of uredinia on flag leaves of RL6078. *Lr*26 produces certain characteristics in the adult plant, but expression of the gene appears to be influenced by genetic background, age of leaf tissue, and temperature.

The *Lr*26 gene for resistance to leaf rust (caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici*) is associated with a translocation between the short arm of rye (*Secale cereale* L.) chromosome 1R and the long arm of wheat (*Triticum aestivum* L.) chromosome 1B (9). Additionally, the rye chromosome segment contains the genes *Yr*9, *Sr*31, and *Pm*8 for resistance to *P. striiformis* West., *P. graminis* Pers. f. sp. *tritici* Eriks. & Henn., and *Erysiphe graminis* DC. f. sp. *tritici* E. Marchal (5). The spring wheat cultivar Veery, developed at CIMMYT from the cultivar cross (Kavkaz × Buho) × (Kalyansona × Bluebird), has inherited the 1BL/1RS translocation from Kavkaz (10).

In Mexico, the cultivars Genaro 81 (Veery 3), Glennson 81 (Veery 1), and Seri 82 (Veery 5) have consistently been slow-rusting in epidemics of leaf rust in the field (15,16). Veery germ plasm is, furthermore, of international significance because of its high-yielding capacity and adaptability to different environments (14). Rajaram and Torres (16) proposed that the slow-rusting characteristics of Veery selections have been derived from the Kalyansona × Bluebird genotype. More recently, Rajaram et al (15) reported that Genaro 81 contains *Lr*3, *Lr*13, and *Lr*26, as well as additional genes for slow leaf-rusting. Several sources of durable resistance to wheat leaf rust are presently attributed to gene combinations involving *Lr*13 (15). In addition to the Veery resistance, this hypothesis is substantiated by the slow-rusting behavior of Pavon S, a Mexican cultivar carrying *Lr*13 in combination with several other resistance genes (15,16).

In this study, we measured components of resistance displayed by wheat genotypes containing *Lr*26. Our objective was to determine whether *Lr*26 also contributes to slow leaf-rusting.

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MATERIALS AND METHODS

Seedlings: Qualitative assessments. Freshly collected urediniospores of isolates 3SA132 and 3SA140 of *P. r.* f. sp. *tritici* were suspended in Soltrol 130 light mineral oil and atomized onto primary leaves of 7-day-old seedlings of the *Lr*26 and leaf rust-susceptible wheat genotypes listed in Table 1. Isolate 3SA132 is virulent to genotypes with the genes *Lr*1, 2a, 2b, 2c, 10, 13, 14a, 14b, 15, 17, 23, and 24 and avirulent to *Lr*3a, 3bg, 3ka, 9, 11, 16, 18, 19, 20, 26, and 30. Except for virulence to *Lr*26, isolate 3SA140 resembles 3SA132. Three sets of plants were inoculated with each isolate. Following incubation in a dark dew chamber for 19 hr, one set of plants was transferred to each of three air-conditioned greenhouse compartments having an ambient temperature of 12–18 C, 16–22 C, and 24–28 C, respectively. Plants to be evaluated at 24–28 C were acclimatized at 16–22 C for 6 hr before placement at the higher temperature. Cool-white fluorescent tubes provided additional illumination of 900 $\mu Em^{-2}sec^{-1}$ for 12 hr daily. Infection types (17) were recorded 9–14 days after inoculation, when uredinia on the susceptible cultivars appeared fully developed. According to the 0–4 cereal rust infection type scale (17), a "0" indicates an immune host response without any macroscopic signs of infection. A susceptible host response, characterized by large uredinia without chlorosis or necrosis, is denoted by a "4," whereas flecking, chlorosis, and necrosis are shown by ";", "c," and "n," respectively. Plus or minus signs indicate pustules that are larger or smaller than the normal size limits.

