Inheritance of Seedling and Adult Plant Resistance to Leaf Rust in Wheat Cultivars Ciano 79 and Papago 86

R. P. SINGH, International Maize and Wheat Improvement Center (CIMMYT), Lisboa 27, Apdo. Postal 6-641, 06600, Mexico, D.F., Mexico, and J. HUERTA-ESPINO, SARH, INIFAP, CIANO, Km. 12. Carret. Norman Borlaug, Apdo. Postal 515, 8500, Cd. Obregon, Son., Mexico

ABSTRACT

Singh, R. P., and Huerta-Espino, J. 1995. Inheritance of seedling and adult plant resistance to leaf rust in wheat cultivars Ciano 79 and Papago 86. Plant Dis. 79:35-38.

Wheat (*Triticum aestivum*) cultivars Ciano 79 and Papago 86 have maintained high levels of resistance to leaf rust, caused by *Puccinia recondita* f. sp. *tritici*, since their release during 1979 and 1986, respectively, in leaf rust-prone northwestern Mexico. Because inheritance of leaf rust resistance for these cultivars is unknown, Ciano 79 and Papago 86 were intercrossed, crossed with the susceptible cultivar Sonora 64, and crossed with the adult plant resistant cultivar Frontana to evaluate the resistance relationship. Inheritance studies were conducted in seedling and/or adult plant growth stages using the parents, F_1 plants, F_2 populations, and F_3 and F_5 lines. The resistance to *P. r. tritici* pathotype TCB/TD in seedlings of Ciano 79 and Papago 86 was conferred by a single gene, *Lr16*. When present alone, *Lr16* confers only moderate resistance in adult plants to the same pathotype. The adult plant resistances of both cultivars were based on the additive interaction between gene *Lr16* and a minimum of two other slow-rusting genes. Besides *Lr16*, one of the two slow-rusting genes was also common in Ciano 79 and Papago 86. The adult plant resistance genes in these cultivars differed from the resistance genes in Frontana.

Wheat (*Triticum aestivum* L.) cultivars Ciano 79 and Papago 86 were released for cultivation in the leaf rust-prone northwestern Mexican states of Sonora and Sinaloa in 1979 and 1986, respectively. Papago 86 is derived from the cross Ciano 79/Pavon 76. Ciano 79 is also cultivated in Brazil and Peru under the names Aruana and Cristina, respectively. Both Ciano 79 and Papago 86 have remained resistant to leaf rust, caused by *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D.M. Henderson, in their areas of cultivation. Singh and Rajaram (17) postulated that these cultivars carry gene *Lr16*, which confers a low disease reaction in seedlings to most Mexican pathotypes of *P. r. tritici*. The presence of additional genes for adult plant resistance in these cultivars has also been reported (17).

The current study was conducted: 1) to determine the genetic basis of leaf rust resistance in seedlings and adult plants of the cultivars Ciano 79 and Papago 86 and 2) to determine the relationship of the resistance in these two cultivars relative to the resistance of the worldwide resistant cultivar Frontana (12,18).

MATERIALS AND METHODS

The leaf rust-resistant cultivars included in the study were Ciano 79 (CIMMYT Wheat Accession BW3209), Papago 86 (BW5012), and Frontana (BW15647). The Mexican cultivar Sonora 64 (BW134) was used as the susceptible parent. Thatcher near-isogenic line RL6005 for *Lr16* was used as a check in the field studies.

The *P. r. tritici* pathotype used in all genetic studies was TCB/TD (15) with the following avirulence/virulence formula: *Lr3ka,9,10,11,16,17,19,21,24,25, 27+31,29,30,32,33,34/1,2a,2b,2c,3, 3bg,13,14a,14b,15,18,20,22b,23,26,28.* Pathotype TCB/TD is common in the areas of Mexico where the study was conducted. Vacuum-dried (13) urediospores of this pathotype are stored at CIMMYT. Fresh inoculum was used in the study and was obtained by multiplying the urediospores on the susceptible cultivar Morocco.

Ciano 79 and Papago 86 were intercrossed and crossed with Sonora 64 and Frontana. Inheritance studies were based on F_1, F_2, individual F_2 plant-derived F_3, and F_5 lines. The F_5 lines were obtained by harvesting a random spike from each F_3 line and a random plant from each F_4 line.

