Plant Breeding **126**, 152—157 (2007)
doi:10.1111/j.1439-0523.2007.01283.x

Genetics of leaf rust resistance in three Americano landrace-derived wheat cultivars from Uruguay

J. A. Kolmer[1], L. M. Oelke[1] and J. Q. Liu[2]

[1]USDA-ARS Cereal Disease Laboratory, Department of Plant Pathology, University of Minnesota, St Paul, MN 5510; E-mail: jkolmer@umn.edu; [2]Pioneer Hi-Bred International Inc., Johnston, IA 50131, USA

With 3 tables

Received May 1, 2006/Accepted June 17, 2006
Communicated by R. A. McIntosh

Abstract

A genetic analysis of the landrace-derived wheat accessions Americano 25e, Americano 26n, and Americano 44d, from Uruguay was conducted to identify the leaf rust resistance genes present in these early wheat cultivars. The three cultivars were crossed with the leaf rust susceptible cultivar 'Thatcher' and approximately 80 backcross (BC1) F_2 families were derived for each cross. The $BC1F_2$ families and selected $BC1F_4$ lines were tested for seedling and adult plant leaf rust resistance with selected isolates of leaf rust, *Puccinia triticina*. The segregation and infection type data indicated that Americano 25e had seedling resistance genes *Lr3*, *Lr16*, an additional unidentified seedling gene, and one adult plant resistance gene that was neither *Lr12* nor *Lr13*, and did not phenotypically resemble *Lr34*. Americano 26n was postulated to have genes *Lr11*, *Lr12*, *Lr13*, and *Lr14a*. Americano 44d appeared to have two possibly unique adult plant leaf rust resistance genes.

Key words: *Triticum aestivum* — *Puccinia triticina* — wheat leaf rust — adult plant resistance — seedling resistance

The wheat accessions Americano 25e, Americano 26n, and Americano 44d, were derived from landraces in Uruguay in the early 20th century (Kohli 1986). Americano 26n and Americano 44d were released by 'A. Boerger' as cultivars in 1918. In Uruguay, these accessions were among the parents used for the early cultivars Artigas (Americano 25e/Americano 26n, 1924), Larranaga (Americano 25e/Pelon 33c, 1926), ACD 11 (Americano 44d/Pelon 33c, 1931) and Porvenir (Americano 26n/Pelon IV, 1935). In Argentina, Americano 26n, also known as Klein Universal I, was used as a parent for Klein Record (1925) and Klein H 51 (1929). Americano 44d, also known as Klein Universal II, was used as a parent for Klein Vencedor (1925), Klein Sin Rival (1925), Klein Ceres (1926) and Klein Titan (1925). Americano 25e was used as a parent for Klein San Martin (1926), Klein Mammuth (1927) and Klein Triunfo (1929). These early Uruguayan and Argentine wheats were subsequently used as parents for later cultivars in both countries and also in Brazil (Kohli 1986).

Wheat leaf rust, caused by *Puccinia triticina* Eriks., is an important disease of wheat in South America and worldwide. In recent years, increased susceptibility to leaf rust has been a major cause of cultivar replacement in Uruguay, as the leaf rust pathogen is genetically diverse and virulent races can rapidly increase (German 1996). Wheat cultivars from South America have been a rich source of important leaf rust resistance genes (Dyck et al. 1966, Dyck and Kerber 1977, 1981). Over 50 leaf rust resistance genes have been mapped and given gene designations (McIntosh et al. 2005), however relatively few genes still condition effective resistance to the leaf rust pathogen. This study was undertaken to identify the leaf rust resistance genes present in accessions of Americano 25e, Americano 26n and Americano 44d, in order to determine if new uncharacterized leaf rust resistance genes are possibly present in these three landrace-derived wheat cultivars.

Materials and Methods

Seed of accessions Americano 25e, Americano 26n and Americano 44d of wheat, *Triticum aestivum* L.,were obtained from Dr Silvia German, INIA – La Estanzuela, Uruguay. Seed of the three Americano accessions, and the leaf rust susceptible wheat 'Thatcher' (Tc), were planted in 15 cm diameter pots that were filled with steamed topsoil and grown in a growth cabinet with a mixture of fluorescent and incandescent bulbs with a 16-h day length. The plants were treated with Nutricote 13-13-13 micronutrients, Type 100 (Plantco Inc., Brampton, ON, Canada). At heading, the 'Thatcher' plants were emasculated, and pollen-shedding anthers from the Americano wheats were used to pollinate the 'Thatcher' female parent. The F_1 seed from each cross was planted and backcrossed as the male parent to 'Thatcher'. Approximately 80 $BC1F_1$ seed were obtained from each of the three crosses. The $BC1F_1$ plants were grown in a greenhouse and selfed to obtain $BC1F_2$ families.

