Postulation of Seedling Leaf Rust Resistance Genes in Selected Ethiopian and German Bread Wheat Cultivars

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ABSTRACT

Leaf rust caused by the fungus *Puccinia triticina* Eriks. is one of the most important foliar diseases of wheat (*Triticum aestivum* L.). Host resistance is the most economical and safest method of controlling the disease. Characterization of the host greatly facilitates the effective utilization of host resistance genes. Gene postulation helps to undertake a quick identification of the probable leaf rust resistance genes (*Lr* genes) present in a large number of wheat cultivars at a time. The objective of this study was to identify the race-specific *Lr*-genes present in 36 wheat cultivars from Ethiopia and Germany. Seventy-six wheat genotypes, including 40 near-isogenic lines (NILs), were tested against 31 isolates of *P. triticina* isolates collected from both countries. *Lr*-genes *Lr*1, 2c, 3, 3ka, 9, 10, 14a, 14b, 13, 16, 18, 21, 23, 27+31, 30, 37, and 44 were postulated to be present in the Ethiopian wheat cultivars. *Lr* genes *Lr*9, 20, and 21 were present in the German wheat cultivars. The *Lr*-genes present in some wheat cultivars could not be postulated because of non-matching virulence combinations with any of the NILs. The results of this study show that most of the wheat cultivars tested do not have adequate resistance for leaf rust, indicating the need for incorporating more effective genes into the target wheat cultivars.

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Abbreviations: APR, adult plant resistance; IT, infection type; NIL, near-isogenic line; QTL, quantitative trait loci.

Leaf rust caused by the fungus *Puccinia triticina* Eriks. is one of the most important foliar diseases of wheat (*Triticum aestivum* L.) worldwide (Dehne and Oerke, 1998; Cherukuri et al., 2005). Yield losses due to leaf rust may be as high as 30 to 50% in cases of severe infections (McIntosh et al., 1995). Use of resistant wheat varieties is the most economical and environmentally friendly method of controlling the disease (Pink, 2002). However, host resistance conferred by a single or a few genes could be easily overcome by the appearance of rust races or pathotypes with new combinations of virulence genes (McDonald and Linde, 2002). The identification of genes that control resistance in the existing wheat cultivars will contribute to the effective management of wheat rusts (Kolmer, 2003). Pyramiding of several resistance genes into a single cultivar is of paramount importance since the combined effects of several genes give the cultivar a wider base of disease resistance (Roelfs et al., 1992), thereby helping to avoid the release of cultivars that are genetically uniform (Statler, 1984; McVeh and Long, 1993; Kolmer, 2003). Before gene pyramiding is practiced, it is advisable to identify genetically different sources of resistance. Gene postulation provides the opportunity

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for quick identification of the probable race-specific seedling leaf rust resistance genes (*Lr* genes) in a large group of wheat lines (Kolmer, 2003). Postulation of genes depends on the principle of gene-for-gene interaction (Flor, 1971) between the host line and *P. triticina* genotype to determine the most probable resistance genes in wheat cultivars tested. Presence of race-specific resistance genes can be postulated on the basis of phenotypic expressions in the form of infection types (ITs) as the wheat lines are infected with a series of pathogen isolates/races (Kolmer, 2003; Wamishe et al., 2004). Infection types produced on near-isogenic wheat lines (NILs), containing specific *Lr*-genes, are the basis for comparing the ITs of wheat cultivars with unidentified genes for leaf rust resistance.

Gene postulation is the most widely used method to identify genes for leaf rust resistance in various wheat cultivars or breeding lines. Many researchers have used this technique for identifying *Lr* genes in a group of wheat genotypes (Wamishe and Milus, 2004). For instance, Statler (1984) identified genes *Lr*1, 2a, 2c, 10, 17, and 18 in 25 hard red spring wheats; McVeh and Long (1993) postulated the presence of genes *Lr*1, 2a, 3, 3ka, 9, 10, 11, 14a, 16, 17, 18, 24, 26, and 30 in 86 hard red winter wheat lines; Kolmer (2003) postulated *Lr*1, 2a, 9, 10, 11, 18, and 26 in a group of 35 soft red winter wheat cultivars and 17 breeding lines; and Wamishe and Milus (2004) postulated genes *Lr*1, 2a, 2c, 3, 3ka, 9, 10, 11, 14a, 18, 20, 23, 24, and 26 to be present in 116 North American wheat lines.

