Postulation of Leaf Rust Resistance Genes in Selected Soft Red Winter Wheats

J. A. Kolmer*

ABSTRACT

Leaf rust, caused by the fungus *Puccinia triticina* Eriks., is a major disease nearly wherever wheat (*Triticum* spp.) is grown in the USA. Soft red winter wheat (*T. aestivum* L.) cultivars with varying degrees of leaf rust resistance are grown in the southern USA. The objective of this study was to characterize the seedling leaf rust resistance present in a group of 35 soft red winter wheat cultivars and 17 breeding lines. Leaf rust infection types (ITs) produced on the cultivars and lines by 16 *P. triticina* isolates were compared with the ITs produced on a standard set of 'Thatcher' near-isogenic lines that differed for single leaf rust resistance genes. Seedling resistance genes *Lr1*, *Lr2a*, *Lr9*, *Lr10*, *Lr11*, *Lr18*, and *Lr26* were postulated to be present in the soft red winter wheat cultivars and lines. Adult plant leaf rust resistance for the cultivars and lines was assessed in field plots at two locations in North Carolina in 2000. Wheat cultivars postulated or genetically determined to have the adult plant resistance genes *Lr12* and *Lr34* had effective leaf rust resistance in the field plots. The soft red winter wheat cultivars and lines that had seedling resistance genes *Lr2a*, *Lr9*, and *Lr26* combined with adult plant resistance were highly resistant to leaf rust. Cultivars and breeding lines that had seedling resistance genes *Lr1*, *Lr10*, *Lr11*, and *Lr18* combined with adult plant resistance had moderate to low levels of leaf rust resistance.

Leaf rust of wheat, caused by the fungus *P. triticina*, is the most widespread and regularly occurring disease of wheat in the USA. The leaf rust pathogen can potentially overwinter on fall-sown wheat in an area from Texas to North Carolina. Localized infections of leaf rust that have survived the winter can often be observed in February in Texas, Louisiana, and Georgia, and occasionally as far north as North Carolina. Wheats grown in the southern USA require some degree of leaf rust resistance since the rust has the potential to be present from the early seedling stage through maturity and harvest. If leaf rust infections become established during the fall after seedling emergence and survive the winter, the rust will have the potential to increase rapidly at the same time the wheat crop is breaking dormancy. Early leaf rust infections usually lead to higher final rust severities, resulting in increased yield losses (Chester, 1946). Wheat cultivars with high levels of race-specific leaf rust resistance will eventually select virulent *P. triticina* races, which results in a loss of leaf rust resistance in these cultivars. Selection of virulent races can occur quickly in the southern USA since leaf rust has the potential to overwinter in much of this area.

Extensive genetic studies of leaf rust resistance have been conducted with hard red spring wheats grown in Canada (Dyck, 1993a,b; Kolmer, 1994; Liu and Kolmer, 1997) and to a much lesser degree with spring wheats grown in the USA (Ezzahiri and Roelfs, 1989). However, relatively few studies of leaf rust resistance have been conducted with soft red winter wheat cultivars that are grown in the southern USA. The objective of this study was to provide an initial description of leaf rust resistance in a group of soft red winter wheat cultivars and breeding lines that are adapted to the southern USA. The approach used in this study is based on gene-for-gene specificity (Flor, 1971; Person, 1959) and has been used to quickly determine the probable identity of seedling leaf rust resistance genes in a group of wheat lines. The low and high ITs produced by a diverse group of *P. triticina* isolates on the lines under study were compared with ITs produced by the isolates on a standard set of near-isogenic Thatcher wheat lines that differ for single leaf rust resistance genes. Leaf rust isolates that produce distinct low ITs on specific *Lr* genes in the Thatcher line series will also produce low ITs to those cultivars that have the same resistance genes. When more than one combination of resistance genes could give the same resistance phenotype, the combination with the lowest number of genes required was used to explain the phenotype. This method has been used to postulate the identity of *Lr* seedling resistance genes in CIMMYT spring wheats (Singh, 1993), hard red winter wheats (McVey and Long, 1993), and European winter wheats (Singh et al., 2001). In this study, the gene postulation method was used to identify the probable genes that condition seedling leaf rust resistance in a group of soft red winter wheat cultivars and breeding lines from the southern USA. Most of the cultivars and lines were included in the 1999 Official Variety Trial for wheat in North Carolina. The field leaf rust resistance of the cultivars and lines also was assessed at two locations in North Carolina and compared with wheat lines that have known seedling and adult plant leaf rust resistance genes to determine if adult plant leaf rust resistance was also present in the soft red winter wheats.

MATERIALS AND METHODS

Seed of 35 commonly grown soft red winter wheat cultivars (FFR 522, FFR 524, FFR 518, FFR 555W, FFR 566, Saluda, Cardinal, Becker, Shelby, Patton, Foster, Terral LA 422, Pocahontas, Jackson, Roane, Pioneer 2684, Pioneer 2691, Pioneer 2580, Pioneer 26R61, Pioneer 2643, Pioneer 26R24, Coker 9474, Coker 9766, Coker 983, Coker 762, Coker 9803, Coker 9704, Coker 9663, Coker 9835, NC Neuse, AGS 2000, SS550, SS520, and Sisson) and 17 advanced breeding lines (NC96-13141, NC96-7197, NC96-13965, NC96-14439, NC96-13129, NC96-13155, VA96W-270, VA96W-346, USG 3408, USG 3209, Pioneer XW681, Pioneer XW682, D95-7763, B93-0390, AR494B-2-2, AR584A-3-1, AR656-5-1, and GA90524-E35)

USDA-ARS, Cereal Disease Laboratory, Dep. of Plant Pathology, Univ. of Minnesota, St. Paul, MN, 55108. Received 7 June 2002. *Corresponding author (jkolmer@umn.edu).

Published in Crop Sci. 43:1266–1274 (2003).

Abbreviations: IT, infection type; M, mixture of small and large uredinia without necrosis; MR, moderate size uredinia with necrosis; MS, moderate size uredinia with chlorosis; R, small uredinia with necrosis; S, large uredinia; TR, trace level of uredinia.

were obtained directly from the respective breeding programs that produced the cultivars and lines (Table 1).

Seed of the cultivars and lines were planted in 40- by 30-cm fiber flats that were filled with a mixture of Metro Mix (Scotts Co., Marysville, OH), soil, and sand. The seeded flats were placed on a greenhouse bench at 18 to 25°C with 8 h of supplemental metal halide lighting. Ten to 15 seeds of each cultivar or line were seeded in clumps in an arrangement of rows with ≈4 cm between each entry in the fiber flats. Each flat could hold up to 30 entries. The seeded fiber flats were watered and then covered with polyethylene sheets for 4 d to ensure uniform distribution of moisture. After 4 d, when the coleoptiles had emerged, the polyethylene sheets were removed and the flats were watered on a daily basis. The seedling flats were fertilized with 20-20-20 NPK at 7 and 14 d after seeding. The 16 Thatcher lines listed in Table 2 were seeded separately in 30- by 20-cm fiber flats.

Sixteen isolates of *P. triticina* collected from Georgia, South Carolina, North Carolina, Virginia, and North Dakota in 1999 (Table 2) (Kolmer, 2002) were used to postulate the presence of seedling leaf rust resistance genes in the soft red winter wheat cultivars and breeding lines. The isolates included in the study were representative of the predominant leaf rust races present in the South Atlantic States (Kolmer, 2002), and other isolates were chosen on the basis of low or high IT to particular leaf rust resistance genes in the Thatcher wheat

Table 1. Pedigrees of soft red winter wheat cultivars and breeding lines tested for leaf rust resistance.