The parents, 100 F_2 plants, and approximately 30 plants of each of the 118 F_5 lines from the crosses of Sonora 64 with Ciano 79 and Papago 86 were evaluated for reaction to leaf rust in the seedling growth stage. In addition, 100 F_2 seedlings from the cross Ciano 79/Papago 86 were evaluated for their reactions to leaf rust. Fully expanded primary leaves of 9-day-old seedlings were inoculated by spraying leaf rust urediospores suspended in the lightweight mineral oil Soltrol 170 at a concentration of 2–3 mg/ml, placed in a dew chamber overnight at 18–20 C, and transferred to a greenhouse maintained at 20–25 C. Between 20 and 30 pustules developed per square centimeter on the leaves. The infection type data were recorded approximately 10 days after inoculation and were based on a 0–4 scale for leaf rust similar to that described by Stakman et al (19) for stem rust.

Approximately 15 F_1 plants, 350 space-planted (15–20 cm between plants) F_2 plants, 118 F_3 lines (approximately 60 plants of each line), and the parents from each cross were tested at the adult plant stage for leaf rust resistance in the field. The F_1 and F_2 populations were evaluated during the 1990–1991 season at Ciudad Obregon (State of Sonora), whereas the F_3 lines were tested at El Batan (near Mexico City) during the 1991 season. The 118 F_5 lines (approximately 60 plants within each line) from the crosses of Sonora 64 with Ciano 79 and Papago 86 were tested for resistance to leaf rust in the field at Ciudad Obregon during the 1992–1993 season. Plots of the parents, F_1 plants, and F_3 and F_5 lines consisted of two 1-m rows seeded 20 cm apart with 70 cm between plots. Rows of the two parents were planted at the beginning of each F_3 or F_5 population, and Sonora 64 was included every 25 rows as the susceptible check.

Leaf rust epidemic was spread in the field from inoculated plants of the susceptible cultivar Morocco planted as clumps at one end of each plot in the 0.5-m path. The visual estimations of adult plant leaf rust severities were based on the modified Cobb scale (10). The host response to infection (reaction) followed the scale described by Roelfs et al (13). The first leaf rust response data were recorded on flag leaves at milk stage when the susceptible check Sonora 64 displayed a response between 80S and 100S. Individual plants in the F_2 populations were classified, whereas the range of severity (the most resistant to the most susceptible plant) was recorded for each F_3 and F_5 line. The average leaf rust severity for each F_5 line was also visually estimated. The F_3 and F_5 lines were evaluated a second time approximately 12–15 days after the first evaluation, when leaf rust had killed leaves of Sonora 64. Previous studies at CIMMYT (18) had shown that the timing of the first rating is critical to identify plants or lines that are similar in susceptibility level to

Accepted for publication 13 September 1994.

the susceptible parent, whereas the second rating time is critical to identify plants or lines that are similar in resistance level to the resistant parent. On the basis of the two data sets, the F_3 and F_5 lines were classified into four categories: HPTR = homozygous parental-type resistance, HPTS = homozygous parental-type susceptibility, SegI = either segregating or homozygous for disease levels higher than that of the resistant parent but lower than that of the susceptible parent, and SegS = segregating with disease levels reaching the susceptible parent's response. Chi-square analyses were carried out to test the distribution of observed F_2, F_3, and F_5 phenotypic frequencies with those expected for crosses involving Sonora 64.

RESULTS

Seedling studies. Table 1 gives the seedling infection types (ITs) displayed by each parent when tested with *P. r. tritici* pathotype TCB/TD. Ciano 79 and Papago 86 displayed IT 1−, which was slightly more resistant than the IT 1+ displayed by RL6005 (tester line for *Lr16*). Sonora 64 and Frontana displayed ITs 4 and 3, respectively.

F_2 families from the crosses of Sonora 64 with Ciano 79 and Papago 86 segregated for resistant-intermediate (ITs 1− to 1+3C) and susceptible (ITs 3 to 4) seedlings in a 3:1 ratio (Table 2), which indicated that a single gene confers seedling resistance. The distributions of F_5 lines in both crosses were also in accordance with a monogenic segregation ratio (Table 2). All 100 F_2 seedlings from the cross Ciano 79/Papago 86 were resistant (IT 1−), which indicated that both parents carry the same seedling gene.