Information on the genetic bases of the Ethiopian wheat cultivars for leaf rust resistance is generally lacking. In addition, information on the type and number of leaf rust resistance genes is very limited for German bread wheat cultivars and infrequent for other European wheat cultivars. Winzeler et al. (2000) postulated leaf rust resistance genes present in some European winter wheat cultivars. However, none of the cultivars considered in our studies were included. Hysing et al. (2006) postulated *lr* genes in the northern European wheat cultivars, including cultivars Lavett, Thasos, and Triso, which were also considered in the current study. It was not possible to postulate leaf rust resistance genes in cultivars Lavett and Triso because of nonmatching virulence combinations with any of the NILs; however, cultivar Thasos was postulated to have no leaf rust resistance gene at all (Hysing et al., 2006).

We designed this study, therefore, to examine the genetic base of leaf rust resistance in 36 bread wheat cultivars from Ethiopia and Germany, respectively, two countries largely differing in wheat production. In Ethiopia, wheat is often grown in low-input systems with rust control relying on cultivar resistance, whereas disease control in high-input wheat production in Germany is ensured by fungicide applications. The postulation of seedling leaf rust resistance genes was done by using *P. triticina* isolates from Ethiopia and Germany and Thatcher-derived NILs, each containing specific leaf rust resistance genes.

MATERIALS AND METHODS

Plant Material

A total of 76 wheat genotypes including 40 Thatcher-derived NILs and 36 wheat cultivars (23 from Ethiopia and 13 from Germany) were used in this study (Tables 1 and 2). The NILs were provided by Dr. V. Lind, Federal Centre for Breeding Research on Cultivated Plants (BAZ), Quedlinburg, Germany. Wheat seedlings were separately raised on a plastic plate filled with seedling substrate (Klasmann-Deilmann GmbH, Geeste, Germany) containing 77 wells, each well accommodating four to six plants of the individual wheat genotype. In each plate, the susceptible cultivar Monopol was used twice as a standard check. After planting, each plate was kept in a cellophane chamber on a greenhouse bench (20 ± 2°C, 16 h illumination) for 7 to 9 d to avoid contamination with airborne pathogens.. At emergence, a liter of maleic hydrazide solution (300 mg L^{-1}) was applied per plate to prevent excessive growth of seedlings.

As shown in Table 1, 40 NILs were tested for their reaction to infection by 31 isolates of *P. triticina* collected from Ethiopia and Germany. Thirty-six bread wheat cultivars possessing unknown *Lr* gene(s) were the target cultivars for gene postulation (Table 2). These cultivars were obtained from the respective German and Ethiopian wheat breeders.

Inoculation and Incubation of Plants

Thirty-one monopustule *P. triticina* isolates collected from Ethiopia and Germany were used to inoculate NILs and wheat cultivars (Table 3). Uredospores (75–100 mg) produced on detached leaf segments were dissolved in 150 mL water containing 2 to 3 droplets of Tween 80 (Merck-Schuchardt, Hohenbrunn, Germany) and 0.2 g of gelatin as detergent and sticker, respectively, to prepare a spore suspension containing 10^5 spores mL^{-1}. Plants in each plate were inoculated (using a hand sprayer) with spore suspension of individual isolates until run-off. The inoculated plants were kept at 100% relative humidity for 24 h at ambient temperature in the dark. Seedlings were then transferred to a growth chamber with 16h/8h light/dark system and a temperature of 20 to 22°C.

Disease Assessment

Scoring of leaf rust symptoms was performed 10 to 12 d after inoculation. Infection types of *P. triticina* on wheat cultivars were quantified using a standard 0 to 4 scale (Long and Kolmer, 1989), where 0 = immune, ; = hypersensitive fleck without uredinia, 1 = small uredinia surrounded by necrosis, 2 = small uredinia surrounded by chlorosis, 3 = moderate size uredinia that may be associated with chlorosis, and 4 = large uredinia without chlorosis. Mixtures of two ITs on the same leaf were represented by ITs, with the most common IT listed first. Designations of + and − were used with the 0 to 4 scale to indicate larger and smaller uredinia than normal, respectively. The isolates were assigned to five-letter race designations based on high and low ITs on 20 Thatcher-derived NILs following the method described by Long and Kolmer (1989).