The isolates of *Puccinia triticina* used in this study, BBBD [59-1], SBDG [59-2], THBJ [99-588], MJBJ [97-406], MCDS [00-520], CBBD [59-3], PBLR [91-1], KFBJ [97-1], TLGF [00-218], MBRK [97-253], MHDS [03-237], TCTD [03-190] and MCRK [03-267] were collected from wheat in the USA and Canada. The isolates were selected for their low infection types to specific *Lr* genes. The leaf rust isolates were stored and inoculated to seedling and adult plants using standard methods (Roelfs et al. 1992).

Fifteen seeds from each $BC1F_2$ family were planted in one 3.5 cm^2 plastic pot in vermiculite (Sunshine Strong-Lite Medium Vermiculite Preminum Grade, JR Johnson Horticultural Supplies, St Paul, MN, USA) and placed in a plastic tray, with six pots per tray. In subsequent tests, $BC1F_4$ lines that had been selected for seedling resistant infection type (IT), were planted in clumps of four to eight plants at the corners of 3.5 cm^2 plastic pots, with six pots per tray. A series of 22 'Thatcher' lines near isogenic for seedling leaf rust resistance genes were planted at the same time for comparison with infection types. The inoculation procedure and growth conditions in the greenhouse were standard procedures that have been previously described (Roelfs et al. 1992).

The seedlings were evaluated for infection type at 10–12 days after inoculation in greenhouse tests. The infection types were classified using a 0–4 scale used by Long and Kolmer (1989). Infection types from 0 to 2^+ were considered as low infection types, and infection types 3^+ to 4, were considered as high. Intermediate infection types

occurred with a 23 (mixture of two to three type uredinia) infection type. The four letter designations for each isolate were based on the three letter codes used in Long and Kolmer (1989), and a fourth letter based on high and low infection types produced by genes *LrB*, *Lr10*, *Lr14a*, and *Lr18*. In the $BC1F_2$ families, the ratio of families that segregated for plants with low infection types, to families homozygous for susceptible plants was used to determine the number of seedling resistance genes that were effective to each *P. triticina* isolate. A 1 segregating : 1 susceptible ratio of families indicated segregation of a single gene, as half of the families would have been derived from $BC1F_1$ plants that were heterozygous for a single resistance gene, and the other half would have been derived from $BC1F_1$ plants that were homozygous susceptible. Similarly, a 3 segregating : 1 susceptible ratio of families indicated segregation of two independent resistance genes since three-quarters of the families would have been derived from $BC1F_1$ plants that were heterozygous for one or two resistance genes, and one-quarter of the families would have been derived from $BC1F_1$ plants that were homozygous susceptible. A 7 segregating : 1 susceptible ratio of families indicated segregation of three independent resistance genes, as seven-eighths of the families would have been derived from $BC1F_1$ plants that were heterozygous for one, two, or three resistance genes, while one-eighth of the families would have been derived from plants that were homozygous susceptible. Goodness of fit of observed ratios to expected ratios was determined using a chi-squared test (Steel and Torrie 1980).

The $BC1F_2$ families from the three crosses were also evaluated in field rust plots for segregation of adult plant leaf rust resistance genes. Approximately 40–50 seeds of each family and a series of near-isogenic 'Thatcher' lines were planted in 2 m rows, spaced 30 cm apart in rust nursery plots at Winnipeg, Manitoba, Canada in 1996. Rows of a mixture of the leaf rust susceptible wheat cultivars Little Club and 'Thatcher', were planted perpendicular to the entries. The spreader rows were inoculated at the tillering stage with a mixture of common leaf rust isolates from Canada in 1995 (Kolmer 1997). The three most common leaf rust phenotypes in Manitoba and Saskatchewan in 1995 were MBRJ, TDGJ and MJBJ. Infections from the naturally occurring leaf rust epidemic in 1996 also occurred in the rust nursery plot. The three most common isolates in 1996 were MBDS, MBRJ and MCDS.

The severity ratings for the adult plants in the field rust nursery test were based on the modified Cobb scale (Peterson et al. 1948). Five to ten flag leaves of each wheat line were evaluated for rust severity and resistance response using the standardized scales (Roelfs et al. 1992). The $BC1F_2$ families and 'Thatcher' lines were rated for leaf rust when the susceptible line 'Thatcher' had leaf rust severity of at least 70%.