Quantitative assessments. The adaxial surface of primary leaves of 9-day-old plants of Kavkaz (obtained from the 1985 International Winter Wheat Rust Nursery), RL6078 (a Thatcher backcross line with *Lr*26 [4]), Gamtoos (= Veery 3, a commercial spring type cultivar in South Africa [22]), and the leaf rust-susceptible genotypes Thatcher and Line E were quantitatively inoculated (2) with 0.4 mg of fresh urediniospores of isolate 3SA140 per milliliter of Soltrol 130 light mineral oil.

After incubation, plants were maintained at 16–22 C in a greenhouse as described above. The latent period was

Table 1. Seedling infection types of wheat cultivars and lines postulated to have *Lr*26 for resistance to *Puccinia recondita* f. sp. *tritici*

Cultivar/line	Infection type[a] produced at temperature					
	12–18 C by isolate		16–22 C by isolate		24–28 C by isolate	
	3SA 140[b]	3SA 132[c]	3SA 140	3SA 132	3SA 140	3SA 132
Kavkaz[d]	4	;	3^-	;	3^-	0;
Glennson 81[e]	4	;	4	;	4	;
Genaro 81[e]	3^{++}	;	3^-	;	4	;
Seri 82[e]	4	;	4	;	3^{++}	;
Veery 6[e]	3^+	;	3^+	;	3^+	;
Veery 7[e]	4	;	4	;	4	;
Veery 8[e]	4	;	4	;	4	;
Veery 9[e]	3^{++}	;	3^{++}	;	4	;
Veery 10[e]	4	;	4	;	4	;
Gamtoos[f]	3^{++}	;	3	;	3^{++}	;
Veery'S[f]	4	;	4	;	4	;
RL6078 (*Lr*26)[g]	4	;	4	;	4	;
Thatcher[h]	4	4	4	4	4	4
Morocco[h]	4	4	4	4	4	4

[a]Infection types are according to a 0–4 scale (17). A "0" indicates no macroscopic sign of infection and a "4" indicates large uredinia without chlorosis or necrosis. Chlorotic flecks are indicated by ";" and plus or minus signs denote pustules that are larger or smaller than the normal size limit.
[b]Isolate 3SA140 is virulent to *Lr*26.
[c]Isolate 3SA132 is virulent to *Lr*26.
[d]Obtained from the International Winter Wheat Rust Nursery.
[e]Obtained from the International Bread Wheat Screening Nursery.
[f] Germ plasm collection, Small Grain Centre, Bethlehem, South Africa.
[g]Obtained from the Winnipeg Research Station, Canada.
[h]Susceptible cultivars.

Table 2. Flag leaf infection types of two wheat cultivars and one line with *Lr*26, and two leaf rust-susceptible genotypes, to isolate 3SA140[a] of *Puccinia recondita* f. sp. *tritici*

Cultivar/line[c]	Infection type[b] produced at temperature	
	12–18 C	24–28 C
Kavkaz	x^-	x^-
Gamtoos	$;1^{+c}$	2^{++c}
RL6078 (*Lr*26)	3	2^{++c}
Thatcher[d]	3^{++}	3^-
Line E[d]	3^{++}	3^+

[a]Isolate 3SA140 is virulent to seedlings with *Lr*26 at both temperatures.
[b]Infection types are according to a 0–4 scale (17). A "0" indicates no macroscopic sign of infection (immune host response) and a "4" indicates large uredinia without chlorosis (c) or necrosis (susceptible host response). Heterogeneous reaction types are designated by "x" and chlorotic flecks by ";". Plus or minus signs indicate pustules that are larger or smaller than the normal size limit.
[c]Plants were inoculated at Zadoks growth stage 55.
[d]Susceptible cultivars.

determined on five leaves per cultivar grown per 10-cm pot. Treatments were replicated five times. On each leaf, a 4-cm-long portion, never closer than 1 cm to either the tip or base 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 inoculation until 40% of the primary uredinia were visible as erumpent structures (1). Assuming an elliptical uredinium shape and using the formula $\pi \times$ length $\times$ width/4, pustule size was estimated from measurements of eight uredinia on each of five leaves per cultivar, 14 days after inoculation.

