Genetics

Genetic Association of Leaf Rust Resistance Gene *Lr34* with Adult Plant Resistance to Stripe Rust in Bread Wheat

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ABSTRACT

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Near-isogenic Thatcher lines (viz., RL6058, RL6077, and Line 920) carrying gene *Lr34* for leaf rust resistance, Frontana, and various other wheat cultivars carrying *Lr34* displayed adult plant resistance to stripe rust in Mexico. F_2 populations or F_3 lines from several intercrosses of wheats carrying *Lr34* did not segregate for susceptibility to stripe rust and leaf rust, indicating that at least one resistance gene was common in each parent. An evaluation of F_3 lines for stripe rust and leaf rust, from the crosses of stripe rust and leaf rust susceptible Jupateco 73S with stripe rust and leaf rust resistant Condor and Jupateco 73R, showed linked segregation for the two diseases. For each disease, resistance was conferred by one partially dominant gene. Because *Lr34* is located on chromosome 7D, the linked *Yr* gene is designated *Yr18*. RL6058, RL6077, Line 920, Condor, or Jupateco 73R could be used as tester genotypes for *Yr18*. The durable adult plant stripe rust resistance of Anza, a related sib of the parent of Condor, is postulated to be attributable to *Yr18*, which is widespread in cultivars from the International Maize and Wheat Improvement Center germ plasm and South American wheats. An additional adult plant stripe rust resistance gene was present in both Sonoita 81 and Tonichi 81.

Additional keyword: *Triticum aestivum*.

The most common diseases of wheat in the world are rusts. Resistant cultivars are the most economical and environmentally safe control measures. Numerous genes conferring resistance to rusts have been identified (7). Several resistances are now ineffective, because rust pathogens were able to overcome them by adding new virulences. However, some cultivars possess durable resistance. Roelfs (13) suggested that genes *Lr12* or *Lr13* in combination with *Lr34* could have conferred durable resistance to leaf (brown) rust caused by *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D. M. Henderson in cultivars such as Frontana and Era. The adult plant resistances of Chinese Spring and Sturdy were attributable to the interaction of *Lr12* and *Lr34* (2). Dyck (1) located *Lr34* in chromosome 7D of wheat. Dyck and Samborski (3) developed near-isogenic lines of Thatcher that carried *Lr34* (viz., RL6058 [Thatcher*6/PI58548], RL6077 [Thatcher*6/PI250413], and Line 920 [Thatcher*6/Lageadinho]). Dyck (2) also indicated that *Lr34* could be linked with leaf tip necrosis of the adult plants. Singh (*unpublished data*) confirmed this observation and also showed the presence of *Lr34* in numerous International Maize and Wheat Improvement Center (CIMMYT)-derived cultivars that were thought to carry *Lr34* (15). The near-isogenic Thatcher lines carrying *Lr34* and various other cultivars known to carry *Lr34* also displayed adult plant resistance to stripe (yellow) rust (caused by *Puccinia striiformis* Westend.) when tested in Mexico and Australia (R. A. McIntosh, *personal communication*). This indicated a possible genetic association between the two traits, because the development of near-isogenic lines for *Lr34* involved various backcrosses with Thatcher; selections were made for leaf rust resistance only.

The objectives of this study were to evaluate the adult plant stripe rust resistance of wheats carrying *Lr34* that were susceptible to stripe rust as seedlings, to estimate the number of genes that confer adult plant resistance to stripe rust and leaf rust in crosses of stripe rust and leaf rust resistant and susceptible wheats, to evaluate the adult plant leaf rust and stripe rust responses of the F_2 or F_3 populations from the crosses of stripe rust resistant wheats that carry *Lr34*, and to test the genetic linkage between *Lr34* and the gene for stripe rust resistance.