	Pedigree
Cultivars	
FFR 522	**IN71761/C797**
FFR 518	**Gore/Balkan//GA80573**
FFR 524	**GA831127//GA821264*3/GA79102**
FFR 555W	**Coker 76-35/3/Doublecrop//VA72-54-14/VA76-52-12//Coker 76-35/3/VA76-52-24/Coker 65-20/Arthur/Kavkaz//Coker 65-20/Arthur**
FFR 566	**Coker 78-23//Coker 68-15**
Saluda	**VA71-54-147/Coker 68-15**
Cardinal	**Logan*2/3/VA63-5-12/Logan//Blueboy**
Becker	**Hart/VA66-54-10**
Shelby	**FL 302/7/C81132/5/Southern Belle/4/Riley/Stoddard/Top/3/Arthur/6/Coker 983**
Patton	**Gentry//Yorkstar*2/Kitakomi Komugi/3/Purdue 8210B1-3-2**
Foster	**KY83-60/Tyler//KY83-75**
Terral LA 422	**FL302/IN76529A5-4**
Pocahontas	**Wheeler*2/C39//Saluda**
Jackson	**Saluda/Coker 762**
Roane	**VA71-54-147/Coker 68-15//IN65309C1-18-2-3-2**
Pioneer 2684	**IN946-A4-18-2/MO W7510//IN5517/3/Caldwell/4/Hunter**
Pioneer 2691	**S77/Abe//Pioneer 2551/3/Hunter**
Pioneer 2580	**Pioneer 2548sib//Pioneer W521/S76**
Pioneer 26R61	**Omega 78/S76/Arthur 71/3/Stadler//Redcoat/Wisconsin 1/5/Coker 747/6/Pioneer 2555sib**
Pioneer 2643	**IN4946A4/MOW7470//W521/3/2553sib//GA80**
Pioneer 26R24	**Aurora/Tyler//Pioneer 2550sib/3/Coker 983/4/Saluda/Coker 797**
Coker 9474	**IN7176A4-31-5-48/Wheeler**
Coker 9766	**Coker 762/Coker 76-16**
Coker 983	**Coker 68-15/4/Potomac/3/Coker 61-19*3//IN 6949A4/Blueboy**
Coker 762	**Coker 68-19/3/Coker 61-19*3/IN4946A-18-2-10-1//Blueboy/4/Coker 65-20*5/WI – 7 Transfer**
Coker 9803	**McNair 1003/Coker 916**
Coker 9704	**Coker 9803/Coker 983**
Coker 9663	**IN71761A4-31-5-48/FL 302**
Coker 9835	**Coker 85-20/Pioneer 2550**
NC Neuse	**Coker 86-29//Stella/CHD75680/3/Coker 9907**
SS550	**Coker 9803/Freedom**
Sisson	**Coker 9803/Freedom**
SS520	**FFR 555W/GA Gore**
AGS 2000	**Pioneer 2551/PF84301//FL 302**
Natchez	**Wakefield/Coker 9877**
Breeding lines	
NC96-13141	**Coker 86-29//Stella/CHD75680/3/Coker 9907**
NC94-7197	**Coker 83-23/Bradford/2/Chancellor/3/Coker 83-20/Caldwell/4/Siouxland/C39**
NC96-13965	**C8629//Stella/CHD45680/3/C8622**
NC96-14439	**Madison/SC840144**
NC96-13129	**Coker 86-29//Stella/CHD75680/3/Coker 9907**
NC96-13155	**Coker 86-29//Stella/CHD75680/3/Coker 9907**
VA96W-270	**Massy *2/Balkan/FFR 511W**
VA98W-346	**Coker 983//GA Andy/VA90-21-20**
USG3408	**Coker 65-20/Arthur*2//Axminster/9*Chancellor/3/2*Saluda/4/Va71-54-147/Coker 68-15**
USG3209	**Saluda/4/Massey*2/3/Massey*3/Balkan//Saluda**
Pioneer XW681	**Pioneer 2555*5/Salaami//Pioneer 2555*4/Stella/3/Pioneer 2555sib/FL 302**
Pioneer XW682	**FL 303sib/Pioneer 2555*4//Stella/Pioneer 2555sib**
B93-0390	**AL850046/Coker 86-23**
AR494B-2-2	**Pioneer 2550/Keiser**
AR584A-3-1	**FL 302/Coker 833/Hunter**
AR656-5-1	**Corin/3/FL 302//Coker 833/Hunter**
GA90524-E35	**Coker 9835//FL302/Gore**
Check Cultivars	
Monon	**Minhardi/Wabash/3/Chinese Spring/Michigan AmberB45//Purplestraw/4/CI 11512/Trumbull/7/Kawvale/5/Fultz/Hungarian//W38/3/ Wabash/4/Fairfield/6/Trumbull*3//Hope/Hussar**
Coastal	**Frondoso//Redhart 3/Noll 28**
Caldwell	**Benhur sib*2/Siete Cerros**
Knox	**Minhardi/Wabash/3/Chinese Spring/Michigan AmberB45//Purplestraw/4/CI 11512/Trumbull**
Sturdy	**Sinvalocho/Witchita//Hope/Cheyenne/3/2*Witchita/4/Seu Seun 27**
Bezostaya 1	**Lutescens 17/Skorospelka**

Table 2. Seedling ITs† of Thatcher near isogenic lines inoculated with 16 virulence phenotypes of the leaf rust fungus *Puccinia triticina* and field severity and response‡ to leaf rust infections at Kinston, NC, in 2000.

Thatcher line-*Lr* gene	FBMT 31-3A	MBGD 21-4	MDRJ 12-1A	TCRJ 3-3A	LBBK 66-1	MBRK 4-2A	MBDS 20-3A	TBRJ 9-1B	MBRJ 16-2B	TFGJ 96-3	KCGD 87-3	TNRJ 86-3	MCGJ 102-1	TLGF 1-1B	MCRK 6-1A	PNMQ CA 80-1	Field Severity Kinston
RL 6003-*Lr1*	;	4	3+	4	3+	3+	3+	3+	3+	3+	;	3+	3+	3+	3+	3+	90 S
RL 6016-*Lr2a*	;1	0	0	4	0	;	0	3+	0	3+	3+	3+	0	3+	0;	;1−	20 M
RL 6047-*Lr2c*	4	;1	;1	4	;1−	;	;1	3+	;1−	3+	3+	3+	;1−	3+	;	3+	30 MR S
RL 6002-*Lr3*	4	4	3+	4	;	3+	3+	3+	3+	3	3+	3+	3+	3+	3+	3+	90 S
RL 6007-*Lr3ka*	4	;2−	3+	4	;2−	3	;2−	3+	3+	;2−	;2−	3+	;2−	2−	3+	3+	70 MS
RL 6010-*Lr9*	0	0	;1−	0	0	0	;	0	0	0	0	3+	0	3+	0	3+	10 MR
RL 6004-*Lr10*	3	;	3+	4	3+	3+	3+	3+	3+	3+	;1	3+	3+	;1−	3+	3+	50 MS
RL 6053-*Lr11*	2−	4	3+	4	;2−	3	2−	3+	3+	3+	3	3+	3+	3	3+	22+	90 S
RL 6013-*Lr14a*	3	3	3+	4	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	;	90 S
RL 6005-*Lr16*	;	;1	;1−	1	;	;1−	;1−	;1−	;1−	;1−	;	;1−	;1−	;1−	;1−	;1−	40 MS
RL 6008-*Lr17*	;1	;1	;1−	2−	;	;1−	3+	;2−	;	;1−	;1−	;1−	;	;1−	;1−	2+	5 R
RL 6009-*Lr18*	3	2+	2+	2	3+	3+	22+	2+	2+	2+	2+	2+	2+	2+	3+	;2+	50 S
RL 6064-*Lr24*	;	;	3+	0	;	;	0;	2+	;	3+	;	3+	;	;	;	3+	0
RL 6078-*Lr26*	;	;	;	3	2+	2−	;1−	;1−	;	3+	3	;	3+	;1−	3	;1−	30 MR
RL 6049-*Lr30*	3	2	3+	4	2−	3	22+	3+	3+	2	2−	3+	2−	2−	3	3+	40 MS
RL 6051-*LrB*	3	22+	2+	2	2	2	3	2+	2+3	2	2	22+	2+3	2+	2+	3+	40 MS

† Infection types: 0 = no flecks or uredinia, 0; = faint hypersensitive flecks, ; = hypersensitive flecks, 1 = small uredinia with necrosis, 2 = small uredinia with chlorosis, 3 = moderate size uredinia, 4 = large uredinia, + indicates slightly larger uredinia, − indicates slightly smaller uredinia, ITs with two symbols denote a range in IT: 2^{2+} indicates a mixture of 2 size uredinia with chlorosis and slightly larger uredinia with chlorosis.

