Temperature-Specific Seedling Resistance and Adult-Plant Resistance to *Puccinia recondita* f. sp. *tritici* in the Wheat Cultivar Glenlea

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ABSTRACT

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In a genetic study conducted in the F_1, F_2, and F_3 generations derived from the cross between line E (leaf rust susceptible) and cultivar Glenlea, a dominant gene for seedling resistance, presumably *Lr*1, and two recessive genes for adult-plant resistance to *Puccinia recondita* f. sp. *tritici* were indicated. Seedling tests with Glenlea and line E/Glenlea progenies at 29–31 C revealed that Glenlea has another gene in addition to *Lr*1. Expression of high-temperature seedling resistance in Glenlea was much more pronounced in progenies of the cross between line E and Glenlea than in the donor parent. Isolates detecting the temperature-specific gene were virulent to *Lr*T2 (a gene for adult-plant resistance in Glenlea) in the seedling stage; some of these isolates, but not all, were virulent to *Lr*13 under similar conditions. Thus, the seedling resistance of Glenlea at 29–31 C is either mediated by the second gene for adult-plant resistance, which has been reported as allelic or closely linked with *Lr*13, or it may be a previously undetected gene. Determination of the specific environmental conditions required for expression of the genes for resistance to *P. r.* f. sp. *tritici* in Glenlea is valuable to breeding programs aimed at developing wheat genotypes with levels of resistance similar to that of Glenlea.

Leaf rust (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*) is probably the most important rust disease of wheat (*Triticum aestivum* L.) worldwide (20). Therefore, resistance to leaf rust should be an objective of most wheat breeding programs. In view of the restricted number of single genes universally resistant to *P. r.* f. sp. *tritici* (22), efforts to provide resistant cultivars should also be centered on the adult-plant type of resistance because this resistance has been effective in cultivars such as Era (12,17) and Glenlea (18,19).

In Canada, the effective resistance against *P. r.* f. sp. *tritici* characteristic of the cultivar Glenlea has been associated with resistance genes *Lr*1, *Lr*T2, and a gene allelic or closely linked to *Lr*13 (11).

The incorporation of more than one gene for resistance to leaf rust in a wheat genotype may result in enhanced levels of resistance (21). Thus, the identification and characterization of an effective combination such as that of Glenlea is important for the exploitation of resistance in other genetic backgrounds.

Considering the concept that parasite: host genotypes are expressed in specific environments (4), seedling tests were conducted to determine whether the genes associated with adult-plant resistance in Glenlea (11) could be detected by manipulating the parasite: genotype:environment interaction. The inheritance of adult-plant resistance in Glenlea, for use of this type of resistance in South African wheat breeding programs, was also studied.

MATERIALS AND METHODS

Pathogen isolates and inoculation procedures. Eight South African isolates of *P. r.* f. sp. *tritici* were used in this study (Table 1). Freshly collected urediniospores suspended in Soltrol 130 light mineral oil (Phillips Chemical Company, Borger, TX) were used as inoculum. Flag leaves of plants in the inheritance study and primary leaves in seedling experiments were inoculated according to the methods of Browder (1,2). A standard suspension of 0.2 mg of urediniospores per milliliter of oil was used in all inoculations.

One hour after inoculation of seedlings and 3 hr after inoculation of adult plants,

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when the oil had evaporated from leaves, the plants were placed in a dew chamber in darkness at 18–20 C for 19 hr. During the last 3 hr in the chamber, leaves were allowed to dry off gradually before placement in a greenhouse where daylight was supplemented with 157.5 μE m^{-2} s^{-1} light emitted by cool-white fluorescent tubes for 12 hr each day.

Resistance of Glenlea seedlings. Three different tests were conducted to evaluate the resistance of Glenlea seedlings in comparison with seedlings of cultivars and lines that possess corresponding genes for resistance, but in different backgrounds. The seedlings were produced in a room at 15–25 C and illuminated by about 35 μE m^{-2} s^{-1} natural daylight. Inoculation of 7-day-old seedlings was as outlined above. Infection types were scored according to the description of Roelfs (16), 8–11 days after inoculation.