Seed from the Tc*2/Americano 25e F_2, and Tc*2/Americano 26n F_2 families that were homozygous susceptible to leaf rust isolate BBBD in the initial seedling tests were planted in 15 cm dia pots (four seeds/pot, two pots/family) and grown to maturity in a greenhouse or growth cabinet. Seeds from 14 Tc*2/Americano 44d F_2 families were planted 15 cm dia pots and grown to maturity in a growth cabinet or greenhouse. Flag leaves of the $BC1F_2$ adult plants were inoculated with isolate BBBD (0.5 mg/0.30 ml) at anthesis, when the flag leaves were fully emerged. Leaf rust infection types were evaluated 14 days after inoculation using the same scale as for the seedling tests. The number of pustules on each flag leaf relative to the 'Thatcher' susceptible control was also noted. Resistant $BC1F_2$ plants were selected and advanced to $BC1F_4$ lines by single seed descent. Flag leaves of adult plant $BC1F_4$ lines derived from Tc*2/Americano 26n were inoculated with leaf rust isolates MCRK, TCTD and BBBD, as these isolates have differential infection types on the 'Thatcher' lines with the adult plant resistance genes *Lr12* and *Lr13*. Adult plants of 'Thatcher', and the 'Thatcher' lines with *Lr12*, *Lr13* and *Lr34*, were also inoculated with the three isolates. Adult plants from derived $BC1F_4$ lines from Tc*2/Americano 25e, and Tc*2/Americano 26n that had been selected for adult plant resistance, 'Thatcher', and the 'Thatcher' line with *Lr34*, were inoculated with isolate THBJ in a greenhouse test.

The $BC1F_4$ lines from the three crosses that had been selected for adult plant resistance in the greenhouse and growth cabinet tests were also evaluated for adult plant resistance in a field rust nursery plot at St Paul, MN, USA in 2005. The $BC1F_4$ lines, and a series of 'Thatcher' lines, were planted perpendicular to a mixture of the leaf rust susceptible cultivars 'Thatcher', Max, Morocco, and Little Club. The spreader rows were inoculated with a mixture of leaf rust phenotypes MJBJ, THBJ, MCRK, TNRJ and TDBG from the 2004 *P. triticina* population in the USA. Infections from the naturally occurring leaf rust epidemic in 2005 also occurred in the rust nursery plot. The $BC1F_4$ lines were evaluated for leaf rust resistance when the susceptible control 'Thatcher' was rated at 70% leaf rust severity.

Results

The Tc*2/Americano 25e F_3 lines segregated in a 3 segregating : 1 susceptible ratio in seedling tests when tested with isolate BBBD, indicating that two independent genes conditioned resistance (Table 1). The segregating families had individual plants with ITs 0;, 2^+ and 3^+. Some families segregated for a single gene as these families had plants with ITs 0; and 3^+ in 3 : 1 ratios, whereas other families segregated for a different gene, with ITs of 2^+ and 3^+ also in 3 : 1 ratios. Ten individual $BC1F_2$ plants with 0; and 2^+ ITs from families that segregated 3 : 1 were selected and grown to obtain $BC1F_3$ lines. Two seeds from each $BC1F_3$ line were grown to obtain $BC1F_4$ lines that were used for additional seedling tests. The same $BC1F_2$ families when tested as seedlings with isolate SBDG, segregated 7 segregating : 1 susceptible indicating that three genes conditioned resistance. The same families that segregated for two genes for resistance to BBBD also segregated for resistance to SBDG. A third independent gene conditioned resistance to SBDG, but not to BBBD. The 15 families that segregated for resistance to SBDG, but were homozygous susceptible to BBBD, had low ITs of $;1^-$ to $;22^+$ to SBDG. Individual $BC1F_2$ plants with low ITs were selected from these families and also advanced to $BC1F_4$ lines. The $BC1F_2$ families segregated 7 segregating : 1 susceptible when tested as adults in a field rust nursery with a mixture of common isolates. This indicated that at least three genes conditioned field resistance in the families derived from Americano 25e.

Table 1: Segregation of leaf rust response in 'Thatcher'*2/Americano 25e and 'Thatcher'*2/Americano 26n derived F_2 families in seedling plants and in field plots

Cross	Leaf rust isolate	Gene(s) detected	Segregating families	Susceptible families	Expected ratio	χ^2
Tc*2/Americano 25e	BBBD	*Lr3*, *Lr16*	56	22	3 : 1	0.42 n.s.
	SBDG	*Lr3*, *Lr16*, +	75	7	7 : 1	0.84 n.s.
	Field mixture[1]		61	9	7 : 1	0.01 n.s.
Tc*2 Americano 26n	BBBD	*Lr11*	35	38	1 : 1	0.12 n.s.
	SBDG	*Lr11*, *Lr14a*	54	18	3 : 1	0.00 n.s.
	Field mixture		55	19	3 : 1	0.02 n.s.
Tc*2/Americano 44d	Field mixture		37	15	3 : 1	0.41 n.s.

[1]Mixture of leaf rust isolates from Canada in 1994 and 1995.