Adult plant studies. The F_1 plants from the crosses of Sonora 64 with Ciano 79 and Papago 86 were scored as 20MSS and 30MSS, respectively (Table 3). The adult plant resistance in both parents was, therefore, partially dominant, because the two resistant parents were scored as 1MR and the susceptible parent as 100S. Plants in F_2 populations from both of the crosses showed a range of leaf rust severity. For analysis, the plants with up to 60% leaf rust were considered to possess at least some resistance (the susceptible parent had disease scores between 80 and 100%) and the plants with 80–100% disease were grouped into the susceptible category (Table 3). Chi-square analyses for ratios expected for independent segregations of two, three, and four genes indicated that, most likely, three genes are present in each resistant parent. The distributions of the F_3 and F_5 lines for each cross also fit the ratio expected for segregation at three loci (Table 4). Since only a few F_3 or F_5 lines were as resistant as Ciano 79 and Papago 86, probably the three genes interacted additively.

To evaluate the adult plant effectiveness of gene *Lr16*, first disease ratings (recorded when Sonora 64 displayed an 80S response) of the F_5 lines from the crosses of Sonora 64 with Ciano 79 and Papago 86 are presented in Table 5 together with the status of *Lr16*. In both crosses, most F_5 lines homozygous for *Lr16* showed less than 1% disease, with a few lines slightly higher (10% or less). Average leaf rust severities for lines segregating for *Lr16* varied from 1 to 60%; in fact, a few plants within some of the lines had disease up to 100%. *Lr16* lacking F_5 lines had leaf rust responses from 1 to 100%. F_5 lines rated to have 1% disease on 6 March (Table 5) were

Table 1. Bread wheat parents, seedling infection type with *Puccinia recondita* f. sp. *tritici* pathotype TCB/TD, and adult plant ratings for three seasons with the same pathotype

Parent	Seedling infection type[a]	Adult plant rating[b]: Ciudad Obregon 1990–1991	El Batan 1991	Ciudad Obregon 1992–1993
Sonora 64	4	100S (N)	100S (N)	100S (N)
Ciano 79	1−	1MR	1MR	1MR
Papago 86	1−	5MR	1MR	5MR
Frontana	3	5MSS	1MSS	5MSS
RL6005 (*Lr16*)	1+	60MSS	80MSS	60MSS

[a]Based on a 0–4 scale (19), where 1 = small-sized uredia surrounded by necrosis, 3 = medium-sized uredia without chlorosis or necrosis, and 4 = large-sized uredia without chlorosis or necrosis; − = uredia somewhat smaller than normal for the infection type and + = uredia somewhat larger than normal for the infection type.

[b]Rating includes two components: disease severity based on modified Cobb scale (10), where 1 = 1%, 5 = 5%, up to 100 = 100%; and host response based on scale described by Roelfs et al (13), where MR = moderately resistant, MSS = moderately susceptible to susceptible, S = susceptible, and (N) = leaves necrotic due to heavy leaf rust infection.

Table 2. Seedling classification and chi-square analysis of F_2 populations and F_5 lines from three crosses inoculated with *Puccinia recondita* f. sp. *tritici* pathotype TCB/TD

Cross	F_2 Number of seedlings[a] R	S	χ^2 3:1, *P* value	F_5 Number of lines[b] HR	Seg	HS	χ^2 7:2:7, *P* value
Sonora 64/Ciano 79	72	28	0.48, $P > 0.25$	49	18	51	0.86, $P > 0.50$
Sonora 64/Papago 86	68	32	2.61, $P > 0.10$	53	19	46	1.87, $P > 0.25$
Ciano 79/Papago 86	100	0	...	...	...	...	...

[a]R = resistant, S = susceptible.

[b]HR = homozygous resistant, Seg = segregating, HS = homozygous susceptible.

Table 3. Responses of F_1 adult plants and classification and chi-square analysis of F_2 plants for various crosses involving Ciano 79 and Papago 86, evaluated in the field with *Puccinia recondita* f. sp. *tritici* pathotype TCB/TD during 1990–1991

Cross	F_1 response[a]	Number of F_2 plants[b] R-I	S	χ^2 ratio and *P* value for ratio 15:1[c]	63:1[d]	255:1[e]
Sonora 64/Ciano 79	20MSS	342	8	9.39, $P < 0.01$	1.19, $P > 0.25$	32.31, $P < 0.01$
Sonora 64/Papago 86	30MSS	340	10	6.88, $P < 0.01$	3.81, $P > 0.05$	54.72, $P < 0.01$
Ciano 79/Papago 86	1MR	350	0	...	...	...
Frontana/Ciano 79	5MS	348	2	19.26, $P < 0.01$	2.24, $P > 0.10$	0.29, $P > 0.50$
Frontana/Papago 86	5MS	346	4	15.58, $P < 0.01$	0.40, $P > 0.50$	5.09, $P < 0.01$

[a]See Table 1 for definitions.