Adult plants. In a series of three experiments, latent period, number of uredinia per square centimeter of flag leaf surface, uredinium size, and infection type (0–4 scale) (17) of isolate 3SA140 of *P. r.* f. sp. *tritici* was determined for certain *Lr*26 genotypes. Latent period and uredinium size were estimated as in the seedling experiment. The density of uredinia was obtained by dividing the number of primary uredinia by the leaf area studied (13). Plants were grown (two per pot) in pots containing 4 kg of soil in a greenhouse at 18–25 C. To facilitate selection of plants at specific growth stages, six plantings were made at weekly intervals. Kavkaz seedlings had been

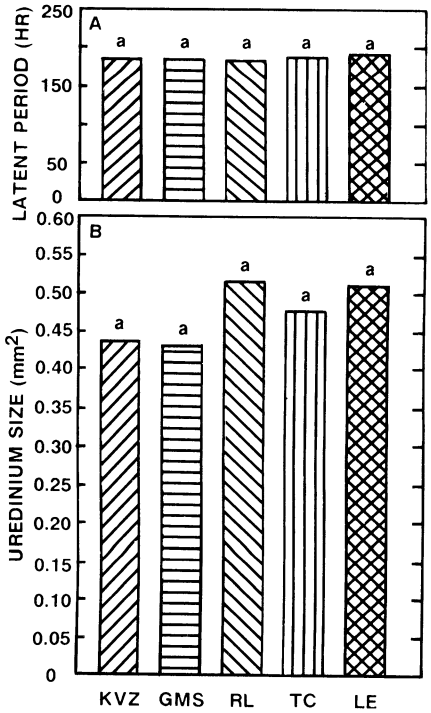

Fig. 1. Latent period (**A**) and uredinium size (**B**) of isolate 3SA140 of *Puccinia recondita* f. sp. *tritici* on seedlings of the *Lr*26 wheat genotypes Kavkaz (KVZ), Gamtoos (GMS), and RL6078 (RL) and the leaf rust-susceptible wheats Thatcher (TC) and Line E (LE). Isolate 3SA140 is virulent to seedlings with *Lr*26. Bars designated with the same lower case letter are not significantly different ($P < 0.05$) according to Tukey's procedure.

vernalized at 4 C for 32 days before each planting. A water-soluble fertilizer containing 6.5, 2.7, and 13.0% of N, P, and K, respectively, was applied (0.5 g per pot) weekly for the duration of the experiments. Flag leaves were quantitatively inoculated (2) using the same inoculum concentration (0.4 mg of spores per milliliter of Soltrol 130 oil), the same distance between the adaxial leaf surface and discharge nozzle, and the same inoculator air pressure in all experiments. To determine the number of spores deposited per square centimeter, three strips of adhesive tape were sprayed using the inoculation device. The number of spores on each of four 1-cm^2 areas per strip were then counted.

Latent period and numbers of uredinia were determined on eight flag leaves per treatment. For uredinium size, the dimensions of 10 uredinia on each of four leaves per treatment were measured. In all three experiments, duplicate sets of inoculated plants were evaluated at 12–18 C and 24–28 C in a greenhouse. At each temperature, measurements for uredinium size were taken on completion of the latent period counts for all entries in that specific experiment.

In the first experiment with adult plants, the above-mentioned components of resistance were measured on Kavkaz, Gamtoos, RL6078, and Thatcher plants inoculated at Zadoks

growth stage 55 (one half of ear emerged) (20). Secondly, Gamtoos and RL6078, also at growth stage 55, were compared to Line E. To determine the effect of adult-plant growth stage on resistance expression, Gamtoos and Thatcher plants were evaluated at growth stages 55 and 73 (early milk).