‡ Rust response: 0 = no flecks or uredinia, TR = trace level of uredinia, R = small uredinia with necrosis, M = mixture of small and large uredinia without chlorosis, MR = moderate size uredinia with necrosis, MS = moderate size uredinia with chlorosis, S = large uredinia.

near-isogenic series of leaf rust differentials. The isolates were assigned four-letter race designations based on high and low IT to 16 Thatcher differential lines (Long and Kolmer, 1989). When the seedlings were 7 to 9 d old, flats of seedlings of the 35 cultivars, 17 breeding lines, and 16 Thatcher lines were inoculated with each test isolate of *P. triticina* by spraying the seedlings with an atomized suspension of ≈1 mg of urediniospores mixed with 0.5 mL of Soltrol 170 oil. After 1 h to allow the oil to evaporate, the inoculated seedling flats were placed in a humidity chamber designed to maintain free moisture on the wheat seedlings at ≈20°C for 16 h, and were then returned to the greenhouse bench. The wheat cultivars, breeding lines, and Thatcher lines were evaluated 12 d after inoculation for IT using the scale in Long and Kolmer, 1989: 0 = no hypersensitive flecks, necrosis, or uredinia—0; = faint hypersensitive flecks—; = distinct hypersensitive flecks—1 = small uredinia surrounded by distinct necrosis—2 = small uredinia surrounded by distinct chlorosis—3 = moderate size uredinia without chlorosis or necrosis—4 = very large uredinia without chlorosis or necrosis. Mixtures of two or more IT were recorded as ITs with the most common IT listed first. Designations of + and − were added as superscripts to the 0 to 4 IT to indicate larger and smaller uredinia than normal, respectively. Generally, IT 0 to 2^+ were considered as low IT, and IT 3 to 4 were considered as high IT. For some isolates on certain wheat lines, IT of 2^+ were considered as high IT, since many or all of the other rust isolates on that particular wheat line had very low IT of 0 to 0;, and none of the isolates produced a 3 to 3^+ IT on those lines. The presence of leaf rust seedling resistance genes in the wheat cultivars and breeding lines was postulated on the basis of comparing low and high IT to the IT of the *P. triticina* isolates on the Thatcher differential lines in Table 1.

The wheat cultivars and breeding lines were planted in field plots at Kinston, NC, and Plymouth NC, in mid-October 1999. Each cultivar and line was planted in a 4-row plot, 1.2 m in length. Each plot was 0.5 m to 1 m apart. Thirty to 40 seeds were planted per plot. Nine cultivars were planted only at Kinston, one cultivar and one breeding line were not planted at either location; and one breeding line was not planted at Kinston. The Thatcher lines in Table 1 were seeded in the same manner in plots at Kinston NC. Seed of the cultivars Monon, Coastal, Caldwell, Knox, Sturdy, and Bezostaya 1 were also seeded at the two locations. These cultivars have been postulated, or have been shown to have adult plant leaf rust resistance genes. Leaf rust infections from the naturally occurring *P. triticina* population in the southeastern USA (Long et al., 2002) were first observed in the plots in mid March 2000. Leaf rust severity and resistance response on the entries were recorded on May 9 at Plymouth and May 15 at Kinston, when the susceptible check cultivar Thatcher had leaf rust severity of 70 to 90%. Powdery mildew and barley yellow dwarf diseases were at low levels at both locations and did not interfere with the leaf rust infections.

RESULTS

Seedling Resistance

Infection types of the 16 *P. triticina* isolates used in this test to the 35 cultivars are listed in Table 3. The ITs to FFR 566 will be used as a detailed example of the logic used to postulate *Lr* seedling resistance genes. Isolates TCRJ and TNRJ produced high IT of 3^+ to cultivar FFR 566. Therefore, the genes *Lr9*, *Lr17*, *Lr18*, *Lr24*, *Lr26*, and *LrB*, which confer resistance to TCRJ

Table 3. Seedling ITs† of soft red winter wheat cultivars inoculated with 16 virulence phenotypes of the leaf rust fungus *Puccinia triticina*.

Line/cultivar	Postulated *Lr* gene(s)	FBMT 31-3A	MBGD 21-4	MDRJ 12-1A	TCRJ 3-3A	LBBK 66-1	MBRK 4-2A	MBDS 20-3A	TBRJ 9-1B	MBRJ 16-2B	TFGJ 96-3	KCGD 87-3	TNRJ 86-3	MCGJ 102-1	TLGF 1-1B	MCRK 6-1A	PNMQ CA80-1
FFR 552	*Lr9*, *Lr18*	0	0	0	0	0	0	0;	0;	0;	0	0	;2^{-}	0	3	0;	;2^{-}
FFR 518	*Lr9*, *Lr10*	0	0	0	0	0	0	0;	0;	0;	0	0	3^{+}	0	;2	0;	3
FFR 524	*Lr18*	3^{+}	12^{-}	12^{-}	2	3^{+}	3^{+}	2^{-}	;2^{-}	2	2	;2^{-}	2	2^{-}	3^{+}	3^{+}	;1
FFR 555W	*Lr10*	3^{+}	0;	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	0;	3^{+}	3^{+}	0;	3^{+}	3^{+}
FFR 566	*Lr1*, *Lr2a*	0	0;	0;	3^{+}	0	0	0;	2^{+}	0;	2^{+}	0	3^{+}	0	22^{+}	0;	;2
Saluda	*Lr11*	;1	33^{+}	3^{+}	3^{+}	;2	3^{+}	;2^{-}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	2^{+}
Cardinal	*Lr10*	3^{+}	;	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	;	3^{+}	3^{+}	0;	3^{+}	2^{+}
Becker	*Lr11*	2	3^{+}	3^{+}	3^{+}	;2^{-}	3^{+}	2	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	2^{+}
Shelby	*Lr10*	3^{+}	;	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	0;	3^{+}	3^{+}	0;	3^{+}	3^{+}
Patton	*Lr10*, *Lr26*	0	;	;	3^{+}	;2^{-}	;2^{-}	;2^{-}	;22^{+}	;	3^{+}	0;	;	3^{+}	0;	3^{+}	0;
Foster	*Lr10*, *Lr26*	0	;	;1^{-}	3^{+}	0;	;1	;2	;22^{+}	;	3	0	;1^{-}	3^{+}	0	3^{+}	;1^{-}
Terral LA 422	?	3^{+}	2^{-}	2^{-}3^{+}	3^{+}	2^{+}3	;12^{-}	22^{+}	3^{+}	3^{+}	3^{+}	3^{+}	2	3^{+}	;2^{-}	0;	;1
Pocahontas	*Lr11*	;2	3^{+}	3^{+}	3^{+}	;2^{-}	3^{+}	2^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	;
Jackson	*Lr1*, *Lr11*	0	33^{+}	3^{+}	3^{+}	0;	3^{+}	2	3^{+}	3^{+}	3^{+}	0	3^{+}	3^{+}	3^{+}	3^{+}	;
Roane	–	3^{+}	3^{+}	33^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3
Pioneer 2684	*Lr10*, *Lr18*	3^{+}	0;	;	;12^{-}	3^{+}	3^{+}	0;	;1^{-}	;1^{-}	;1	0;	;	;1^{-}	0;	3^{+}	0;
Pioneer 2691	*Lr1*, *Lr3*, *Lr18*	0	;2	;2^{-}	;2^{-}	0	3^{+}	2^{-}	;2	;2	;2	0	;2^{-}	;2	33^{+}	3	3^{+}
Pioneer 2580	*Lr11*	;	3^{+}	3^{+}	3^{+}	0	3^{+}	;1^{-}	3	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	3^{+}	;2
Pioneer 26R61	*Lr11*, *Lr26*	0	;	;	2^{+}	;2	;2	;1	;2^{-}	;	3^{+}	3^{+}	;	3^{+}	0	3^{+}	;
Pioneer 2643	*Lr1*, *Lr18*	0	;	;	;	2^{+}	3^{+}	;	;	;	;	;	;	;	3^{+}	3^{+}	;
Pioneer 26R24	*Lr18*	3^{+}	2^{+}	;1^{-}	;1	3^{+}	3^{+}	;	;2	;1^{-}	;1^{-}	;2^{-}	;2	;2^{-}	3^{+}	3^{+}	;1
Coker 9474	*Lr2a*, *Lr9*	0	0	0	0	0	0	0	0	0	0	0	3^{+}	0	3^{+}	0;	0;
Coker 9766	*Lr2a*, *Lr9*	0	0	0	0	0	0	0	0	0	0	0	3^{+}	0	3^{+}	0;	0;
Coker 983	*Lr2a*, *Lr9*	0	0;	0;	0	0	0	0	0	0;	0	0	3^{+}	0	3^{+}	0;	0;
Coker 762	*Lr2a*, *Lr9*	0	0	0	0	0	0	0	0	0	0	0	3^{+}	0	3^{+}	0;	0;
Coker 9803	*Lr10*, *Lr18*	3^{+}	;	;1	;2	3^{+}	3^{+}	;1^{-}	;1^{-}	2	;2^{-}	0;	;	;2^{-}	;	33^{+}	;1^{-}
Coker 9704	*Lr10*, *Lr18*	3^{+}	;	2^{-}	3^{+}	3^{+}	3^{+}	;1^{-}	3^{+}	2	;2^{-}	0;	;1^{-}	;2^{-}	;	3^{+}	;1
Coker 9663	*Lr2a*, *Lr9*, *Lr10*	0	0;	0	0	0	0	0;	0	0	0	0;	3^{+}	0	;	0;	0;
Coker 9835	*Lr2a*, *Lr9*	0	0;	0;	0	0	0	0	0	0;	0	0	3^{+}	0	3^{+}	0;	0;
NC Neuse	*Lr1*, *Lr2a*	0	0;	0;	2^{+}	0	0	0;	2^{+}	0;	2^{+}	0	2^{+}	0	2^{+}	0;	0;
AGS 2000	*Lr10*, *Lr26*	0	0;	;1^{-}	3^{+}	;1^{-}	;1^{-}	2	;1^{-}	;	3^{+}	;	;	3^{+}	;	2^{+}	0;
SS 550	*Lr26*	;	;	;1	3^{+}	2	;1^{-}	2	2	;1^{-}	3^{+}	3^{+}	;1^{-}	3^{+}	0;	3^{+}	;2
SS 520	*Lr11*, *Lr18*	;2	2	2^{-}	;2	;1	3^{+}	;2^{-}	;2	;1^{-}	;1	;1^{-}	;2	;2^{-}	33^{+}	3^{+}	;1
Sisson	*Lr26*	;	0;	;	3^{+}	22^{+}	;1^{-}	22^{+}	2	;1^{-}	3^{+}	3^{+}	;1^{-}	3^{+}	0;	3^{+}	;2
Natchez	*Lr9*, *Lr10*	0	0;	0	0	0	0	0	0	0	0	0	3^{+}	0	0	0;	3