MATERIALS AND METHODS

The cultivars and near-isogenic lines carrying *Lr34* used in the studies are listed in Table 1. Thatcher and its near-isogenic lines (viz., RL6058, RL6077, and Line 920) were developed by P. L. Dyck (Agriculture Canada, Winnipeg, Canada). Frontana, a Brazilian cultivar, carries durable resistance to leaf rust conferred by the interaction of *Lr34* with other genes (3,12,13,16). The Australian cultivar Condor (University of Sydney accession W3749) is from the cross WW15*2/WW80; WW15 is a sister line of the U.S. spring wheat cultivar Anza, which is from CIMMYT germ plasm. The cultivars Tobari 66 (CIMMYT accession BW30), Sonoita 81 (BW4105), Tonichi 81 (BW4026), Opata 85 (BW3414), and Jupateco 73 were released in Mexico. The number after the name indicates the year of release (e.g., Tobari 66 was released in 1966). Jupateco 73R (BW17890) and Jupateco 73S (BW17891) are reselections from the cultivar Jupateco 73 and were selected for leaf rust resistance (based on *Lr34*) and leaf rust susceptibility, respectively. Myna (BW17886), Parula (BW17887), Trap (BW17888), and Yaco (BW17889) are advanced breeding lines of the CIMMYT wheat improvement program. The parentages of these wheats are described by Villareal and Rajaram (18).

Between 116 and 133 F_3 lines (obtained from individual F_2 plants) from each of the crosses of Jupateco 73S with Jupateco 73R, Condor, Tobari 66, Sonoita 81, and Tonichi 81 were evaluated independently for leaf rust and stripe rust. The data were used for the estimation of the number of genes conferring resistance. Data from the crosses of Jupateco 73S with Jupateco 73R and Condor were also used for the study of linkage between resistances to stripe rust and leaf rust. The maximum recombination frequency (r) between the genes, which could have remained undetected at the 0.05 probability level for a population of n F_3 lines, was calculated from the following expression (4): $(1 - r)^2 = (0.05)^{1/n}$. F_3 lines were used in these studies instead of F_2 or backcross populations, because the same family could be evaluated at one location with stripe rust and at other locations with leaf rust. Between 37 and 101 F_3 lines from each of 17 intercrosses between wheats thought to carry *Lr34* were independently classified, and the commonality of stripe rust and leaf rust resistances in these parents was studied. Similarly, F_2 populations from 10 additional intercrosses were also evaluated.

The pathotype 14E14 (6) of *P. striiformis* used for seedling and adult plant studies carries virulences for the stripe rust resistance genes *Yr2,3,6,7* as well as the resistance gene known in Australia as *YrA* (19). The *P. r. tritici* pathotype was TBD/TM (14) with the avirulence/virulence formula: *Lr3ka,9,11,16,19,21, 23,24,25,26,29,30,32,33,34/1,2a,2b, 2c,3,3bg,10,13,14a,14b,15,17, 18,20,27+31,28*. This pathotype was chosen because it lacked virulence for *Lr34* but was virulent for other named *Lr* genes in the cultivars (15,16). Seedlings (8–9 days old) of the parents were inoculated by spraying urediospores suspended in a lightweight mineral oil (Soltrol 170, Phillips 66 Co., Bartiesville, OK), placed in a dew chamber overnight at 18–20 C for leaf rust and 13–15 C for stripe rust, and transferred to a greenhouse where temperature varied between 14 and 17 C. Gene *Lr34* confers some seedling resistance to leaf rust at low temperatures (3). Infection type (IT) data were recorded when the susceptible Thatcher expressed high ITs (approximately 2 wk after inoculation for leaf rust and 3 wk for stripe rust) and were based on a 0–4 scale (17) for leaf rust and on a 0–9 scale (8) for stripe rust.

TABLE 1. Cultivars with seedling infection types (IT) observed at 14–17 C and adult plant field responses to stripe rust and leaf rust during 1990 and 1991