The Tc*2/Americano 26n F_2 families were classified 1 segregating : 1 susceptible when tested with isolate BBBD in seedling tests (Table 1) indicating that a single gene conditioned resistance to isolate BBBD. The low ITs in the segregating families varied from ;2^- to 2^+. Ten individual plants with low ITs were selected from different $BC1F_2$ families and advanced to $BC1F_4$ lines. The $BC1F_2$ families segregated 3 segregating : 1 susceptible when tested with isolate SBDG in seedling tests. The families that segregated for a single resistance gene to isolate BBBD also segregated for resistance to SBDG. A second genetically independent gene in the $BC1F_2$ families conditioned resistance to isolate SBDG, but not to BBBD. Individual plants with ITs ;1^- to ;2^- from the 19 families segregating for resistance to SBDG, but homozygous susceptible to BBBD, were advanced to $BC1F_4$ lines. The $BC1F_2$ families segregated 3 segregating : 1 susceptible when tested as adults in a field rust nursery with a mixture of common isolates indicating that at least two genes conditioned field resistance in the families derived from Americano 26n.

The Tc*2/Americano 44d F_2 families did not segregate when tested with isolates BBBD and SBDG, all were homozygous susceptible indicating that Americano 44d had no genes conditioning seedling resistance to these isolates. The $BC1F_2$ families segregated 3 segregating : 1 susceptible as adult plants in the field rust nursery indicating that two genes for adult plant resistance conferred resistance in Americano 44d.

Adult plants from 11 pooled Tc*2/Americano 25e F_2 families that were homozygous susceptible to isolate BBBD as seedlings, were inoculated with BBBD in a greenhouse test. The $BC1F_2$ plants from these families segregated 28 resistant : 61 susceptible plants, fitting a 3 : 5 ratio ($\chi^2 = 1.32$, P = 0.17). In a population of pooled $BC1F_2$ plants a 3 : 5 ratio is expected for the segregation of a single gene since one-half of the $BC1F_1$ plants would produce $BC1F_2$ progeny that would segregate in a 3 resistant : 1 susceptible ratio, while the other $BC1F_1$ plants would produce only homozygous susceptible progenies. This model also assumes that plants heterozygous for the resistance gene could be distinguished from plants that were homozygous susceptible. Resistant plants with ITs ;33^+ and 23, were selected and advanced by single seed descent to $BC1F_4$ lines for further testing. Adult plants from 16 pooled Tc*2/Americano 26n F_2 families that were homozygous susceptible as seedlings to isolate BBBD were tested with BBBD. The $BC1F_2$ plants from these families segregated 78 resistant : 45 susceptible plants, fitting a 39 : 25 ratio ($\chi^2 = 0.314$, P = 0.57). A 39 : 25 segregation ratio is expected for a $BC1F_2$ population if one-quarter of the $BC1F_1$ plants produced $BC1F_2$ progeny in 15 resistant : 1 susceptible ratios; one-half produced $BC1F_2$ progeny in a 3 resistant : 1 susceptible ratio, and one-quarter were homozygous susceptible. This model again assumes that plants heterozygous for resistance gene(s) can be distinguished from plants that are homozygous susceptible. Plants with ITs ;1^- to ;2^- were selected and advanced by single seed descent to $BC1F_4$ lines. Adult plants from 14 pooled families of Tc*2/Americano 44d tested with isolate BBBD segregated 56 resistant : 82 susceptible, which fit a single gene segregation ratio of 3 : 5 ratio ($\chi^2 = 0.55$, P = 0.45). Plants with IT of 23 were selected and advanced by single seed descent to $BC1F_4$ lines.

Derived Tc*2/Americano 25e and Tc*2/Americano 26n F_4 lines that had been selected for seedling resistance to isolates BBBD and SBDG were tested as seedlings to the isolates listed in Table 2. The 'Thatcher' near-isogenic lines with genes *Lr1*, *Lr2a*, *Lr2c*, *Lr3*, *Lr9*, *Lr16*, *Lr24*, *Lr26*, *Lr3ka*, *Lr11*, *Lr17*, *Lr30*, *LrB*, *Lr10*, *Lr14a*, *Lr18*, *Lr3bg*, *Lr14b*, *Lr20*, *Lr23*, *Lr28*, and *Lr33* were inoculated with the same isolates. Lines 5.1 and 80.1 derived from Tc*2/Americano 25e had low ITs of 0; to isolates BBBD and SBDG, and high IT of 3^+ to all other isolates, and these responses were identical ITs to the 'Thatcher' line with *Lr3*. Lines 57.1 and 58.1 from Tc*2/Americano 25e had ITs of 3^+ and 2^+3 to isolates MHDS, MJBJ, and THBJ, and low ITs to all other isolates; these ITs were similar to the 'Thatcher' line with *Lr16*. Line 68.1 from Tc*2/Americano 25e had low IT to only isolates SBDG (;1^-) and MCDS (;23). None of the tested 'Thatcher' lines had similar low infection types to only SBDG and MCDS. The 'Thatcher' line with *Lr23* had distinct low ITs to SBDG, and MCDS, however it had a low IT of ;12^- to isolate MHDS, and intermediate to high ITs to all other isolates. Line 4.1 derived from Tc*2/Americano 25e had very low ITs to isolates BBBD and SBDG, which indicated it had *Lr3*. However it also had low-intermediate IT to isolates MJBJ, THBJ and MBRK, indicating an additional seedling resistance gene that was not