† Infection types: 0 = no flecks or uredinia, 0; = faint hypersensitive flecks, ; = hypersensitive flecks, 1 = small uredinia with necrosis, 2 = small uredinia with chlorosis, 3 = moderate size uredinia, 4 = large uredinia, $^{+}$ indicates slightly larger uredinia, $^{-}$ indicates slightly smaller uredinia, ITs with two symbols denote a range in IT: 22^{+} indicates a mixture of 2 size uredinia with chlorosis and slightly larger uredinia with chlorosis.

and/or TNRJ (Table 2), cannot be present in FFR 566. Of the remaining possible genes, *Lr2a* conditioned very low IT of 0 or 0; to the M-isolates, and genes *Lr1* and *Lr10* conditioned low IT of ; and ;1, respectively, to KCGD. However, FFR 566 had an IT of 22^+ to race TLGF, which had a low IT of $;1^-$ to *Lr10*, and an IT of 3^+ to *Lr1*. Therefore, FFR 566 was postulated to have *Lr1* and *Lr2a*. The 22^+ IT of FFR 566 to TLGF cannot be explained by the presence of *Lr1* and *Lr2a*; however, it is possible that the genetic background of FFR 566 (adult plant leaf rust resistance genes) may have lowered the seedling IT to race TLGF. NC Neuse had the same pattern of high and low IT to the 16 *P. triticina* isolates, which indicated that it also most likely had resistance genes *Lr1* and *Lr2a*.

The cultivar Jackson had low IT of 0 to 2 to isolates FBMT, LBBK, KCGD, MBDS, and PNMQ, and high IT of 3^+ to all other isolates. FBMT and KCGD are avirulent to *Lr1*, and LBBK, MBDS, and PNMQ are avirulent to *Lr11*. Jackson most likely has *Lr1* and *Lr11*. Pioneer 2691 had high IT of 3 to 3^+ to isolates MBRK, TLGF, MCRK, and PNMQ, and low IT of 0 to ;2 to all other isolates. MBRK, MCRK, and TLGF are virulent to *Lr1*, *Lr3*, and *Lr18*, while PNMQ is virulent to *Lr1* and *Lr3*. LBBK is avirulent to *Lr3*, and virulent to *Lr1* and *Lr18*. Pioneer 2691 may have *Lr1*, *Lr3*, and *Lr18*. The 3^+ IT of PNMQ to Pioneer 2691 may have been a misclassification, since *Lr18* can be particularly temperature sensitive in expression of resistance in greenhouse conditions. Pioneer 2643 had high IT of 2^+ to 3^+ to isolates LBBK, MBRK, TLGF, and MCRK, and low IT of 0 to; to all other isolates. Pioneer 2643 most likely has *Lr1* and *Lr18*. The Coker wheats 9474, 983, 9766, 762, and 9835 had high IT of 3^+ to isolates TNRJ and TLGF, and low IT of 0 to 0; to all other isolates. TNRJ and TLGF are virulent to *Lr2a* and *Lr9*. The Coker wheats 9474, 983, 9766, 762, and 9835 most likely have *Lr2a* and *Lr9*. Coker 9663 had low IT of ; to TLGF and low IT of 0 to 0; to all other isolates except TNRJ, which had a high IT of 3^+. Since TLGF had a low IT to *Lr10* and Coker 9663 and TNRJ had a high IT, Coker 9663 most likely has *Lr2a*, *Lr9*, and *Lr10*. FFR 522 had a high IT of 3 to TLGF, low IT of $;2^-$ to both TNRJ and PNMQ, and low IT of 0 to 0; to all other isolates. FFR 522 most likely has *Lr9* and *Lr18* since TLGF has a high IT to both genes, and TNRJ and PNMQ had low IT to *Lr18*. FFR 518 and Natchez had high IT of 3 to 3^+ to isolates TNRJ and PNMQ, low IT of ;2 to TLGF, and low IT of 0 to 0; to all other isolates. Since TNRJ and PNMQ had high IT to both *Lr9* and *Lr10*, and TLGF had high IT to *Lr9* and low IT to *Lr10*, FFR 518 and Natchez most likely have *Lr9* and *Lr10*.