	Stripe rust			Leaf rust		
	Seedling	Adult plant response[b]		Seedling	Adult plant response	
Cultivar	IT[a]	1990	1991	IT[c]	1990	1991
Thatcher	8	60–80S	80–100S	3+	100S	80S
RL6058	7–8	5–10M	5–15M	3−	40MSS	15MSS
RL6077	7–8	. . .	5–15M	3−	. . .	20MSS
Line 920	7–8	5–10M	5–15M	3−	40MSS	15MSS
Frontana	7	5–15M	0–10M	3−	TMSS	TMSS
Condor	8	10–20M	10–30M	3−	40MSS	20MSS
Tobari 66	7	T–10M	T–15M	3−	10MSS	5MSS
Sonoita 81	7–8	T–10M	5–15M	3−	10MSS	10MSS
Tonichi 81	7–8	T–5M	T–5M	3−	5MS	TMS
Opata 85	7–8	5–15M	15–40M	3−	10MS	5MS
Jupateco 73R	7–8	T–15M	5–15M	3−	40MSS	30MSS
Jupateco 73S	7–8	80–100S	80–100S	3+	100S	100S
Myna	7–8	T–15M	5–15M	3−	10MSS	5MSS
Parula	7–8	TM	T–10M	3−	TMS	TMS
Trap	7–8	T–5M	T–15M	3−	TMS	TMS
Yaco	7–8	TM	T–5M	3−	TMS	TMS

[a] Seedling IT scale of 0–9 is based on McNeal et al (8), in which ITs 7,8, and 9 are considered high or susceptible.

[b] Adult plant disease estimation is based on modified Cobb scale (11) and has two components: disease severity and infection type (IT). T = trace severity; 5 = 5% severity; etc.; M = moderately resistant to moderately susceptible IT; MS = moderately susceptible IT; MSS = moderately susceptible to susceptible IT; and S = susceptible IT.

[c] Seedling IT scale of 0–4 is based on Stakman et al (17), in which IT 3 indicates medium-sized uredia rarely with chlorosis or necrosis; + = uredia somewhat larger than normal for the IT; − = uredia considerably smaller than normal for the infection type.

The adult plant studies involving *P. striiformis* were done during 1990 at El Batan and during 1991 at Toluca; both locations are in the highlands near Mexico City. The 1990 parental response data are from a natural epidemic (largely consisting of pathotype 14E14), whereas the 1991 parental response data and data for all genetic studies are from nurseries artificially inoculated with pathotype 14E14. The parental, adult plant responses to *P. r. tritici* are those observed in the field at El Batan during 1990 and 1991 (Table 1). However, some F_2 and F_3 results were from tests done during previous crop cycles and at Ciudad Obregon in northwestern Mexico. Pathotype TBD/TM was used to inoculate nurseries in each year or location.

Field plots of parents and F_3 lines consisted of two 1-m rows seeded 20 cm apart with 70 cm between plots. Each plot consisted of approximately 40 plants. F_2 plants were space-planted (10–15 cm between plants). The leaf rust epiphytotic was created at El Batan, and the stripe rust epiphytotic was created at Toluca; they were created by inoculating susceptible spreader rows planted as clumps at one end of each plot. The disease estimation on adult plants was according to the modified Cobb Scale (11).

RESULTS

Thatcher, its near-isogenic lines carrying *Lr34*, and other wheats included in the study displayed high seedling ITs (susceptible reactions) ranging from 7 to 8 (Table 1) for stripe rust. It was evident that no seedling-effective *Yr* gene conferred resistance to the pathotype 14E14 used in the study.

Seedlings of Thatcher and Jupateco 73S displayed IT 3+ with leaf rust, whereas all other lines were recorded as 3− (Table 1). This type of IT is observed in Mexico for lines with *Lr34* when tested at low temperatures (R. P. Singh, *unpublished*). The effectiveness of *Lr34* gradually decreases with increase in temperature. These cultivars displayed ITs 3 to 3+ when tested at 23–25 C (data not presented). Adult plants of Thatcher and Jupateco 73S were highly susceptible to both rusts, whereas all other wheats displayed low to intermediate disease severities (Table 1). The data for stripe rust response include the range of severity observed in the plot with the most frequently occurring reaction (M = moderately resistant to moderately susceptible).

The distribution of the F_3 lines for adult plant stripe rust resistance for crosses involving Jupateco 73S and five resistant wheats is given in Table 2. Resistance in Jupateco 73R, Condor, and Tobari 66 was controlled by one gene, because the observed distributions of F_3 lines were in accordance with the segregation expected for one locus. Sonoita 81 and Tonichi 81 appeared to carry two independently inherited genes, because the F_3 line distributions conformed to the expected ratio of seven homozygous resistant/eight segregating/one homozygous susceptible for segregation at two independent loci. According to disease ratings on plants within segregating F_3 lines, resistance in each wheat appeared to be partially dominant; most of the plants displayed higher disease ratings than the resistant parents but less than Jupateco 73S.