Statistical analyses. All experiments were arranged in completely randomized designs, and the data were analyzed for variance accordingly. Tukey's test ($P < 0.05$) was used to indicate significant differences between means.

RESULTS

Seedlings. At 16–22 C and 24–28 C, Kavkaz and certain Veery selections displayed slightly lower infection types to isolate 3SA140 than did line RL6078 and the leaf rust-susceptible cultivars (Table 1). When tested at 12–18 C, no indication of resistance genes other than *Lr*26 in Kavkaz and Veery accessions was evident. Isolate 3SA132 was avirulent (infection types 0; or ;) to all *Lr*26 genotypes (Table 1). Quantitative assessment of latent period and the size of uredinia of isolate 3SA140 revealed that Kavkaz, Gamtoos, and RL6078 did not differ significantly from Thatcher and Line E (Fig. 1).

Adult plants. Kavkaz and Gamtoos had low infection types at 12–18 C and 24–28 C on flag leaves following inoculation with the *Lr*26-virulent isolate 3SA140 (Table 2). RL6078

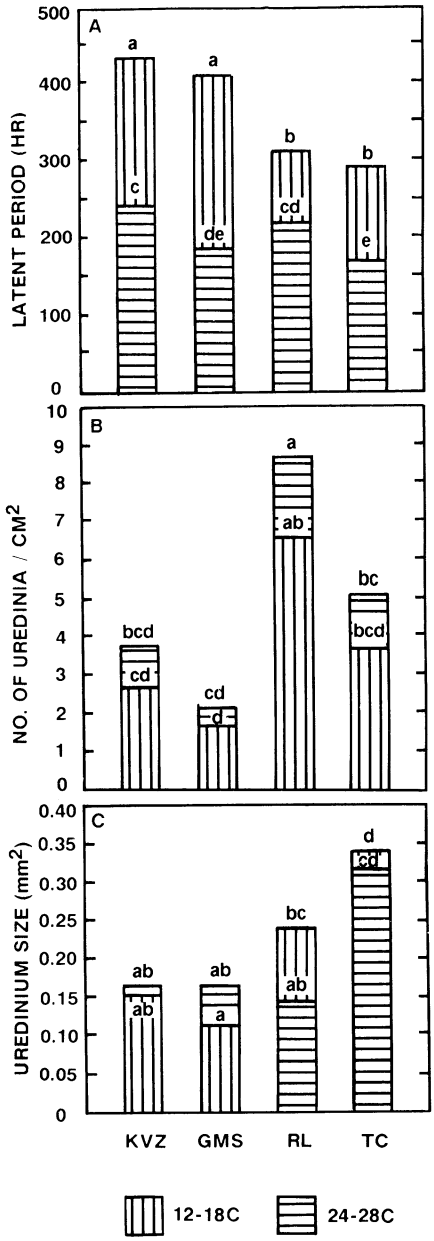

Fig. 2. The effect of two temperature regimes on latent period (**A**), uredinium density (**B**), and uredinium size (**C**) of isolate 3SA140 of *Puccinia recondita* f. sp. *tritici* in flag leaves of Kavkaz (KVZ) (*Lr*26+), Gamtoos (GMS), (*Lr*26+), RL6078 (RL) (Thatcher:*Lr*26), and Thatcher (TC) (susceptible host). Isolate 3SA140 is virulent to seedlings with *Lr*26. Bars designated with the same lower case letter are not significantly different ($P < 0.05$) according to Tukey's procedure.