[b]R-I = resistant-intermediate (severity of 60% or less), S = susceptible (severity of 80% or more).

[c]Expected for independent segregations of two dominant genes.

[d]Expected for independent segregations of three dominant genes.

[e]Expected for independent segregations of four dominant genes.

rated again 12 days later and grouped according to the most severe individual plant reactions within each line (Table 6). These lines now had a diverse response. All five HPTR lines (1% rust) in Sonora 64/Ciano 79 and all seven HPTR lines (1–5% rust) in Sonora 64/Papago 86 were homozygous for *Lr16*. The most resistant *Lr16*-lacking lines in Sonora 64/Ciano 79 and Sonora 64/Papago 86 crosses had up to 10 and 30% leaf rust severity, respectively. These results clearly indicate that: 1) *Lr16* also confers some resistance in adult plants, 2) other genes that confer resistance only in adult plants are also present in Ciano 79 and Papago 86, and 3) *Lr16* interacts additively with these additional adult plant effective genes.

The F_1 plants from the Ciano 79/Papago 86 cross had resistance levels similar to the two parents (Table 3). All F_2 plants were also scored as resistant-intermediate (Table 3). Segregation for leaf rust was evident in the F_3, but the highest severity was 10% (Table 7), indicating that the two parents share some common genes.

The F_1 plants from the crosses of Frontana with Ciano 79 and Papago 86 were scored as 5MS, and only a few F_2 plants were susceptible (Table 3). Although none of the 118 F_3 lines was homozygous-susceptible, plants in some lines from each cross were as susceptible as Sonora 64 (Table 7). These results indicate that the genes for adult plant resistance identified in Ciano 79 and Papago 86 are different from those in Frontana.

DISCUSSION

A single gene, most likely *Lr16* (17), confers seedling resistance in Ciano 79 and Papago 86 to the Mexican pathotype

Table 4. Distribution and chi-square test for F_3 (grown during 1991) and F_5 (grown during 1992–1993) lines from the crosses of susceptible and resistant cultivars, when tested in the field for the adult plant responses to *Puccinia recondita* f. sp. *tritici* pathotype TCB/TD

		Number of lines[a]				
Cross	Generation	HPTR	HPTS	SegI	SegS	χ^2 and P value[b]
Sonora 64/Ciano 79	F_3	0	1	51	66	2.43, $P > 0.25$
	F_5	5	8	91	14	3.67, $P > 0.25$
Sonora 64/Papago 86	F_3	2	2	72	42	1.24, $P > 0.50$
	F_5	7	6	94	11	2.91, $P > 0.25$

[a] HPTR = homozygous for parental-type resistance (homozygous for all resistance alleles); HPTS = homozygous for parental-type susceptibility (homozygous, lacking all resistance alleles); SegI = either segregating or homozygous for disease levels higher than that of the resistant parent but less than that of the susceptible parent (homozygous for at least one resistance allele); SegS = segregating with disease levels reaching the susceptible parent's response (heterozygous for at least one locus and homozygous for susceptibility alleles at other loci).
[b] Ratios in F_3 = 1 HPTR:1HPTS:36 SegI:26 SegS and in F_5 = 0.0837 HPTR:0.0837 HPTS:0.7383 SegI:0.0944 SegS; these are expected for independent segregations at three loci.