Table 2: Seedling leaf rust infection types[1] of derived F_4 lines from Tc*2/Americano 25e and Tc*2/Americano 26n, and 'Thatcher' lines near-isogenic for leaf rust resistance genes

Cross	Line	BBBD	SBDG	THBJ	MJBJ	MCDS	CBBD	PBLR	KFBJ	TLGF	MBRK	MHDS	Gene(s)
Tc*2/Americano 25e	5.1	0;	0;	2^+3^+	33^+	3^+	3^+	3^+	3^+	3^+	3^+	3^+	*Lr3*
	80.1	0;	0;	33^-	3^+	3^+	3^+	3^+	3^+	3^+	3^+	3^+	*Lr3*
	57.1	1^+	1	2^+3	3^+	;23	1^+	2^+	1	1^+2^+	1^+2	3^+	*Lr16*
	58.1	1	;1^-	33^+	3^+4	2^+3	1^+	1^+2^+	1	1^+2	1^+2	3^+	*Lr16*
	68.1	3^+	;1^-	3^+	3^+	;23	3^+	3^+	3^+	3^+	3^+	3^+	+
	4.1	0;	0;	;2^+3	;123	;23	3^+	3^+	3^+	3^+	3^+2;	3^+	*Lr3*, +
Tc*2/Americano 26n	1.1	22^+	2^+	;22^+	—	2^+	—	;22^+	—	3^+	3^+	—	*Lr11*
	14.1	2^+	2^+	2^+	—	22^+	—	2^+	—	3^+	3^+	—	*Lr11*
	56.1	3^+	;2	3^+	—	3^+	—	;123	—	3^+	3^+	—	*Lr14a*
	26.1	3^+	;2	3^+	—	3^+	—	;123	—	3^+	3^+	—	*Lr14a*
	12.1	22^+	;1	2	—	2^+	—	;123	—	3^+	3^+	—	*Lr11*, *Lr14a*
	8.1	22^+	;2	22^+	—	22^+	—	;1^-	—	3^+	3^+	—	*Lr11*, *Lr14a*
'Thatcher' lines	RL 6002 Tc*Lr3*	0;	;	3^+	3^+	3^+	3^+	3^+	3^+	3^+	3^+	3^+	—
	RL 6011 Tc*Lr11*	2^-	2	2	2^-	2	22^-	2	2	3^+	3^+	;2^-	—
	RL 6013 Tc*Lr14a*	3^+	2	3^+	3^+	3^+	3^+	;123	3^+	3^+	3^+	3^+	—
	RL 6005 Tc*Lr16*	1^+	1	2^+3	3^+	1^+2	1^+2	22^+	;1	1^+	1^+	3	—
	RL 6012 Tc*Lr23*	2^+3	;	2^+3	22^+	;2^-	22^+	3	2^+3	2^+3	2^+3	;12^-	—

[1]As described in Long and Kolmer (1989).

Lr3 or *Lr16*, or the gene conditioning resistance to only SBDG and MCDS.

Lines 1.1 and 14.1 derived from Tc*2/Americano 26n had high ITs of 3^+ to isolates TLGF and MBRK, which are also virulent to the 'Thatcher' line with *Lr11* (Table 2). Lines 56.1 and 26.1 derived from Tc*2/Americano 26n had a mesothetic response of ;123 to isolate PBLR; a $;2^-$ IT to isolate SBDG, and high ITs to all other isolates. The 'Thatcher' line with *Lr14a* also had low-ITs to only PBLR and SBDG. The lines 12.1 and 8.1 had high-ITs to isolates TLGF and MBRK, mesothetic IT ;123 to isolate PBLR, and intermediate ITs ;2 to 22^+ to all other isolates. These lines most likely have both *Lr11* and *Lr14a*.