The F_3 lines from 17 intercrosses involving the stripe rust and leaf rust resistant wheats were independently classified for responses to both diseases (Table 3). Except for two lines in the Condor and Opata 85 cross, all lines in each cross were homozygous resistant (HR). The two lines in the Condor and Opata 85 cross segregated for leaf rust and stripe rust resistances; this could have resulted from a technical error or from outcrossing. The F_2 populations from 10 intercrosses involving the resistant wheats also did not segregate for susceptibility to both rusts (Table 4). These results demonstrate that each cultivar carried at least one common gene that conferred resistance to stripe rust and leaf rust. Because five intercrosses involved Thatcher near-isogenic lines carrying *Lr34* (RL6058 or Line 920) and six crosses involved Condor, which carries only one gene (presumably *Lr34*), the common gene for stripe rust resistance in each cross must be very closely linked to *Lr34*.

In two crosses, Jupateco 73S with Jupateco 73R and Jupateco 73S with Condor, the distribution of F_3 lines (Table 5) for leaf rust response also conformed with that expected for segregation at one locus ($\chi^2$1:2:1 = 2.06; $P > 0.25$ for Jupateco 73S and Jupateco 73R; and $\chi^2 = 2.81$; $P > 0.1$ for Jupateco 73S and Condor). Because the same two crosses also carried one gene for stripe rust resistance (Table 2), the reactions of F_3 lines for stripe rust and leaf rust were compared (Table 5). Of the 29 F_3 lines classified as HR for leaf rust, 28 were HR and one was segregating (Seg) for response to stripe rust. Similarly, of the 29 lines HR for stripe rust, 28 were HR and one was Seg for leaf rust. All 64 lines Seg for leaf rust response were also Seg for stripe rust response, and all 23 lines homozygous susceptible (HS) for leaf rust were HS for stripe rust. Similar results were obtained in the Jupateco 73S and Condor cross, in which the

TABLE 2. Distribution of F_3 lines in the crosses of various adult plant stripe rust resistant wheats with stripe rust susceptible Jupateco 73S

Cultivar crossed with Jupateco 73S	Number of F_3 lines with reaction[a]			χ^2 ratio and value	P[b]	Number of genes
	HR	Seg	HS			
Jupateco 73R	29	65	23	1:2:1 = 2.06	>0.25	1
Condor	23	68	25	1:2:1 = 3.52	>0.10	1
Tobari 66	43	64	26	1:2:1 = 4.53	>0.05	1
Sonoita 81	57	62	4	7:8:1 = 1.96	>0.25	2
Tonichi 81	63	49	6	7:8:1 = 4.46	>0.05	2

[a] Reaction categories are HR = homozygous resistant; Seg = segregating; and HS = homozygous susceptible.
[b] P values higher than 0.05 indicate nonsignificant values of χ^2.

TABLE 3. Distribution of F_3 lines in various intercrosses of resistant wheats independently tested for adult plant responses to stripe rust and leaf rust

Cross	Number of F_3 lines with reaction[a]		
	HR	Seg	HS
Condor × Tonichi 81	39	0	0
Condor × Yaco	66	0	0
Condor × Parula	56	0	0
Condor × Trap	62	0	0
Condor × Myna	40	0	0
Condor × Opata 85	37	2	0
Tonichi 81 × Parula	60	0	0
Tonichi 81 × Myna	60	0	0
Parula × Myna	45	0	0
Tobari 66 × Trap	100	0	0
Sonoita 81 × Trap	100	0	0
Opata 85 × Trap	78	0	0
Frontana × Opata 85	91	0	0
Frontana × Trap	85	0	0
Frontana × Sonoita 81	101	0	0
Frontana × RL6058	79	0	0
Trap × RL6058	92	0	0

[a] Reaction categories are HR = homozygous resistant; Seg = segregating; and HS = homozygous susceptible.