Table 5. Relationship of the seedling response to the average leaf rust severity on adult plants of F_5 lines, scored on 6 March 1993 when susceptible parent Sonora 64 had 80% leaf rust severity

	Seedling	Number of F_5 lines with average leaf rust severity[b]											
Cross	response[a]	1	5	10	20	30	40	50	60	80	90	100	Total
Sonora 64/Ciano 79	HR	46	2	1	0	0	0	0	0	0	0	0	49
	Seg	3	3	2	4	2	1	2	1	0	0	0	18
	HS	10	3	8	4	5	6	3	4	6	2	0	51
Sonora 64/Papago 86	HR	48	4	1	0	0	0	0	0	0	0	0	53
	Seg	7	1	2	2	2	1	2	2	0	0	0	19
	HS	7	6	5	8	5	5	1	3	1	4	1	46

[a] HR = homozygous resistant, (*Lr16* homozygous), Seg = segregating for *Lr16*, HS = homozygous susceptible (*Lr16* absent).
[b] Based on modified Cobb scale (10).

Table 6. Distribution of F_5 lines grouped by plants of greatest leaf rust severity, scored on 18 March 1993, that had displayed 1% leaf rust on 6 March

	Seedling	Number of F_5 lines with plants of greatest leaf rust severity[b]								
Cross	response[a]	1	5	10	20	30	40	60	80	Total
Sonora 64/Ciano 79	HR	5	4	5	12	4	9	6	1	46
	Seg	0	0	0	0	2	1	0	0	3
	HS	0	0	3	2	2	1	2	0	10
Sonora 64/Papago 86	HR	3	4	3	7	5	9	15	2	48
	Seg	0	0	0	0	1	3	2	1	7
	HS	0	0	0	0	3	2	1	1	7

[a] HR = homozygous resistant (*Lr16* homozygous), Seg = segregating for *Lr16*, HS = homozygous susceptible (*Lr16* absent).
[b] Based on modified Cobb scale (10).

Table 7. Distribution of F_3 lines grouped by plants of greatest leaf rust severity in crosses of resistant cultivars tested with *Puccinia recondita* f. sp. *tritici* pathotype TCB/TD at El Batan during 1991

	Number of F_3 lines with plants of greatest leaf rust severity[a]								
Cross	1	5	10	20	30	40	60	80	100
Ciano 79/Papago 86	85	25	8	0	0	0	0	0	0
Frontana/Ciano 79	56	18	9	9	8	7	4	4	3
Frontana/Papago 86	47	19	13	6	7	8	7	6	5

[a] Based on modified Cobb scale (10).

TCB/TD of *P. r. tritici*. The presence of additional genes for adult plant resistance is evident in both cultivars because they are highly resistant as adult plants, whereas the near-isogenic Thatcher line (RL6005) for *Lr16* is moderately susceptible even with the *Lr16*-avirulent pathotype (Table 1). Our results indicate that the adult plant resistance of both cultivars involves additive interaction between *Lr16* and a minimum of two additional partially effective genes. Papago 86, which is derived from the cross Ciano 79/Pavon 76, shares *Lr16* and one of the two adult plant resistance genes with Ciano 79. Pavon 76 is known to carry slow-rusting resistance to leaf rust that has remained durable (11,12). Therefore, the second adult plant effective gene in Papago 86 could be derived from Pavon 76. Gene *Lr16* is known to interact additively with genes *Lr13* and *Lr34* (5,14). However, Ciano 79 and Papago 86 lack both genes (16,17). German and Kolmer (5) observed the additive interaction of *Lr16* with *Lr34* when the *Lr16*-avirulent pathotypes were used. Virulence for *Lr16* has been identified in Texas and eastern Mexico just across the Texas border (8,15). However, pathotypes with virulence for *Lr16* have not been identified in northwestern Mexico (15) where Ciano 79 and Papago 86 are grown. One reason for this could be that *Lr16* is present in these cultivars in combination with two other adult plant effective genes. At least in Ciano 79, the two additional genes confer an acceptable level of resistance, as demonstrated by the response of the three F_5 lines that lack *Lr16* (Table 6). Combination of the two adult plant genes from Papago 86 resulted in moderate disease levels (Table 6). The response to infection of these F_5 lines was moderately susceptible to susceptible (MSS), indicating that the genes are slow-rusting (2) or partial (9) in nature. Therefore, at least part of the non-*Lr16* resistance in these two cultivars could be durable in nature, since most known durable rust resistances are attributed to a few additive partial resistance genes (1,3,4,6,7,18). The adult plant resistance of Frontana to common Mexican pathotypes of *P. r. tritici* is based on the interaction of *Lr34* with two or three additional additive genes and forms the basis of durable resistance in several CIMMYT-derived wheats (18). The resistances of Ciano 79 and Papago 86, most importantly their non-*Lr16* component, are genetically different from that of Frontana. Crosses of Ciano 79 and Papago 86 with high-yielding wheats carrying the Frontana-derived resistance should result in various new diverse combinations of adult plant effective genes.