In the first seedling experiment, the resistance of Glenlea was compared with that of Era (*Lr*10, *Lr*13, *Lr*T2, + [12,17]), Manitou (*Lr*13 [20]), Sinton (*Lr*10, *Lr*13, + [17]), and line E (susceptible check). Of the genes assumed to reside in the wheat genotypes studied, *Lr*1 and *Lr*10 are expressed in seedlings (3), whereas *Lr*T2 and *Lr*13 are usually considered genes for adult-plant resistance, but can be detected in seedlings under certain conditions (9,15). In Glenlea, the gene associated with *Lr*13 was expressed in the adult stage (11). Seedlings were inoculated with isolates 3SA121, 3SA122, 3SA123, 3SA126, 3SA127, and 3SA128 (Table 1) and kept at 17–19 C and 30–32 C in two greenhouse compartments.

In the second experiment, seedlings derived from a cross between line E and Glenlea were evaluated for resistance to isolates 3SA121 or 3SA127 of *P. r.* f. sp. *tritici*. Seedlings were grown from remnant seeds of an inheritance study (described later in this paper). F_2, F_3, and F_4 seedlings were tested at 30–32 C. One test with F_3 seedlings was conducted at 15–17 C. The genotypes Glenlea, line E, Thatcher, and a Thatcher backcross line (RL6003) with gene *Lr*1 were included in each inoculation.

In the third seedling experiment, the resistance of Glenlea was compared with that of Thatcher backcross lines with genes *Lr*T2, *Lr*T3, *Lr*T2 + *Lr*T3, four families from line E/Glenlea F_5 progenies (lines H9, H10, H11, and H12), and with line E, Thatcher, and Manitou (*Lr*13). *Lr*T2 was included in this study because it conditions resistance in Glenlea. *Lr*T3 was tested because it has been reported (9) to enhance the effect of *Lr*T2 in certain combinations. The Thatcher near-isogenic lines were supplied by P. L. Dyck, Agriculture Canada, Winnipeg. Seven-day-old seedlings were inoculated with isolates 3SA121 (avirulent to Glenlea at 31 C) and 3SA127 (virulent to Glenlea at 31 C) of *P. r.* f. sp. *tritici* and kept at 16–18 C and 28–30 C until infection types were scored.

Inheritance of resistance. The reaction of flag leaves of F_1 and F_2 plants derived from a cross between Glenlea and line E was recorded 14 days after inoculation. Plants from both the F_1 and F_2 generations were grown before and after inoculation in a greenhouse at 20–24 C with additional illumination of 157.5 μE m^{-2} s^{-1} provided by fluorescent tubes for 12 hr each day.

One hundred ninety-eight F_3 families were grown in a greenhouse at 15–21 C and, due to segregation for maturity and limited dew chamber space, eight inoculations were carried out over a period of 21 days. F_1, F_2, and F_3 plants were inoculated with isolate 3SA62 of *P. r.* f. sp. *tritici* (Table 1). Flag leaves of F_1 plants were inoculated at Romig growth stage 13 (6), and those of F_2 and F_3 plants were inoculated when most plants were between late-boot and flowering stages (Romig scale 11–16). In all inoculations, line E and Glenlea were included as checks. Plants were grown in soil in 5-kg pots (3–8 plants per pot). A water-soluble fertilizer (6.5:2.7:13.0 NPK) was applied as a soil drench (0.5 g per pot) 3 wk after planting and weekly thereafter for the duration of the experiments. Inoculated F_3 plants were placed in a greenhouse at 15–21 C until evaluation of reaction types.

One hundred eighty F_2 seedlings from the cross between line E and Glenlea were tested for resistance to isolate 3SA57 (Table 1). Inoculated seedlings were maintained in a greenhouse at 19–23 C with illumination as described above. The ratio of resistant to susceptible plants was determined 11 days after inoculation. Chi-square values for F_2 and F_3 ratios were calculated (23).