TABLE 4. Number of plants in F_2 populations independently classified for stripe rust and leaf rust in intercrosses of resistant wheats that did not segregate for susceptibility

Cross	Number of resistant plants	
	Stripe rust	Leaf rust
Line 920 × Opata 85	345	215
Line 920 × Parula	289	305
Line 920 × Tonichi 81	316	278
Frontana × Yaco	304	345
Frontana × Parula	178	340
Frontana × Tonichi 81	184	260
Frontana × Myna	165	321
Trap × Yaco	148	295
Trap × Parula	156	340
Trap × Tonichi 81	168	315

response of only one of 116 lines did not match. Because no HS line to leaf rust or HR line to stripe rust, or vice-versa, was obtained, the three nonmatching lines among 233 classified in the two crosses could have resulted from misclassifications. For a population of 233 F_3 lines, the maximum recombination frequency (r), which could have remained undetected at 0.05 probability level, was 0.64%.

Comparisons of leaf rust and stripe rust responses were not possible for the other three crosses of resistant wheats with Jupateco 73S, because segregation occurred for additional, adult plant-effective genes for stripe rust resistance (Table 2) or leaf rust resistance (data not presented).

DISCUSSION

The *Lr34*-carrying cultivars Frontana (3) and Tezanos Pintos Precoz (R. P. Singh, *unpublished*) were extensively used by the Mexican-Rockefeller Program in the 1950s. Several CIMMYT-derived cultivars carried *Lr34* and adult plant resistance to stripe rust. *Lr34* is also linked with leaf tip necrosis (2). Singh (*unpublished*) failed to recover recombinants for the above two traits. In the present study, recombination did not occur between *Lr34* and the gene for stripe rust resistance. Therefore, the presence of leaf tip necrosis could aid selection for *Lr34* and/or stripe rust resistance. The linked segregation of *Lr34* and the gene for stripe rust resistance explained why all wheats with *Lr34*, including the three near-isogenic Thatcher lines in which *Lr34* was independently derived from three different wheats, also carried adult plant resistance to stripe rust. Johnson (5) and Rajaram et al (12) indicated that Anza carries durable resistance to stripe rust. Condor and Anza, closely related wheats, carry *Lr34* and display very similar seedling and adult plant stripe rust and leaf rust responses. The durable stripe rust resistance of Anza is conferred by the gene that is linked to *Lr34*. Like *Lr34*, the linked stripe rust resistance gene is partially effective but usually confers an adequate level of resistance. The effectiveness of this resistance has also been reported in Australia (R. A. McIntosh, *unpublished*), the United Kingdom (5), and is apparent in data from other parts of the world (CIMMYT database). However, at some locations, such as Quito (Ecuador) and Njoro (Kenya), resistance levels are often inadequate. Durable resistance to stripe rust occurs in some European winter wheats such as Little Joss, Hybride de Bersee, and Cappelle-Desprez (5), and U.S. wheats such as Gaines, Nugaines, and Luke (9,10). In each case, resistance was controlled by the additive effects of two or three adult plant genes (5,9,10). The possible association of one or more of these genes with chromosome 7D is not known. An adult plant resistance gene *Yr16* in Cappelle-Desprez was located on chromosome 2D (20). Published reports of the presence of *Lr34* in winter wheats are limited to Sturdy (2).

Because *Lr34* is located on chromosome 7D (1), the linked gene for stripe rust resistance must also be located on that chromosome. No other designated *Yr* gene occurs on chromosome 7D (7). Therefore, the gene closely linked to *Lr34* is hereby designated *Yr18*. It is possible that *Lr34* and *Yr18* are pleiotropic. However, additional studies that test this possibility are required. RL6058, RL6077, Line 920, Condor, Anza, or Jupateco 73R could be used as tester genotypes for *Yr18*.

Additional adult plant stripe rust resistance gene(s) were identified in the cultivars Sonoita 81 and Tonichi 81. Observations (not presented) on the F_3 lines from the cross Jupateco 73S and Tonichi 81 indicated that *Yr18* and the second adult plant gene may interact and produce enhanced levels of resistance. Such interactions are common for stripe rust (5,9,10). Therefore, adding partially effective, additive genes to cultivars already carrying *Yr18* or *Lr34* by selection for higher levels of resistance should be possible.