FFR 555W, Cardinal, and Shelby had low ITs of ; to 0; to isolates MBGD, KCGD, and TLGF, which are avirulent to *Lr10*, and high ITs of 2^+ to 3^+ to all other isolates. FFR 555W, Cardinal, and Shelby most likely have *Lr10*. Pioneer 2684 and Coker 983 had high ITs of 3^+ to FBMT, LBBK, MBRK, and MCRK, and low ITs of 0; to ;2 to all other isolates. FMBT, LBBK, MBRK, and MCRK are virulent to *Lr10* and *Lr18*. Pioneer 2684 and Coker 9803 most likely have *Lr10* and *Lr18*. Coker 9704 had low ITs of 0; to ; to isolates MBGD, KCGD, and TLGF, which indicated that Coker 9704 may have *Lr10*. Coker 9704 had IT of 3^+ to isolates LBBK, MBRK, and MCRK, which are virulent to *Lr10* and *Lr18*, and high IT of 3^+ to isolates TCRJ and TBRJ that had low IT to *Lr18*. Coker 9704 most likely has *Lr10* and may also have *Lr18*. The temperature instability of resistance expression for *Lr18* may have resulted in IT for TCRJ and TBRJ to Coker 9704 being misclassified. Coker 9704 had low IT of ;1 to 2 to all other isolates that had high IT to *Lr10* and low IT to *Lr18*. Patton, Foster, and AGS 2000 had high ITs of 2^+ to 3^+ to isolates TCRJ, TFGJ, MCGJ, and MCRK, which had high IT to *Lr10* and *Lr26*. Patton, Foster, and AGS 2000 had low IT to KCGD, which had high IT to *Lr26* and low IT to *Lr10*. Patton, Foster, and AGS 2000 had low IT of 0 to ;1 to all other isolates. Patton, Foster, and AGS 2000 most likely have *Lr10* and *Lr26*. Saluda, Becker, Pocahontas, and Pioneer 2580 had low IT of ;1 to 2^+ to isolates FBMT, LBBK, MBDS, and PNMQ, which had IT of $;2^-$ to 22^+ to *Lr11*. Saluda, Becker, Pocahontas, and Pioneer 2580 most likely have *Lr11*. Pioneer 26R61 had high ITs of 2^+ to 3^+ to isolates TCRJ, TFGJ, KCGD, MCGJ, and MCRK that had high IT to *Lr11* and *Lr26*, and low IT of 0 to ;2 to all other isolates. Pioneer 26R61 most likely has *Lr11* and *Lr26*. Pioneer 26R24, and FFR 524 had high IT to isolates FBMT, LBBK, MBRK, TLGF, and MCRK, which had high IT to *Lr18*, and low ITs of $;1^-$ to 2^+ to all other isolates. Pioneer 26R24 and FFR 524 most likely have *Lr18*. SS 520 had high ITs of 3 to 3^+ to isolates TLGF, MBRK, and MCRK, and low ITs of ;1 to 2 to all other isolates. TLGF, MBRK, and MCRK are the only isolates with high IT to *Lr11* and *Lr18*, which are likely present in SS 520. SS 550 and Sisson had a high IT of 3^+ to isolates TCRJ, TFGJ, KCGD, MCGJ, and MCRK, and low ITs of ; to 22^+ to all other isolates. TCRJ, TFGJ, MCGJ, and MCRK have high IT to *Lr26* that is likely present in SS 520 and Sisson. Roane had high ITs of 3 to 3^+ to all isolates, which indicated that Roane lacked any seedling *Lr* genes. Terral LA 422 had high IT of 3^+ to isolates FBMT, TCRJ, TBRJ, MBRJ, TFGJ, KCGD, MCGJ, IT of 2^+3 to LBBK and MDRJ, and low ITs of 0; to 2 to the other isolates. It was not possible to designate *Lr* genes for Terral LA 422 using the low and high ITs generated by the isolates used in this study.

The ITs of 17 soft red winter wheat breeding lines to the 16 *P. triticina* isolates are listed in Table 4. ARB494B-2-2 had ITs 0 and 0; to isolates FBMT and KCGD, which are avirulent to *Lr1*. ARB494B-2-2 most likely has *Lr1*. USG3408 had low ITs of 0 to ;2 to isolates FBMT, LBBK, MBDS, KCGD, and PNMQ that had low IT to *Lr1* or *Lr11*. USG3408 most likely has *Lr1* and *Lr11*. USG3209 had high IT of 3^+ to isolates TCRJ, TFGJ, MCGJ, and MCRK, which have high IT to *Lr1* and *Lr26*. USG3408 had low IT of 0 to ;2 to all other isolates. USG3408 most likely has *Lr1* and *Lr26*. NC96-13141 and B93-0390 had high ITs to isolates TNRJ and TLGF, and low ITs to all other isolates. Isolates TNRJ and TLGF are virulent to *Lr2a* and *Lr9*. NC96-13141 and B93-0390 most likely have *Lr2a* and *Lr9*. GA90524-

E35 and NC96-13129 had a high IT of 3^+ to TNRJ and a low IT of 0 to ; to all other isolates. TNRJ is virulent to genes *Lr2a*, *Lr9*, and *Lr10*, which are most likely in GA90524-E35 and NC96-13129. AR656-5-1 had high IT of 3 to 3^+ to isolates TCRJ, TBRJ, TFGJ, and TNRJ, which are virulent to *Lr2a* and *Lr10*. AR656-5-1 had low ITs of 0 to ;1 to all other isolates. AR656-5-1 most likely has *Lr2a* and *Lr10*. AR584A-3-1 had high ITs of 3 to 3^+ to isolates TNRJ and PNMQ, and low ITs of 0 to 0; to all other isolates. TNRJ and PNMQ had high IT to *Lr9* and *Lr10*, which are most likely in AR584A-3-1. VA98W-346 had ITs of 2^+ to 3^+ to isolates TCRJ, TFGJ, MCGJ, MCRK, and low ITs of 0; to 2 to all other isolates. TCRJ, TFGJ, MCGJ, and MCRK had high ITs to *Lr10* and *Lr26*, which are most likely in VA98W-346. VA96W-270 had a high IT of 3^+ to isolates TCRJ, TFGJ, KCGD, MCGJ, and MCRK, and low ITs of ; to 22^+ to all other isolates. TCRJ, TFGJ, MCGJ, and MCRK have a high IT to *Lr26* that is likely present in VA96W-270. NC94-7197 had a high IT of 3^+ to isolate MCRK and low ITs of 0; to 2^- to all other isolates. MCRK is the only isolate virulent to both *Lr18* and *Lr26*, which are likely present in NC94-7197. NC96-13965 had low IT of 0 to $;2^-$ to all the isolates used in this test. The identity of *Lr* gene(s) could not be postulated for this line since none of the isolates produced a high IT. Gene postulations could not be derived based on the pattern of high and low IT produced by the isolates on NC96-14439, NC96-13155, and Pioneer XW681.

Field Resistance

The 35 cultivars in the test generally had similar leaf rust severity at Plymouth and Kinston in 2000 (Table 5). The cultivars FFR 522 (*Lr9*, *Lr18*), FFR 518 (*Lr9*, *Lr10*), Natchez (*Lr9*, *Lr10*), FFR 566 (*Lr1*, *Lr2a*), NC Neuse (*Lr1*, *Lr2a*), Patton (*Lr10*, *Lr26*), Terral LA 422 (?), Coker 9766 (*Lr2a*, *Lr9*), Coker 762 (*Lr2a*, *Lr9*), and Coker 9663 (*Lr2a*, *Lr9*, *Lr10*) were highly resistant with 0% (0) or trace level of infection (TR) leaf rust ratings at one or both locations. All of these highly resistant cultivars were postulated to have combinations of *Lr2a*, *Lr9*, or *Lr26*. Compared with Thatcher, which was rated at 90 S (large uredinia), the Thatcher lines with *Lr2a*, *Lr9*, and *Lr26* had leaf rust ratings of 20 M, 10 MR (moderate size uredinia with necrosis), and 30 MR, respectively, in plots at Kinston (Table 1). The leaf rust resistance genes *Lr2a*, *Lr9*, and *Lr26* most likely interact with effective adult plant resistance genes to condition high levels of resistance in these cultivars.

Other cultivars with *Lr2a*, *Lr9*, or *Lr26*: Foster (*Lr10*, *Lr26*), Coker 983 (*Lr2a*, *Lr9*), Coker 9835 (*Lr2a*, *Lr9*), and Pioneer 26R61 (*Lr11*, *Lr26*) had intermediate to high leaf rust severity at the two locations. Although *Lr2a*, *Lr9*, and/or *Lr26* were present in these cultivars, they were not highly resistant, which might be attributed to less effective adult plant resistance in these cultivars. Some cultivars, Cardinal (*Lr10*), Shelby (*Lr10*), Pocahontas (*Lr11*), AGS 2000 (*Lr10*, *Lr26*), Pioneer 2691 (*Lr1*), Pioneer 2643 (*Lr1*, *Lr11*), Pioneer 26R24 (*Lr18*),

Table 4. Seedling ITs† of soft red winter wheat breeding lines inoculated with 16 virulence phenotypes of the leaf rust fungus *Puccinia triticina*.