RESULTS

Resistance of Glenlea seedlings. Infection types produced at 17–19 C and 30–32 C on Glenlea and other wheat genotypes that possess different genes for resistance are shown in Table 2. Manitou (*Lr*13) was susceptible at both temperatures to all isolates, except isolates 3SA122 and 3SA128, which were avirulent to *Lr*13 at the higher temperature. Era was resistant to all isolates tested at 30–32 C, except isolate 3SA126. Isolate 3SA127 was virulent to Era at 17–19 C but avirulent at 30–32 C, indicating an unknown gene for temperature-specific seedling resistance. Sinton was susceptible to isolate 3SA121 and only moderately resistant to isolates 3SA122 and 3SA123 at 17–19 C. At

Table 1. Avirulence/virulence[y] combinations of isolates of *Puccinia recondita* f. sp. *tritici* used to study the expression and inheritance of resistance to leaf rust in the wheat cultivar Glenlea

Isolate	Leaf rust resistance (*Lr*) genes[z]
3SA57, 3SA122	*Lr*1,2a,2b,3ka,11,15,17,20,24,30/3a,3bg,10,14a,16
3SA62, 3SA126	*Lr*3a,3bg,3ka,11,16,20,24,30/1,2a,2b,10,14a,15,17
3SA121	*Lr*3a,3bg,3ka,10,11,14a,16,17,20,24,30/1,2a,2b,15
3SA123	*Lr*3a,3bg,3ka,10,11,14a,16,17,20,30/1,2a,2b,15,24
3SA127	*Lr*3a,3bg,3ka,11,16,20,30/1,2a,2b,10,14a,15,17,24
3SA128	*Lr*2a,2b,3bg,15,16,17/1,3a,3ka,10,11,14a,20,24,30

[y] Avirulence/virulence characteristics were determined at 18–24 C.
[z] South African leaf rust differential genes.

Table 2. Infection types produced by six isolates of *Puccinia recondita* f. sp. *tritici* at two temperatures on primary leaves of adult-plant resistant wheat cultivars and of a susceptible control line

	Infection type[z] observed with isolates at different temperatures											
	3SA121		3SA122		3SA123		3SA126		3SA127		3SA128	
Cultivar or line	18 C	31 C	18 C	31 C	18 C	31 C	18 C	31 C	18 C	31 C	18 C	31 C
Era (*Lr*10, 13, T2, +)	;	;c	3	;c	;c	;c	3	3	3	;12	3	;c
Glenlea (*Lr*1, *Lr*T2, +)	3+	;12	0;	0;	3+	;12	3+	3+	3+	3	3++	;12
Manitou (*Lr*13)	4	3	4	;1cn	4	3+	4	4	4	4	4	;1cn
Sinton (*Lr*10, 13, +)	3	;c	2+3	;cn	2–	;1c	3+	3+	4	4	3+	2=
Line E (check)	3++	3++	3++	3++	3++	3++	3++	3++	3++	3++	3++	3++

[z] As described in Roelfs (16), where a semicolon indicates a fleck reaction, plus and minus signs denote sizes larger and smaller than normal for an infection type, the letter c indicates chlorosis, and the letter n indicates necrosis.

30–32 C, Sinton was highly resistant to isolates 3SA121, 3SA122, 3SA123, and 3SA128. Sinton was susceptible to isolates 3SA126 and 3SA127 at both temperatures. Glenlea was resistant at 30–32 C to isolates 3SA121, 3SA122, 3SA123, and 3SA128 and suceptible to isolates 3SA126 and 3SA127. It was susceptible at 17–19 C to all isolates except 3SA122, which lacks virulence to *Lr*1.