The F_4 derived lines from Tc*2/Americano 25e, Tc*2/Americano 26n, and Tc*2/Americano 44d that had been selected for adult plant resistance to isolate BBBD were tested for resistance in rust nursery field plots and as adult plants in greenhouse tests with the isolates listed in Table 3. The 'Thatcher' lines with adult plant resistance genes *Lr12*, *Lr13* and *Lr34*, were included in the tests. Pavon 76, a cultivar with genes *Lr1*, *Lr10*, *Lr13,* and *Lr46* was included in the field plot test. Adult plants of line 6.2 from Tc*2/Americano 26n had low IT to isolates TCTD and BBBD, and high IT to isolate MCRK, very similar ITs to the 'Thatcher' line with *Lr13*. Adult plants of line 3.1 derived from Tc*2/Americano 26n had low ITs to isolates MCRK, and BBBD, and high IT to isolate TCTD, very similar to the 'Thatcher' line with *Lr12*. Adult plants of lines 21.1 and 2.2 derived from Tc*2/Americano 26n had low ITs to TCTD, MCRK and BBBD, indicating that these lines had both *Lr12* and *Lr13*. Lines 6.2, 3.1, 21.1 and 2.2 were susceptible in the field plots.

Lines 11.1, 21.2 and 47.2 derived from Tc*2/Americano 25e had effective resistance in the field plot test, with ratings of 30–40 MR–MS (Table 3). Adult plants of line 11.1 had IT $;2^-$ when tested with isolate THBJ in the greenhouse. Lines 16.1, 23.1, 39.2 and 42.2, derived from Tc*2/Americano 44d, were resistant in the field test, with ratings 20 M to 20 MRMS. Adult plants of lines 16.1 and 23.1 had IT ;23 when tested with isolate THBJ in the greenhouse. Adult plants of lines 39.2 and 42.2 had a lower IT $;2^-$ in the greenhouse. The lines with adult plant resistance derived from Americano 25e and Americano 44d had neither *Lr12* nor *Lr13*, since the 'Thatcher' lines with these genes were susceptible in the field in 2005, and also since isolate THBJ is virulent to adult plants with these genes. The derived lines with adult plant resistance did not resemble the 'Thatcher' line with *Lr34*, since they had more chlorosis and necrosis in the greenhouse and field plot tests than the 'Thatcher' line with *Lr34*. Adult plants with *Lr34* typically have small to moderate size uredinia with little or no necrosis or chlorosis. The $BC1F_4$ lines with adult plant resistance derived from Americano 25e and Americano 44d were homozygous susceptible as seedlings with isolates BBBD and SBDG.

Discussion

Americano 25e was determined to have genes *Lr3*, *Lr16*, an additional seedling gene that conditioned resistance to isolates SBDG and MCDS, and at least one adult plant resistance gene that conditioned resistance to the current leaf rust population in rust nursery plots. Americano 26n was determined to have genes *Lr11*, *Lr12*, *Lr13* and *Lr14a*. Americano 44d had at least one and possibly two adult plant resistance genes conditioning resistance in rust nursery plots. Since the Americano wheat cultivars were used as parents in Uruguay in the 1920s to produce the first wheat cultivars specifically bred in South America, it is likely that the leaf rust resistance genes in these landrace-derived wheats can also be found in other wheat cultivars from the Southern Cone region.

Resistance gene *Lr16* is present in South American wheats such as the Uruguayan cultivars 'Estanzuela Pelon 90', 'Estanzuela Calandria' and 'Estanzuela Halcon' (German 1996), and the Argentine cultivar 'Buck Manatial' (Dyck 1989). The presence of *Lr16* in these wheat cultivars could trace to early wheats derived from Americano 25e, or also to more recent wheat lines derived from CIMMYT or North America. Resistance gene *Lr3* has been found in many wheats worldwide, including the Argentine cultivar Sinvalocho (Haggag and Dyck 1973). Gene *Lr11* is present in many of the soft red winter wheats in the USA (Kolmer 2003), and was also found in the Argentine cultivar 'El Gaucho' (Samborski and Dyck 1976). Gene *Lr12* has been found in wheats derived from

Table 3: Adult plant infection types[1] and field rust severities for F_4 lines from Tc*2/Americano 26n and Tc*2/Americano 44d

Cross	Line	MCRK	TCTD	BBBD	THBJ	Field	Gene(s)
	'Thatcher'	4	4	4	4	70 S	—
	RL 6011 Tc*Lr12*	22^+	3^+	2	4	70 S	—
	RL 4031 Tc*Lr13*	3^+	$;2^+$	;1	4	70 S	—
	RL 6058 Tc*Lr34*	23 f[2]	2^+	2 f	23 f	Tr[3]-20 M	—
	Pavon 76 *Lr1*, *Lr10*, *Lr13*, *Lr46*	—	—	—	—	Tr-20 M	
Tc*2/Americano 26n	6.2	3^+	$;2^+$	$;12^+$	—	70 S	*Lr13*
	3.1	2	3^+	22^+	—	70 S	*Lr12*
	21.1	2	$;2^+$	$;12^-$	—	80 S	*Lr12*, *Lr13*
	2.2	2	$;2^+$	;1	—	70 S	*Lr12*, *Lr13*
Tc*2/Americano 25e	11.1	—	—	—	$;2^-$	30–40 MRMS	+
	21.2	—	—	—	—	30 MRMS	+
	47.2	—	—	—	—	30 MRMS	+
Tc*2/Americano 44d	16.1	—	—	—	;23 f	20 M	+
	23.1	—	—	—	;23 f	20 MRMS	+
	39.2	—	—	—	$;2^-$	10–20 MRMS	+
	42.2	—	—	—	$;2^-$	20 M	+

[1]As described in Long and Kolmer (1989).
[2]Few pustules compared to 'Thatcher'.
[3]Tr, trace level of infection; $<1\%$.