Line/cultivar	Postulated *Lr* gene(s)	FBMT 31-3A	MBGD 21-4	MDRJ 12-1A	TCRJ 3-3A	LBBK 66-1	MBRK 4-2A	MBDS 20-3A	TBRJ 9-1B	MBRJ 16-2B	TFGJ 96-3	KCGD 87-3	TNRJ 86-3	MCGJ 102-1	TLGF 1-1B	MCRK 6-1A	PNMQ CA80-1
NC96-13141	*Lr2a, Lr9*	0	0;	0;	0;	0	0	0;	0;	0;	0	0	3^+	0	3^+	0;	0;
NC94-7197	*Lr18, Lr26*	;	;	;	$;2^-$	$;2^-$	2^-	;	;	;	$;1$	$;1$	;	$;1^-$	0;	3^+	0;
NC96-13965	?	0	0;	0	0	0	0;	0	0	0	0	0	$;2^-$	0	$;1^-$	0;	0;
NC96-14439	?	0;	3^+	3^+	3^+	$;1^-$	0	;	3^+	3^+	3^+	3	3	3^+	$;2^-$	2^+	$;2^-$
NC96-13129	*Lr2a, Lr9, Lr10*	0	0	0	0	0	0	0	0	0	0	0	3^+	0	;	0;	0;
NC96-13155	?	0	0;	0;	2^+	0	0	0	2^+	0;	3^+	0	;	0	$;2^-$	0;	0;
VA96W-270	*Lr26*	;	;	;	3^+	$;1^-$	$;2^-$	;	$;1^-$	;	3^+	3^+	;	3^+	0;	3^+	;
VA98W-346	*Lr10, Lr26*	;	0;	0;	2^+	$;2^-$	$;1^-$	;	$;1^-$	;	3^+	$;1^-$	0;	3^+	0	3^+	0;
USG3408	*Lr1, Lr11*	0	3^+	3^+	3^+	;1	3^+	$;2^-$	3^+	3^+	3^+	0	3^+	3^+	33^+	3^+	;2
USG3209	*Lr1, Lr26*	0	;	$;1^-$	3^+	;2	2^-	;	2	$;1^-$	3^+	0	;	3^+	0;	3^+	;
Pioneer XW681	?	1	;	;	3^+	2^+3	3^+	;2	$;2^-$	;	3^+	3^+	;	3^+	;	3^+	;
Pioneer XW682	*Lr10, Lr26*	;1	;	;	3^+	0;	2	;	$;2^-$	$;1^-$	3^+	;	;	3^+	;	3^+	;
B93-0390	*Lr2a, Lr9*	0	0	0	0	0	0	0	0	0	0	0	3^+	0	3^+	0;	0;
AR494B-2-2	*Lr1*	0	3^+	3^+	3^+	3^+	3^+	3^+	3^+	3^+	3^+	0;	3^+	3^+	3^+	3^+	3^+
AR584A-3-1	*Lr9, Lr10*	0	0	0	0	0	0	0	0	0	0	0	3^+	0	0	0	3^+
AR656-5-1	*Lr2a, Lr10*	0	0;	0	3^+	0	0;	0	3	0	3^+	0;	3^+	0	;	0;	0;
GA90524-E35	*Lr2a, Lr9, Lr10*	0	0;	0	0	0	0;	;	0	0	0	0	3^+	0	;	0;	0;

† Infection types: 0 = no flecks or uredinia, 0; = faint hypersensitive flecks, ; = hypersensitive flecks, 1 = small uredinia with necrosis, 2 = small uredinia with chlorosis, 3 = moderate size uredinia, 4 = large uredinia, $^+$ indicates slightly larger uredinia, $^-$ indicates slightly smaller uredinia, ITs with two symbols denote a range in IT: 22^+ indicates a mixture of 2 size uredinia with chlorosis and slightly larger uredinia with chlorosis.

Table 5. Leaf rust severity† and resistance‡ response of soft red winter wheat cultivars and breeding lines at two locations in North Carolina in 2000.

	Plymouth	Kinston	*Lr* genes postulated
Cultivars			
FFR 522	0–5 R	TR	*Lr9*, *Lr18*
FFR 518	0	0	*Lr9*, *Lr10*
FFR 524	10 MR MS	30 M	*Lr18*
FFR 555W	50 MS	20 MR MS	*Lr10*
FFR 566	5 MR	TR	*Lr1*, *Lr2a*
Saluda	–§	70 MS	*Lr11*
Cardinal	–	5 M	*Lr10*
Becker	–	90 S	*Lr11*
Shelby	5 R MR	20 M	*Lr10*
Patton	5 R	TR	*Lr10*, *Lr26*
Foster	–	20 MR MS	*Lr10*, *Lr26*
Terral LA 422	TR	TR	?
Pocahontas	30 MR MS	30 MR MS	*Lr11*
Jackson	50 S	90 S	*Lr1*, *Lr11*
Roane	10 M	5 R	–
Pioneer 2684	40 M	40 M	*Lr10*, *Lr18*
Pioneer 2691	5 M	20 M	*Lr1*
Pioneer 2580	30 M	50 M	*Lr11*
Pioneer 26R61	5 M	10 R	*Lr11*, *Lr26*
Pioneer 2643	10 M	30 M	*Lr1*, *Lr18*
Pioneer 26R24	20 MR MS	20 MR MS	*Lr18*
Coker 9474	–	–	*Lr2a*, *Lr9*
Coker 9766	–	0	*Lr2a*, *Lr9*
Coker 983	–	40 S	*Lr2a*, *Lr9*
Coker 762	–	0	*Lr2a*, *Lr9*
Coker 9803	10 M	10 MR	*Lr10*, *Lr18*
Coker 9704	5 M	10 M	*Lr10*, *Lr18*
Coker 9663	0	0	*Lr2a*, *Lr9*, *Lr10*
Coker 9835	–	50 M	*Lr2a*, *Lr9*
NC Neuse	0	TR	*Lr1*, *Lr2a*
AGS 2000	5 R MR	5 R	*Lr10*, *Lr26*
SS 550	20 MR MS	30 MR MS	*Lr26*
SS 520	20 MR MS	20 R MR	*Lr11*, *Lr18*
Sisson	20 R MR	20 R MR	*Lr26*
Natchez	TR	0	*Lr9*, *Lr10*
Breeding lines			
NC96-13141	0	0	*Lr2a*, *Lr9*
NC94-7197	5 R MR	5 R	*Lr18*, *Lr26*
NC96-13965	0	0	?
NC96-14439	TR	5 R	?
NC96-13129	0	0	*Lr2a*, *Lr9*, *Lr10*
NC96-13155	TR	TR	?
VA96W-270	20 MR MS	10 R MR	*Lr26*
VA98W-346	5 R	10 R	*Lr10*, *Lr26*
USG3408	10 M	30 M	*Lr1*, *Lr11*
USG3209	–	–	*Lr1*, *Lr26*
Pioneer XW681	50 M	50 M	?
Pioneer XW682	50 M	20 MR MS	*Lr10*, *Lr26*
B93-0390	TR	–	*Lr2a*, *Lr9*
AR494B-2-2	30 MS	30 MR MS	*Lr1*
AR584A-3-1	TR	0	*Lr9*, *Lr10*
AR656-5-1	60 MS	5 R	*Lr2a*, *Lr10*
GA90524-E35	0	0	*Lr2a*, *Lr9*, *Lr10*
Check cultivars			
Monon	50 MR MS	40 MR MS	*Lr12*
Coastal	50 S	60 S	*Lr13*
Caldwell	10 R MR	0	*Lr12* + APR¶
Knox	–	5 MR	*Lr12* + APR
Sturdy	5 R	5 MR	*Lr10*, *Lr12*, *Lr34*#
Bezostaya 1	–	10 MR MS	*Lr3*, *Lr34*#

† Infection types: 0 = no flecks or uredinia, 0; = faint hypersensitive flecks, ; = hypersensitive flecks, 1 = small uredinia with necrosis, 2 = small uredinia with chlorosis, 3 = moderate size uredinia, 4 = large uredinia, $^{+}$ indicates slightly larger uredinia, $^{-}$ indicates slightly smaller uredinia, ITs with two symbols denote a range in IT: 22^{+} indicates a mixture of 2 size uredinia with chlorosis and slightly larger uredinia with chlorosis.

‡ Rust response: 0 = no flecks or uredinia, TR = trace level of uredinia, R = small uredinia with necrosis, M = mixture of small and large uredinia without chlorosis, MR = moderate size uredinia with necrosis, MS = moderate size uredinia with chlorosis, S = large uredinia.