Seedlings from the F_2, F_3, and F_4 generations segregated for resistance to isolates 3SA121 and 3SA127 (Table 3). Because the number of F_2 plants and F_3 families tested was statistically insufficient, conclusions on the genetics of seedling resistance could not be made. Line E, Thatcher, and RL6003 (*Lr*1) were susceptible to isolates 3SA121 or 3SA127 at 15–17 C and 30–32 C. Isolate 3SA121 produced infection types ;1, ;12, 3, and 3+ on F_2 seedlings evaluated at 30–32 C. Isolate 3SA127, virulent to Glenlea at 30–32 C, produced the low infection types X, 2⁻, and 2+3 on individual plants in eight of the 24 F_3 families tested at 30–32 C with this culture. Isolate 3SA121, avirulent to Glenlea at 30–32 C, produced low infection types in the range ;c to 2+3 in 17 of the 21 F_3 families tested at this temperature. Isolate 3SA121 was virulent to Glenlea at 15–17 C, but produced low infection types in the range ;1 to 2+3 in 14 of the 25 F_3 families evaluated at the lower temperature. In the F_4 generation tested at 30–32 C with isolate 3SA121, low infection types (;n to X2) were observed in seven of the eight families evaluated. Isolate 3SA127 depicted low infection type ;12c at 30–32 C in four out of eight different F_4 families.

In the test designed to determine whether the high-temperature seedling resistance of Glenlea was due to genes *Lr*T2, *Lr*T3, or *Lr*13, isolate 3SA121 produced low infection types at 28–30 C only on Glenlea and lines H9, H10, and H11 (Table 4). At 16–18 C, isolate 3SA121 was virulent to all seedlings evaluated except line H11, which exhibited an intermediate reaction. All the cultivars and lines tested in this experiment were susceptible to isolate 3SA126 at both temperatures (Table 4).

Inheritance of resistance. The segregation for seedling resistance to isolate 3SA57 of *P. r.* f. sp. *tritici* in a F_2 population derived from the cross between line E and Glenlea indicated a single dominant gene (Table 5). Infection types of the resistant plants were 0; or ;c.

All adult F_1 plants were susceptible (Table 5). In the F_2 population the observed ratio indicated segregation of two recessive genes for adult-plant resistance (Table 5). The infection types on the flag leaves of plants displaying resistance were ;c, ;1c, and 2c. Z-reactions (16), where the larger uredinia are produced toward the base of the leaf, were common. Of the 198 F_3 families evaluated, 92 were homozygous resistant, eight were homozygous susceptible, and 98 families segregated for adult-plant resistance (Table 5). Resistant F_3 plants were characterized by flag leaf infection types in the range ; to Z4. Again, Z-reactions were common. Reactions of Glenlea were resistant (X) and of line E were susceptible (3++).

DISCUSSION

The segregation of a single dominant gene for resistance to isolate 3SA57 in seedlings derived from Glenlea agrees with the report of Dyck et al (11). Data from the present study do not identify the gene involved, but Canadian studies indicated it was *Lr*1 (11). Moreover, in

Table 3. Detection of seedling resistance at two temperatures to isolates 3SA121 and 3SA127 of *Puccinia recondita* f. sp. *tritici* in the F_2, F_3, and F_4 generations of the cross between line E and Glenlea[z]

Isolate	Generation	No. of plants or families	Temperature (C)	Ratio		
				Resistant	Segregating	Susceptible
3SA121	F_2	34	31	11		23
	F_3	21	31	3	14	4
	F_3	25	16	6	8	11
	F_4	8	31	5	2	1
3SA127	F_3	24	31	0	8	16
	F_4	8	31	4	0	4

[z] Line E and *Lr*1, a gene for seedling resistance in Glenlea, were susceptible to both isolates at 16 and 31 C.

Table 4. Infection types produced by isolates 3SA121 and 3SA126 of *Puccinia recondita* f. sp. *tritici* at two temperatures on primary leaves of lines derived from the wheat cultivar Glenlea and of lines with the genes *Lr*T2 and *Lr*T3

Cultivar or line	Infecton type[z] observed with isolates at different temperatures			
	3SA121		3SA126	
	17 C	29 C	17 C	29 C
Glenlea	3–	;12c	3–	3
Line E	3++	3+	3+	3++
Thatcher	3+	3+	3	3++
Manitou (*Lr*13)	3+	3	3++	3++
Line 897 (*Lr*T2)	3+	3	3+	3
RL6058 (*Lr*T2)	3	3	3+	3
Line 896 (*Lr*T3)	3	3	3+	3
RL6050 (*Lr*T2 + T3)	3	3	3	3
Line H9	3++	;12=c	4	3++
Line H10	3+	;1=c	3+	3++
Line H11	2+3	;1=cn	3+	3++
Line H12	3++	3++	3++	3++

[z] As described in Roelfs (16), where a semicolon indicates a fleck reaction, plus and minus signs denote sizes larger and smaller than normal for an infection type, the letter c indicates chlorosis, and the letter n indicates necrosis.