ACKNOWLEDGMENTS

We thank Maarten van Ginkel for reviewing and Gene Hettel for editing the manuscript.

LITERATURE CITED

1. Broers, L. H. M., and Jacobs, T. 1989. The inheritance of host plant effect on latency period of wheat leaf rust in spring wheat. II: Number of segregating factors and evidence for transgressive segregation in F_3 and F_5 generations. Euphytica 44:207-214.
2. Caldwell, R. M. 1968. Breeding for general and/or specific plant disease resistance. Pages 263-272 in: Proc. Int. Wheat Genet. Symp. 3rd. K. W. Finlay and K. W. Shepherd, eds.
3. Dyck, P. L. 1991. Genetics of adult-plant leaf rust resistance in 'Chinese Spring' and 'Sturdy' wheats. Crop Sci. 31:309-311.
4. Ezzahiri, B., and Roelfs, A. P. 1989. Inheritance and expression of adult plant resistance to leaf rust in Era wheat. Plant Dis. 73:549-551.
5. German, S. E., and Kolmer, J. A. 1992. Effect of gene *Lr34* in the enhancement of resistance to leaf rust of wheat. Theor. Appl. Genet. 84:97-105.
6. Knott, D. R., and Padidam, M. 1988. Inheritance of resistance to stem rust in six wheat lines having adult plant resistance. Genome 30:283-288.
7. Kuhn, R. C., Ohm, H. W., and Shaner, G. 1980. Inheritance of slow leaf-rusting resistance in Suwon 85 wheat. Crop Sci. 20:655-659.
8. Marshall, D. 1989. Virulence of *Puccinia recondita* and cultivar relationships in Texas from 1985 to 1987. Plant Dis. 73:306-308.
9. Parlevliet, J. E. 1988. Strategies for the utilization of partial resistance for the control of cereal rusts. Pages 48-62 in: Breeding Strategies for Resistance to the Rusts of Wheat. N. W. Simmonds and S. Rajaram, eds. CIMMYT, Mexico City.
10. Peterson, R. F., Campbell, A. B., and Hannah, A. E. 1948. A diagrammatic scale for estimating rust severity on leaves and stems of cereals. Can. J. Res. Sect. C. 26:496-500.
11. Rajaram, S., Singh, R. P., and Torres, E. 1988. Current CIMMYT approaches in breeding wheat for rust resistance. Pages 101-118 in: Breeding Strategies for Resistance to the Rusts of Wheat. N. W. Simmonds and S. Rajaram, eds. CIMMYT, Mexico City.
12. Roelfs, A. P. 1988. Resistance to leaf and stem rusts in wheat. Pages 10-22 in: Breeding Strategies for Resistance to the Rusts of Wheat. N. W. Simmonds and S. Rajaram, eds. CIMMYT, Mexico City.
13. Roelfs, A. P., Singh, R. P., and Saari, E. E. 1992. Rust Diseases of Wheat: Concepts and Methods of Disease Management. CIMMYT, Mexico City.
14. Samborski, D. J., and Dyck, P. L. 1982. Enhancement of resistance to *Puccinia recondita* by interactions of resistance genes in wheat. Can. J. Plant Pathol. 4:152-156.
15. Singh, R. P. 1991. Pathogenicity variations of *Puccinia recondita* f. sp. *tritici* in wheat-growing areas of Mexico during 1988 and 1989. Plant Dis. 75:790-794.
16. Singh, R. P. 1993. Resistance to leaf rust in 26 Mexican wheat cultivars. Crop Sci. 33:633-637.
17. Singh, R. P., and Rajaram, S. 1991. Resistance to *Puccinia recondita* f. sp. *tritici* in 50 Mexican bread wheat cultivars. Crop Sci. 31:1472-1479.
18. Singh, R. P., and Rajaram, S. 1992. Genetics of adult-plant resistance of leaf rust in 'Frontana' and three CIMMYT wheats. Genome 35:24-31.
19. Stakman, E. C., Stewart, D. M., and Loegering, W. Q. 1962. Identification of physiologic races of *Puccinia graminis* var. *tritici*. U.S. Agric. Res. Serv. E-617 (rev.).