TABLE 5. Relationship of the adult plant leaf rust and stripe rust reactions of the F_3 lines in the crosses of Jupateco 73S with Jupateco 73R and Condor

		Stripe rust reaction		
Cross	Reaction[a]	HR	Seg	HS
Jupateco 73S × Jupateco 73R	HR	28	1	0
	Seg	1	64	0
	HS	0	0	23
Jupateco 73S × Condor	HR	23	1	0
	Seg	0	67	0
	HS	0	0	25

[a] Reaction categories are HR = homozygous resistant; Seg = segregating; and HS = homozygous susceptible.

LITERATURE CITED

1. Dyck, P. L. 1987. The association of a gene for leaf rust resistance with the chromosome 7D suppressor of stem rust resistance in common wheat. Genome 29:467-469.
2. Dyck, P. L. 1991. Genetics of adult-plant leaf rust resistance in 'Chinese Spring' and 'Sturdy' wheats. Crop Sci. 31:309-311.
3. Dyck, P. L., and Samborski, D. J. 1982. The inheritance of resistance to *Puccinia recondita* in a group of common wheat cultivars. Can. J. Genet. Cytol. 24:273-283.
4. Hanson, W. D. 1959. Minimum family sizes for the planning of genetic experiments. Agron. J. 51:711-715.
5. Johnson, R. 1988. Durable resistance to yellow (stripe) rust in wheat and its implications in plant breeding. Pages 63-75 in: Breeding Strategies for Resistance to the Rusts of Wheat. N. W. Simmonds and S. Rajaram, eds. CIMMYT, Mexico, D.F.
6. Johnson, R., Stubbs, R. W., Fuchs, E., and Chamberlain, N. H. 1972. Nomenclature for physiological races of *Puccinia striiformis* infecting wheat. Trans. Br. Mycol. Soc. 58:475-480.
7. McIntosh, R. A. 1988. Catalogue of gene symbols for wheat. Pages 1225-1313 in: Proc. Int. Wheat Genet. Symp. 7th. T. E. Miller and R. M. D. Koebner, eds. Inst. Plant Sci. Res., Cambridge, England.
8. McNeal, F. H., Konzak, C. F., Smith, E. P., Tate, W. S., and Russell, T. S. 1971. A uniform system for recording and processing cereal research data. USDA-ARS Bull. 34-121. 42 pp.
9. Milus, E. A., and Line, R. F. 1986. Number of genes controlling high-temperature, adult-plant resistance to stripe rust in wheat. Phytopathology 76:93-96.
10. Milus, E. A., and Line, R. F. 1986. Gene action for inheritance of durable, high-temperature, adult-plant resistance to stripe rust in wheat. Phytopathology 76:435-441.
11. 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. C. 26:496-500.
12. 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, D.F.
13. 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, D.F.
14. Singh, R. P. 1991. Pathogenicity variations of *Puccinia recondita* f. sp. *tritici* and *P. graminis* f. sp. *tritici* in wheat-growing areas of Mexico during 1988 and 1989. Plant Dis. 75:790-794.
15. 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.
16. Singh, R. P., and Rajaram, S. 1992. Genetics of adult-plant resistance to leaf rust in 'Frontana' and three CIMMYT wheats. Genome. 35:24-31.
17. Stakman, E. C., Stewart, D. M., and Loegering, W. Q. 1962. Identification of physiologic races of *Puccinia graminis* var. *tritici*. USDA-ARS Bull. E-617. Rev. ed. U.S. Gov. Print. Off., Washington, DC.
18. Villareal, R. L., and Rajaram, S. 1988. Semidwarf bread wheats: Names, parentages, pedigrees, and origins. CIMMYT, Mexico, D.F.
19. Wellings, C. R., McIntosh, R. A., and Hussain, M. 1988. A new source of resistance to *Puccinia striiformis* f. sp. *tritici* in spring wheats (*Triticum aestivum*). Plant Breed. 100:88-96.
20. Worland, A. J., and Law, C. N. 1986. Genetic analysis of chromosome 2D of wheat I. The location of genes affecting height, day-length insensitivity, hybrid dwarfism and yellow-rust resistance. Z. Pflanzenzüchtg. 96:331-345.