§ Not planted at location.

¶ Adult plant resistance.

Determined by genetic analysis.

Coker 9803 (*Lr10*, *Lr18*), and Coker 9704 (*Lr10*) had intermediate levels of leaf rust severity from 5 M to 30 MR MS (moderate size uredinia with chlorosis). The Thatcher line with *Lr1* had a leaf rust rating of 90 S, *Lr10* was 50 MS, *Lr11* was 90 S, and *Lr18* was 50 S in plots at Kinston (Table 1), which indicated that these genes conditioned little or no field resistance by themselves. The leaf rust resistance in field plots of the cultivars with seedling genes *Lr1*, *Lr10*, *Lr11*, or *Lr18*, must be mostly due to the expression of adult plant resistance. The cultivars FFR 555W (*Lr10*), Saluda (*Lr11*), Becker (*Lr11*), Jackson (*Lr1*, *Lr11*), Pioneer 2684 (*Lr10*, *Lr18*) and Pioneer 2580 (*Lr11*) had field leaf rust severities of 20 MR MS to 90 S, which indicated that these cultivars had less effective adult plant resistance.

The seedling leaf rust resistance genes in Terral LA 422 could not be identified, yet this cultivar was highly resistant at both locations. Terral LA 422 likely has an effective combination of seedling and adult plant resistance genes. Roane, which was determined to lack seedling *Lr* genes, had intermediate leaf rust severity at both locations. The field resistance in Roane must be due to adult plant resistance genes.

Lines NC96-13141 (*Lr2a*, *Lr9*), NC96-13129 (*Lr2a*, *Lr9*, *Lr10*), B93-0390 (*Lr2a*, *Lr9*), AR584A-3-1 (*Lr9*, *Lr10*), and GA90524-E35 (*Lr2a*, *Lr9*, *Lr10*) were highly resistant with 0 to TR leaf rust severity at both Plymouth and Kinston. These highly resistant breeding lines most likely all had either *Lr2a* or *Lr9*. Lines NC96-13965, NC96-14439, and NC96-13155 were also highly resistant with 0 to TR rust ratings at both locations. Lines with *Lr26*: NC94-7197 (*Lr18*, *Lr26*), and VA98W-346 (*Lr10*, *Lr26*), also had good resistance ratings between 5 R (small uredinia with necrosis) to 10 R at both locations. Other lines with genes *Lr1*, *Lr10*, *Lr11*, *Lr18*, and *Lr26* had intermediate to high levels of leaf rust infection. Pioneer XW681 was rated at 50 *M* for leaf rust severity at both locations. Line AR656-5-1 (*Lr2a*, *Lr10*) was resistant at 5 R in Kinston, but was more susceptible at Plymouth with a rating of 60 MS.

Adult Plant Resistance Cultivars

Monon, which has been postulated to have *Lr12*, had an intermediate level of leaf rust resistance with ratings of 50 MR MS and 40 MR MS, respectively, in Plymouth and Kinston (Table 5). Coastal, which has been postulated to have *Lr13*, was susceptible with ratings of 50 S and 60 S. Caldwell and Knox, which have been postulated to have *Lr12* plus additional adult plant resistance, were highly to moderately resistant with readings between 0 to 10 R MR. The hard red winter wheat cultivar Sturdy, which has been shown by genetic analysis to have *Lr10*, *Lr12*, and *Lr34* (Dyck, 1991), had good resistance with ratings of 5 R and 5 MR at the two locations. Bezostaya 1, which has been shown by genetic analysis to have *Lr3* and *Lr34* (P.L. Dyck, 1993, personal communication), was rated at 10 MR MS at Kinston.

DISCUSSION

On the basis of the leaf rust ITs in this study, it was postulated that genes *Lr1*, *Lr2a*, *Lr9*, *Lr10*, *Lr11*, *Lr18*,

and *Lr26* are common in soft red winter wheats. A virulence survey of *P. triticina* in the South Atlantic states (Georgia, South Carolina, North Carolina, Virginia) in 1999 indicated that virulence to *Lr2a* was found in 42% of isolates, virulence to *Lr9* was in 23%, and virulence to *Lr26* was in 16% of isolates. In 2000, in plots at Kinston, the Thatcher lines with *Lr2a*, *Lr9*, and *Lr26* had some effective field rust resistance compared with Thatcher. The frequency of *P. triticina* isolates at Kinston in 2000 with virulences to *Lr2a*, *Lr9*, or *Lr26* must have been at sufficiently low levels in order for these genes to provide effective resistance. Cultivars known to have the adult plant resistance genes *Lr12* and *Lr34* also had good leaf rust resistance in field plots. In the 1999 virulence survey of the South Atlantic states, most of the *P. triticina* isolates tested for virulence to adult plants of the Thatcher line with *Lr12* were avirulent, and all the isolates tested produced smaller and fewer uredinia on adult plants of the Thatcher line with *Lr34* compared with Thatcher. It is most likely that the high level of leaf rust resistance displayed by cultivars such as FFR 522, FFR 518, FFR 566, Patton, Coker 9766, Coker 762, and Coker 9663 is due to the combination of seedling leaf rust resistance genes *Lr2a*, *Lr9*, or *Lr26*, combined with effective adult plant genes such as *Lr12* and *Lr34*. Adult plant gene *Lr13* may also be present in the soft red winter wheats in this study; however, the cultivar Coastal, postulated to have *Lr13*, was susceptible in both field plot locations, and almost all of the isolates tested in the 1999 virulence survey were virulent to adult plants of the Thatcher line with *Lr13* (Kolmer, 2002). It is unlikely that *Lr13* contributes effective leaf rust resistance in the soft red winter wheats grown in North Carolina.

Effective adult plant resistance genes must be common in the soft red winter wheats. Cultivars such as Shelby (*Lr11*), Cardinal (*Lr11*), and Pioneer 2643 (*Lr1*, *Lr11*) did not have any effective seedling resistance genes, yet had intermediate levels of leaf rust resistance in the field plots. The effective field resistance in lines with *Lr1*, *Lr10*, *Lr11*, or *Lr18* is most likely due to adult plant resistance genes, since the Thatcher lines with these seedling genes had little or no effective resistance in plots at Kinston, and virulence to these resistance genes is common in *P. triticina* isolates in the southeastern USA (Kolmer, 2002; Long et al., 2002).

The sources of adult plant leaf rust resistance in soft red winter wheats most likely trace back to the wheat landrace Chinese Spring and the Brazilian cultivars Frondoso and Frontiera (Caldwell et al., 1957). Caldwell et al. (1954) described the cultivar Knox as having a "mature plant" type of leaf rust resistance. The leaf rust resistance in Knox was derived from Chinese Spring, which was later shown to have the adult plant resistance genes *Lr12* and *Lr34* (Dyck, 1991). Since Knox had good resistance at both Plymouth and Kinston, it most likely has both *Lr12* and *Lr34*. Monon has adult plant resistance with a phenotype much like *Lr12* and also has Chinese Spring in its pedigree. Knox and Monon were subsequently used as leaf rust resistant parents in the soft red winter wheats. The Brazilian cultivars Frondoso and Frontiera that most likely have *Lr13* (Roelfs, 1988) were used as leaf rust resistant parents in the crosses that developed 'Atlas 66', 'Atlas 50', Coastal, and 'Coker 47-27' (Caldwell et al., 1957).

The identities of the seedling resistance genes were postulated on the basis of gene-for-gene specificity. However, there are obvious limitations to this approach for analysis of leaf rust resistance genes in wheat. The *P. triticina* isolates that were used in this study were not adequate to identity all of the seedling *Lr* genes that were present in the cultivars and breeding lines. A more diverse collection of *P. triticina* isolates may have allowed the postulation of leaf rust resistance genes in Terral LA 422, and the breeding lines NC96-14439, NC96-13155, and Pioneer XW681. Breeding line NC96-13965 had low IT to all of the isolates used in this study. This line would be a good candidate for further genetic analysis to conclusively determine the number and identity of leaf rust resistance genes it carries.