Table 5. Segregation ratios of genes for resistance to isolates 3SA57 and 3SA62 of *Puccinia recondita* f. sp. *tritici* in F_1, F_2, and F_3 progenies of the cross between line E and Glenlea

Generation	Isolate	Number of plants or families			Total no. of plants	Expected ratio	χ^2	*P*
		Resistant	Segregating	Susceptible				
Seedlings								
F_2	3SA57	139		41	180	3:1	0.474	0.50–0.25
Adult plants								
F_1	3SA62	0		49	49			
F_2	3SA62	79		121	200	7:9	1.468	0.25–0.10
F_3	3SA62	92	98	8	3461	7:8:1	1.890	0.50–0.25

the latter report, Glenlea showed negligible seedling resistance in addition to that conferred by *Lr*1. In the study with South African isolates of *P. r.* f. sp. *tritici*, extremely high levels of seedling resistance in Glenlea derivatives were observed. Although it was most readily detected at 29–31 C, some line E/Glenlea families exhibited seedling resistance at 16–17 C. Furthermore, line E/Glenlea progenies displayed seedling resistance at 31 C to isolate 3SA127 despite the fact that this isolate is virulent to Glenlea at 31 C. Apparently the gene for high-temperature seedling resistance is inhibited in Glenlea because its expression in the line E background was much more pronounced. Temperature specificity in the wheat leaf rust association has often been described (4,7). Our study also emphasized the importance of pathogen genotype and supported the view of Browder and Eversmeyer (5) that the phenotypic expression resulting from the interaction between host and parasite genotype is adapted to a specific environment.

The adult-plant resistance of Glenlea was conferred by two recessive genes. Dyck et al (11) also found two genes for adult-plant resistance in Glenlea, but the genes segregated in a dominant manner in crosses with lines RL6011 (*Lr*12) and RL6044 (*Lr*22a). However, genetic background (8,10), temperature (14), or the genetic constitution of the pathogen (13) may influence the degree of dominance of *Lr* genes.

The relationship between the genes for adult-plant resistance in Glenlea and the gene for high-temperature seedling resistance is not clear. Infection type studies showed that the South African isolates of *P. r.* f. sp. *tritici* tested could not detect *Lr*T2, a gene previously reported to be present in Glenlea (11). The temperature-specific gene identified in our study was detected in a way similar to that reported for *Lr*13 (15). However, isolates 3SA121 and 3SA123 are both virulent to *Lr*13 at 31 C, but avirulent to Glenlea at the same temperature. Although genetic evidence was not provided in our study, the temperature-specific gene in Glenlea appears to be the same gene described earlier as linked or allelic to *Lr*13 (11).

Complementary effects between genes for resistance to *P. r.* f. sp. *tritici* have been reported for the pairs *Lr*T2 and *Lr*T3 (9) and *Lr*13 and *Lr*16 (21). The highly effective resistance to leaf rust in Glenlea could probably be ascribed to the combination of *Lr*T2 and the gene linked or allelic to *Lr*13. Furthermore, presently unidentified corresponding gene pairs could also be responsible for enhancement of resistance. The presence of such unidentified interactions was suggested by the infection types listed in Table 2. Although we assumed that *Lr*10, *Lr*13, and *Lr*T2 occurred in more than one background, expression of these genes for resistance to *P. r.* f. sp. *tritici* in their respective backgrounds was not similar. However, data from our study suggested that by manipulating components of the parasite:host:environment interaction (4) potentially valuable genes for resistance to leaf rust could be identified for exploitation in wheat breeding programs.

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