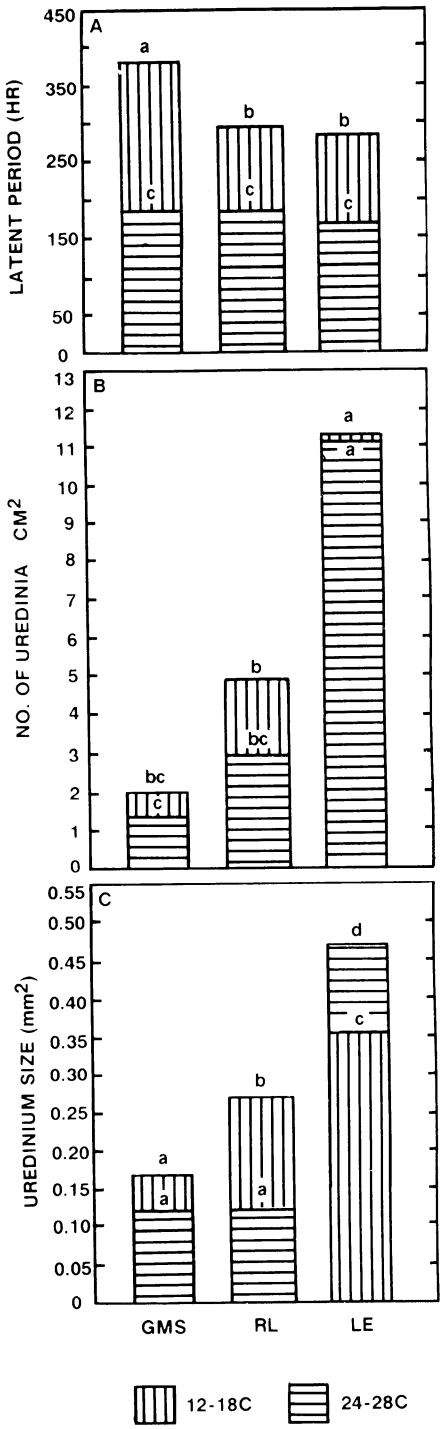

Fig. 3. The effect of two temperature regimes on latent period (**A**), uredinium density (**B**), and uredinium size (**C**) of isolate 3SA140 of *Puccinia recondita* f. sp. *tritici* in flag leaves of Gamtoos (GMS) (*Lr*26+), RL6078 (RL) (Thatcher:*Lr*26), and Line E (LE) (susceptible host). Isolate 3SA140 is virulent to seedlings with *Lr*26. Bars designated with the same lower case letter are not significantly different ($P < 0.05$) according to Tukey's procedure.