'Chinese Spring' and 'Exchange' (Dyck et al. 1966, Dyck 1991). Athwal and Watson (1954) indicated that a wheat cultivar from Uruguay also had *Lr12*. Gene *Lr13* is found in many wheats from South America, particularly those derived from 'Frontana' (Dyck et al. 1966). However, wheat culitvars developed before 'Frontana', such as 'Klein Anniversario', and 'Klein Cometa' also had *Lr13* (McIntosh et al. 1995). Gene *Lr14a* originated from 'Yaroslav' emmer, and was transferred to common wheat through the cultivars 'Hope' and 'H-44' (McIntosh et al. 1995). It was surprising to find that *Lr14a* was present in the lines derived from Americano 26n, as it would seem unlikely that an early landrace-derived cultivar would have a gene originally derived from an emmer wheat.

The lines with adult plant resistances derived from Americano 25e and Americano 44d may have new uncharacterized gene(s) for leaf rust resistance. Based on isolate specificity, this resistance was not conditioned by *Lr12* or *Lr13*, and these lines had rust resistance phenotypes that were distinct from those characteristic of *Lr34* or *Lr46*, with more distinct chlorosis and necrosis. Americano 26n and Americano 44d were speculated to be early sources of *Lr13* and *Lr34* in South American wheats (Roelfs 1988). However, we found no evidence for the presence of *Lr34* in either of these cultivars. Results from using a microsatellite marker diagnostic for *Lr34* confirmed that Americano 25e, Americano 26n, and Americano 44d lacked *Lr34* (J. A. Kolmer, unpublished data). The field resistance in the $BC1F_2$ families derived from Americano 26n was likely due to *Lr12* and *Lr13*, as the 'Thatcher' lines with these genes were both partially resistant (80 MR S) in the rust nursery plots in Winnipeg in 1996. The segregation data from the $BC1F_2$ families in Winnipeg in 1996 suggested a single adult plant resistance gene in Americano 25e, and two genes in Americano 44d. Many of the $BC1F_2$ families derived from Americano 44d had late maturity compared with 'Thatcher', making field assessments of their responses more difficult, because late maturing families can appear to be resistant due to a shorter exposure time of comparable leaves with the leaf rust inoculum. The variation for infection type observed in the greenhouse test in adult plants of the $BC1F_4$ lines derived from Americano 44d supported the field data that more than one adult plant resistance gene was likely present in this cultivar. The results from a pooled F2 adult plant population of Tc*2/Americano 44d in growth cabinet tests indicating segregation of a single gene may have underestimated the number of genes as it was be difficult at times to distinguish ITs 2^+3^+ from IT 3^+. The field resistance in Americano 25e was most likely conditioned by *Lr16*, and an uncharacterized adult plant gene(s). The uncharacterized seedling resistance gene in Americano 25e conditioned resistance to only two isolates in the seedling tests, so it would be unlikely that this gene would contribute to field resistance. Gene *Lr3* does not condition effective field resistance since nearly every current leaf rust isolate in North America is virulent to this gene (Kolmer et al. 2005). As there is no pedigree information regarding the origin of the Americano wheats, it is impossible to speculate if the adult plant resistances in Americano 25e and Americano 44d are conditioned by the same or different genes. The 'Thatcher' lines with the adult plant resistances derived from Americano 25e and Americano 44d will be further crossed to 'Thatcher' to clarify the numbers of resistance genes and to develop mapping populations to determine their chromosome locations. Barcellos et al. (2000) described two uncharacterized adult plant leaf rust resistance genes in the Brazilian cultivar 'Toropi'. Mishra et al. (2005) described a new adult plant resistance gene in Indian germplasm that was not *Lr34*.

Early landrace-derived accessions, such as the Americano lines from Uruguay, would have been subjected to natural selection for a number of generations for yield stability and thus indirectly for disease resistance. These accessions are potentially new sources of leaf rust resistance genes. However, the early landrace accessions could also be highly heterogeneous as these initial selections were held and increased by different breeding programs in South America. Genetic analysis of other stocks of these three landrace-derived accessions may have indicated the presence of other leaf rust resistance genes such as *Lr34*, as this gene had been found in a number of wheat cultivars from South America.