Table 1. List of Thatcher-derived near-isogenic lines (NILs) used for virulence analysis and gene postulation studies.

NIL	Resistance gene	Pedigree
RL6003	*Lr*1	Tc*6/Centenario
RL6016	*Lr*2a	Tc*6/Webster
RL6019	*Lr*2b	Tc*6/Carina
RL6047	*Lr*2c	Tc*6/Loros
RL6002	*Lr*3	Tc*6/Democrat
RL6042	*Lr*3bg	Bage/Tc*8
RL6007	*Lr*3ka	Tc*6/Klein Aniversario
RL6010	*Lr*9	Transfer/Tc*6
RL6004	*Lr*10	Tc*6/Exchange
RL6053	*Lr*11	Tc*2/Hussar
TC6011	*Lr*12	Exchange/Tc*6
RL4031	*Lr*13	Tc*6/Frontana
RL6013	*Lr*14a	Selkirk/Tc*6
RL6006	*Lr*14b	Tc*6/M. Escobar
RL6052	*Lr*15	Tc*6/Kenya W1483
RL6005	*Lr*16	Tc*6/Exchange
RL6008	*Lr*17	K.Lucero/Tc*6
RL6009	*Lr*18	Tc*7/Africa43
RL6040	*Lr*19	Tc*7/Tr.4 A.elong.
RL6092	*Lr*20	Tc*6/Jimmer
RL6043	*Lr*21	Tc*6/RL5406 Tetra C
RL6044	*Lr*22	Tc*6/RL 5404 Tetra C
RL6012	*Lr*23	Lee 310/Tc*6
RL6064	*Lr*24	Tc*6/Agent
RL6084	*Lr*25	Tc*6/Transec
RL6078	*Lr*26	Tc*6/St-1-25
W3021	*Lr*27+31	Gatcher[W3021]
RL6079	*Lr*28	Tc*6/C-77-1
RL6080	*Lr*29	Tc*6/CS7D-Ag#11
RL6049	*Lr*30	Tc*6/Terenzio
RL5494-1	*Lr*32	Tc*6/Ae. Sq.
RL6057	*Lr*33	Tc*6/PI58548 (1+gene)
RL6058	*Lr*34	Tc*6/PI58548 (2+gene)
RL5711	*Lr*35	Tc*6/RL 5711
RL6081	*Lr*37	Tc*8/VPM1
RL6097	*Lr*38	Tc*6/T7Kohn
RL6147	*Lr*44	Tc*6/*T. spelta*
RL6051	*Lr*B	Tc*6/Carina
RL6107	*Lr*W	Tc*6/V336
Thatcher	*Lr*Tc	Marquis/Iumillo/2/Marquis/Kanred

Table 2. List of wheat cultivars used for gene postulation.

Cultivar†	Pedigree
Bobitcho (HAR 2419) E	PEG/PF70354/KAL/BB/ALD/3/MRNG
Galama (HAR 604) E	4777(2)//FNK/GB/3/PVN''S''
Tussie (HAR 1407) E	COOK/VEE''S''//DOVE''S''/SERI
Shinna (HAR 1868) E	GOV9A7//MUS''S''/3/R37/GHL121//KAL/BB/4/ANI''S''
Dereselign E	NA‡
ET-13A2 E	ENKOY/UQ105
Sirbo (HAR 2192) E	VS73.600/MRL/3/BOW//YR/TRF
K6295-4A E	ROMANYxGB-GAMENYA
Hawi (HAR 2501) E	CHIL/PRL
Mitike (HAR 1709) E	BOW28 RBC
Simba (HAR 2536) E	PRL/VEE6//MYNA/VUL
Katar (HAR 1899) E	COOK/VEE''S''//DOVE''S''/SERI/3/BJY''S''
Wetera (HAR 1920) E	MON''S''-BUC''S''
K6290 Bulk E	AFM/*ROMANY
Abola (HAR 1522) E	BOW''S''/BUC''S''
Magal (HAR 1595) E	F371/TRM//BUC''S''/3/LIRA''S''
Wabe (HAR 710) E	MRL''S''-BUC''S''
Dashen E	KVZ/BUHO''S''//KAL/BB
Pavon-76 E	VCM//CNO//7C/3/KAL/BB
Dodota (HAR 2508) E	BJY/COC//PRL/BOW
Morocco E	NA
Tura (HAR 1775) E	ARO YR SEL.60/89
Kubsa (HAR 1685) E	ND VG9144//KAL/BB/3/YACO"S"/4VEE#5"S"
Munk G	NA
Lavett G	NA
Granny G	NA
Monsun G	NA
Fasan G	NA
Epos G	NA
Perdix G	NA
Triso G	NA
Monopol G	NA
Quattro G	NA
Thasos G	NA
Naxos G	NA
Tybalt G	NA