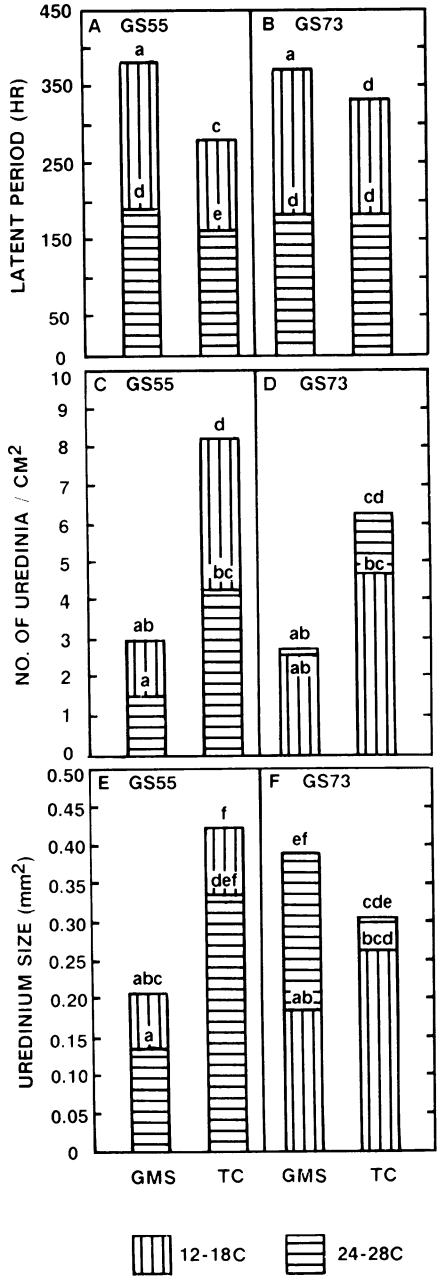

Fig. 4. The effects of temperature and adult-plant growth stage on latent period (**A,B**), uredinium density (**C,D**), and uredinium size (**E,F**) of isolate 3SA140 of *Puccinia recondita* f. sp. *tritici* in flag leaves of Gamtoos (GMS) (*Lr*26+) and Thatcher (TC) (susceptible host). Isolate 3SA140 is virulent to seedlings with *Lr*26. Bars designated with the same lower case letter are not significantly different ($P < 0.05$) according to Tukey's procedure.

produced infection type 2^{++c} at 24–28 C but exhibited a susceptible reaction at the lower temperature (Table 2). Thatcher and Line E were susceptible to isolate 3SA140 at both temperature ranges. However, uredinia on Thatcher leaves were smaller at 24–28 C than at 12–18 C.

In the quantitative experiments, the inoculation device deposited 24±3 urediniospores per square centimeter. The latent period, determined at 12–18 C for Kavkaz and Gamtoos in the first experiment, differed from those of RL6078 and Thatcher, which were similar (Fig. 2A). At 24–28 C, the latent period calculated for Gamtoos was equal to that of Thatcher, whereas Kavkaz and RL6078 reacted similarly. Although temperature did not significantly influence the number or size of uredinia on flag leaves of any of the cultivars, fewer uredinia developed on leaves of Kavkaz and Gamtoos than on RL6078 and Thatcher (Fig. 2B and C). Uredinia on Kavkaz and Gamtoos, as well as on RL6078 tested at 24–28 C, were smaller than those on Thatcher (Fig. 2C).

The latent periods, measured at 24–28 C in the second experiment, were statistically similar for Gamtoos, RL6078, and Line E (Fig. 3A). In all three genotypes, the latent period was significantly increased at the lower temperature regime but was most extended in Gamtoos. Fewer and smaller uredinia developed on the flag leaves of Gamtoos and RL6078 than on the leaf rust-susceptible Line E (Fig. 3B and C). Uredinia on RL6078 were significantly smaller at 24–28 C than at 12–18 C (Fig. 3C).

Differences in adult-plant growth stage did not extensively influence the length of latent period or the uredinium density on Gamtoos (Fig. 4A–D). Except for plants (growth stage 73) at 12–18 C, fewer uredinia developed per unit leaf area on Gamtoos than on Thatcher (Fig. 4C and D). At both temperatures, the uredinia on Gamtoos plants inoculated at growth stage 55 were smaller than on Thatcher (Fig. 4E and F). However, the size of uredinia on Gamtoos and Thatcher plants at growth stage 73 was statistically similar. The marked increase in uredinium area on the more mature Gamtoos plants was encountered only at 24–28 C (Fig. 4E and F).

DISCUSSION

From a wheat-breeding point of view, the slow-rusting resistance displayed by Veery lines would preferably be independent of *Lr*26. The gene is associated with deleterious dough-mixing properties (4) that are usually discriminated against in quality evaluations. Furthermore, the durability of *Lr*26-related resistance to *P. r.* f. sp. *tritici* is questionable. In Europe (18,23) and South Africa (12), virulence to *Lr*26 appeared shortly after the release of cultivars containing this gene. Long et al (8) also reported that virulence to *Lr*26 was increasing in the United States, partly because CIMMYT-developed cultivars with *Lr*26 were being grown more widely in North America.