References

Athwal, D. S., and I. A. Watson, 1954: Inheritance studies with certain leaf rust resistant varieties of *Triticum vulgare* VIII. Proc. Linn. Soc. N. S. W. **82,** 272—284.

Barcellos, A. L., A. P. Roelfs, and M. I. B. de Moraes-Fernandes, 2000: Inheritance of adult plant leaf rust resistance in the Brazilian wheat cultivar Toropi. Plant Dis. **84,** 90—93.

Dyck, P. L., 1989: The inheritance of leaf rust resistance in wheat cultivars Kenyon and Buck Manantial. Can. J. Plant Sci. **69,** 1113—1117.

Dyck, P. L., 1991: Genetics of adult-plant leaf rust resistance in 'Chinese Spring' and 'Sturdy' wheats. Crop Sci. **24,** 309—311.

Dyck, P. L., and E. R. Kerber, 1977: Inheritance of leaf rust resistance in wheat cultivars Rafaela and Eap 26127 and chromosome location of gene *Lr17*. Can. J. Genet. Cytol. **19,** 355—358.

Dyck, P. L., and E. R. Kerber, 1981: Aneuploid analysis of a gene for leaf rust resistance derived from the common wheat cultivar Terenzio. Can. J. Genet. Cytol. **23,** 405—409.

Dyck, P. L., D. J. Samborski, and R. G. Anderson, 1966: Inheritance of adult-plant leaf rust resistance derived from the common wheat varieties Exchange and Frontana. Can. J. Genet. Cytol. **8,** 665—671.

German, S. 1996: Genetics of leaf rust resistance of selected Uruguayan wheat cultivars. PhD Thesis. University of Manitoba, Winnipeg, Manitoba.

Haggag, M. E. A., and P. L. Dyck, 1973: The inheritance of leaf rust resistance in four common wheat varieties possessing genes at or near the *Lr3* locus. Can. J. Genet. Cytol. **15,** 127—134.

Kohli, M. M., 1986: Wheat varieties of the Southern Cone Region of South America. Names: Pedigrees and Origins. CIMMYT, Mexico D. F., Mexico.

Kolmer, J. A., 1997: Physiological specialization of *Puccinia recondita* f. sp. *tritici* in Canada in 1995. Can. J. Plant Pathol. **19,** 166—170.

Kolmer, J. A., 2003: Postulation of leaf rust resistance genes in selected soft red winter wheats. Crop Sci. **43,** 1266—1274.

Kolmer, J. A., D. L. Long, and M. E. Hughes, 2005: Physiological specialization of *Puccinia triticina* on wheat in the United States in 2003. Plant Dis. **89,** 1201—1206.

Long, D. L., and J. A. Kolmer, 1989: A North American system of nomenclature for *Puccinia recondita* f. sp. *tritici*. Phytopathology **79,** 525—529.

McIntosh, R. A., C. R. Wellings, and R. F. Park, 1995: Wheat Rusts: Atlas of Resistance Genes. CSIRO Australia, Kluwer Academic Publishers, Dordrecht, The Netherlands.

McIntosh, R. A., Y. Yamazaki, K. M. Devos, J. Dubcovsky, J. Rogers, and R. Appels, 2005: Catalogue of Gene Symbols for Wheat. KOMUGI Integrated Wheat Science Database. Available at: http://www.shigen.nig.ac.jp/wheat/komugi/genes/symbol/ClassList.jsp. Last accessed August 3, 2006.

Mishra, A. N., K. Kaushal, S. R. Yadav, G. S. Shirsekar, and H. N. Pandey, 2005: A leaf rust resistance gene, different from *Lr34*,

associated with leaf tip necrosis in wheat. Plant Breeding **124,** 517—519.

Peterson, R. F., A. B. Campbell, and A. E. Hannah, 1948: A diagrammatic scale for estimating rust intensity on leaves and stems of cereals. Can. J. Res. **26,** 496—500.

Roelfs, A. P., 1988: Resistance to leaf and stem rusts in wheat. In: N. W., Simmonds, and S. Rajaram (eds), Breeding Strategies for Resistance to the Rusts of Wheat, 10—22. CIMMYT, Mexico, D. F., Mexico.

Roelfs, A. P., R. P. Singh, and E. E. Saari, 1992: Rust Diseases of Wheat: Concepts of and Methods of Management. CIMMYT, Mexico, D. F., Mexico.

Samborski, D. J., and P. L. Dyck, 1976: Inheritance of virulence in *Puccinia recondita* on six backcross lines of wheat with single genes for resistance to leaf rust. Can. J. Bot. **54,** 1666—1671.

Steel, R. D., and J. H. Torrie, 1980: Principles and Procedures of Statistics. McGraw-Hill Book Co., New York.