Most of the isolates used in this test were virulent to *Lr11*, making it difficult to postulate the presence of *Lr11* in certain wheat lines. Only two isolates, TNRJ, and TLGF, were virulent to *Lr2a* and *Lr9*. Since TNRJ and TLGF are both virulent to *Lr11*, it would be impossible using these two isolates to identify the presence of *Lr11* in wheat lines with *Lr2a* and *Lr9*. *Lr11* is likely very common in soft red winter wheats since it was derived from Hussar, which was used as an early parent (Caldwell et al., 1957). Similarly, only isolate LBBK was avirulent to *Lr3*, which is in the wheat Mediterranean (Dyck and Samborski, 1968). Since many of the soft red winter wheats were derived from Mediterranean, it is likely that *Lr3* is also present in these wheats. More isolates of *P. triticina* that are avirulent to *Lr3* would be needed to postulate the presence of *Lr3*.

The seedling gene *Lr9* is an important component of leaf rust resistance in many of the soft red winter wheat cultivars and breeding lines. This gene was initially used in the cultivars Riley 67 and Arthur 71, released in 1967 and 1971. Isolates of *P. triticina* with virulence to *Lr9* were detected only a few years after the release of these cultivars (Shaner et al., 1972); however, *Lr9* still provides some effective resistance to leaf rust. The gene *Lr18* is also likely present in a number of the soft red winter wheats. This gene can be difficult to detect in seedling tests, since it is particularly temperature sensitive (Long and Kolmer, 1989; McIntosh et al., 1995). At high greenhouse temperatures (>25°C) the resistance response conditioned by *Lr18* becomes very difficult to evaluate. The ambiguities regarding the presence of *Lr18* in the cultivars and breeding lines used in this study is most likely due to this temperature sensitivity. The origin of *Lr18* in the soft red winter wheat germplasm is not clear since this gene was most likely derived from *T. timopheevi* (Zhuk.) Zhuk.

Gene *Lr26* is likely present in the cultivars Foster, Patton, AGS 2000, SS 550, Sisson, and Pioneer 26R61. This gene is located on the wheat-rye 1B-1R translocation (McIntosh et al., 1995). Although the Thatcher line with *Lr26* had effective leaf rust resistance compared with Thatcher in field plots at Kinston, *P. triticina* isolates with virulence to this gene have increased in response to the limited use of *Lr26* in the soft red wheats.

Increased use of *Lr26* in wheats in the southeastern states will erode the effectiveness of this gene. Gene *Lr1* is in the soft red winter wheats 'Tyler' and 'Blueboy', which also had *Lr10*. Many of the isolates in the southeastern USA are virulent to *Lr1* and *Lr10*. Isolate TLGF, which is avirulent to *Lr10*, was common in 1999 in the South Atlantic states (Kolmer, 2002). Isolates with virulence to *Lr2a*, *Lr9*, and *Lr10*, such as isolates TNRJ and TLGJ, have increased in frequency in 2000 and 2001 (Long et al., 2002) in response to the cultivation of wheats with these resistance genes in the southeastern USA.

The results of this study indicated that the cultivars and breeding lines with the best leaf rust resistance in field plots most likely have combinations of effective seedling and adult plant resistance genes. The adult plant resistance *Lr34* is likely very common in the soft red winter wheat germplasm. Isolates of *P. triticina* that are fully virulent to adult plants with *Lr34* have not been detected (Kolmer, 1997, 2002), which indicates that wheat lines with this gene should have a generalized nonspecific resistance to leaf rust. *Lr34* conditions an incomplete, partial resistance to leaf rust that is manifested by smaller and fewer pustules at the flag leaf stage in the initial phase of the leaf rust epidemic. Wheat lines that only have *Lr34* for effective resistance can appear to be susceptible later in the epidemic when severity levels on these lines are often equal to the susceptible check lines. Wheat lines that have *Lr34* and effective seedling resistance genes often display higher levels of leaf rust resistance than lines that have only *Lr34* or the seedling resistance genes (Samborski and Dyck, 1982; German and Kolmer, 1992). Lines with *Lr34* and effective seedling resistance genes also have lower seedling IT to avirulent isolates (German and Kolmer, 1992). This ability to interact with other genes for high levels of leaf rust resistance has undoubtedly helped *Lr34* to be selected in the various breeding programs in the southeastern USA.

ACKNOWLEDGMENTS

I thank P. Murphy for assistance in planting the field trial and for encouragement.

REFERENCES

Caldwell, R.M., L.E. Compton, J.F. Schafer, and F.L. Patterson. 1954. Knox, a new leaf rust resistant and stem rust escaping soft winter wheat. Phytopathology 44:483–484.

Caldwell, R.M., J.F. Schafer, L.E. Compton, and F.L. Patterson. 1957. A mature-plant type of wheat leaf rust resistance of composite origin. Phytopathology 47:690–692.

Chester, K.S. 1946. The nature and prevention of the cereal rusts as exemplified in the leaf rust of wheat. Chronica Botanica Co., Waltham, MA.

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. 1993a. Inheritance of leaf rust and stem rust resistance in 'Roblin' wheat. Genome 36:289–293.

Dyck, P.L. 1993b. The inheritance of leaf rust resistance in the wheat cultivar Pasqua. Can. J. Plant Sci. 73:903–906.

Dyck, P.L., and D.J. Samborski. 1968. Genetics of resistance to leaf rust in the common wheat varieties Webster, Loros, Brevit, Carina, Malakof and Centenario. Can. J. Genet. Cytol. 10:7–17.

Ezzahiri, B., and A.P. Roelfs. 1989. Inheritance and expression of adult plant resistance to leaf rust in Era wheat. Plant Dis. 73:549–551.

Flor, H.H. 1971. Current status of the gene-for-gene concept. Annu. Rev. Phytopathol. 9:275–296.

German, S.E., and J.A. Kolmer. 1992. Effect of gene *Lr34* in the enhancement of resistance to leaf rust of wheat. Theor. Appl. Genet. 84:97–105.

Kolmer, J.A. 1994. Genetics of leaf rust resistance in three western Canada spring wheats. Plant Dis. 78:600–602.

Kolmer, J.A. 1997. Virulence in *Puccinia recondita* f. sp. *tritici* isolates from Canada to genes for adult-plant resistance to wheat leaf rust. Plant Dis. 81:267–271.

Kolmer, J.A. 2002. Virulence phenotypes of *Puccinia triticina* in the South Atlantic States in 1999. Plant Dis. 86:288–291.

Liu, J.Q., and J.A. Kolmer. 1997. Genetics of leaf rust resistance in Canadian spring wheats AC Domain and AC Taber. Plant Dis. 81:757–760.

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

Long, D.L., J.A. Kolmer, K.J. Leonard, and M.E. Hughes. 2002. Physiologic specialization of *Puccinia triticina* on wheat in the United States in 2000. Plant Dis. 86:981–986.

McIntosh, R.A., C.R. Wellings, and R.F. Park. 1995. Wheat rusts: An atlas of resistance genes. CSIRO, North Ryde, NSW, Australia, and Kluwer Academic Publ., Dordrecht, The Netherlands.

McVey, D.V., and D.L. Long. 1993. Genes for leaf rust resistance in hard red winter wheat cultivars and parental lines. Crop Sci. 33: 1373–1381.

Person, C. 1959. Gene-for-gene relationships in host:parasite systems. Can. J. Bot. 37:1101–1130.

Roelfs, A.P. 1988. Resistance to leaf and stem rusts in wheat. p. 10–22. *In* N.W. Simmonds and S. Rajaram (ed.) Breeding strategies for resistance to the rusts of wheat. CIMMYT, Mexico, D.F.

Samborski, D.J., and P.L. Dyck. 1982. Enhancement of resistance to *Puccinia recondita* by interactions of resistance genes in wheat. Can. J. Plant Pathol. 4:152–156.

Shaner, G., J.J. Roberts, and R.E. Finney. 1972. A culture of Puccinia recondita virulent to the wheat cultivar Transfer. Plant Dis. Rep. 56:827–830.

Singh, R.P. 1993. Resistance to leaf rust in 26 Mexican wheat cultivars. Crop Sci. 33:633–637.

Singh, D., R.F. Park, and R.A. McIntosh. 2001. Postulation of leaf (brown) rust resistance genes in 70 wheat cultivars grown in the United Kingdom. Euphytica 120:205–218.