The consistent slow-rusting behavior of Veery lines in Mexico, however, suggests that adequate leaf rust control in certain wheat-growing areas can be achieved by exploiting this genotype. According to the components of resistance measured in all our adult-plant inoculations, Gamtoos was repeatedly slow-rusting. Considering the latent period, the highest degree of slow-rusting in Gamtoos was displayed at 12–18 C. This is in contrast with the high-temperature adult-plant response of RL6078, but agrees with the results of Kaul and Shaner (6), who found that adult-plant resistance to leaf rust generally decreased in warmer environments. The slow-rusting resistance of Veery germ plasm most probably emanates from the interaction between the components of host resistance and pathogen genotype in a specific environment. This phenomenon has been thoroughly reviewed by Browder (3) and was also recognized by Kaul and Shaner (6). Not only is postinoculation temperature important, but infection type can be influenced by temperature conditions experienced before inoculation (6).

Without further studies, the high-temperature response of RL6078 cannot be attributed to *Lr*26 alone. Linkage drag is apparently a fairly common phenomenon in developing sets of near-isogenic lines (24,25). Genes for slow-rusting or temperature-specificity, distinct from *Lr*26, could have been retained in RL6078. Because of the assumed limited pairing between the donor parent 1R and the homeologous Thatcher 1B chromosome arms, it is unlikely that even several generations of backcrossing would have eliminated most of the rye chromatin other than the *Lr*26 locus.

Because only one *Lr*26-virulent race of *P. r.* f. sp. *tritici* was used in our study, it is not known whether the high-temperature flag leaf expression of RL6078 is race-specific. In Kavkaz and Gamtoos, the genetic background undoubtedly contributed to adult-plant resistance, but our study did not allow identification of those factors. The detection of *Lr*13 in Veery germ plasm, as reported by Rajaram et al (15), was also not possible with pathotype 3SA140 because of its virulence to this gene. Differentiation between *Lr*26 and leaf rust-susceptible genotypes was almost negligible in our evaluation of seedling resistance. Therefore, the involvement of an adult-plant resistance gene in Veery, such as *Lr*13, seems plausible. *Lr*13 has been shown to interact with *Lr*16 in the Canadian cultivar Columbus to produce higher levels of resistance than either gene alone (19). Similar interaction with *Lr*26 is not unlikely. Long et al (7) also noted leaf rust resistance in addition to that conferred by *Lr*26 in Kavkaz but did not report on its identity.

The slight variation in primary leaf infection types of certain Veery lines did not provide clear evidence of seedling resistance genes other than *Lr*26. Thus, it appears that the background resistance of Kavkaz could be different from that in Veery. Variation also seems to occur within Veery germ plasm. The South African cultivar Gamtoos, for example, does not have *Lr*3, as has been reported for the Mexican cultivar Genaro 81 (15), although both cultivars originated from the same Veery selection (22).

Although the breakdown of adult-plant resistance, as evidenced by larger uredinia on Gamtoos plants at growth stage 73, was not confirmed in a second replicated study, the phenomenon was in accordance with previous reports. Vanderplank (21) mentioned that slow-rusting resistance in cereals is frequently less effective at postanthesis growth stages. In this regard, Ohm and Shaner (11) have shown that slow-rusting resistance to leaf rust was reduced after flowering but, nevertheless, suggested that serious yield losses should be prevented by the delayed progress of the disease during sensitive host growth stages. The slightly less effective postanthesis resistance of Gamtoos should, therefore, not disqualify Veery germ plasm as a valuable source of resistance to leaf rust.

Genetic studies, using pathotypes 3SA132 and 3SA140 at different temperature regimes, should identify the inheritance and number of leaf rust resistance genes in Kavkaz and Veery. In addition to the identity of the major resistance genes, elucidation of the factors responsible for slow leaf-rusting would also contribute to our understanding of the resistance mechanisms in these genotypes. Once the slow-rusting genes have been isolated, various combinations with other *Lr* genes could be attempted to establish genetically more diverse sources of resistance to leaf rust. If such studies show that *Lr*26 forms an essential part of the resistance complex, the priorities of effective leaf rust control, compared to specific standards for milling and baking quality, should be considered.

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