†E: wheat cultivars from Ethiopian, G: wheat cultivars from Germany

‡NA, not available.

RESULTS

The presence of genes for seedling leaf rust resistance was postulated for 36 wheat cultivars on the basis of the comparison of ITs of *P. triticina* isolates on the cultivars to ITs produced on Thatcher-derived NILs, each containing a specific leaf rust resistance gene.

The ITs of 40 Thatcher-derived NILs, produced after inoculation with 31 isolates of *P. triticina*, are listed in Table 3. Table 4 presents the ITs of wheat cultivars produced as a result of infection by the same 31 *P. triticina* isolates used to infect the NILs. Cultivars Bobitcho and Tussie from Ethiopia and Tybalt from Germany had low ITs to all isolates of *P. triticina* tested, ITs similar to that of NILs containing the *Lr*9, 19, 24, 26, 29, 38, and *Lr*W, making the postulation of genes in these cultivars difficult. In such cases where two or more possible gene combinations were present to explain the phenotype, the lowest number of genes required to explain the phenotype was used. Therefore, *Lr*9 was taken as the most likely gene present in these cultivars.

Cultivars Galama and K-6295-4A had low ITs to *P. triticina* isolates BGJTG-1, FGJTJ-3, SBJPQ-1, SBJPR-1, SBJPQ-2, SBJPR-2, BGJRH, BGJTG-2, BGGTJ,

Table 3. Seedling infection types (ITs)† of Thatcher-derived near-isogenic lines (NILs) inoculated with 31 *Puccinia triticina* isolates.

NIL	Race‡														
	MBTTS-1	FGKTJ	FGJTJ-1	BGJTG-1	MGTTS	FGJTJ-2	FGJTJ-3	SBJPQ-1	FGGTJ	SBJPR-1	SBJPQ-2	SBJPR-2	MGKTS	MBTTS-2	BGJRH
*Lr*1	4	0	0	;	3+	0;	0	4	0	4	3	4	4	4	0
*Lr*2a	;	1	1+	;	;	2–	1–	3+	;	4	3+	4	;	;	;
*Lr*2b	3–	2	2	;	1	2	2	4	2	4	4	4–	3–	3	;
*Lr*2c	1+	3	3	1	1	3–	3–	4	3	4	4	4	1	2	2–
*Lr*3	4	4	4–	;	4	3	3+	;	4	;	1	;	3	4	;
*Lr*3bg	4	4	3	;	3+	4–	4–	1–	4–	;	1+	;	3+	4–	1
*Lr*3ka	3–	;	1+	;	3	;	1	;	2	;	;	;	2+	3+	;
*Lr*9	;	0	0;	0	0;	0	0	;	0	1	1	;	;	2–	0
*Lr*10	4	3+	4–	4	4–	4–	4–	1	3	2+	2–	1	4	4	4
*Lr*11	4	4	4	4	4–	4	4	4	4	4	4	4–	4	4	4
*Lr*12	4	4	4	4	4	4	4	3–	4	4	4	4	3+	4	4
*Lr*13	4	4	4	4	4	4–	3	4	4	4	3+	4	3–	4	4
*Lr*14a	4	4–	4	3+	4–	4–	4–	4	4	3	4	3	3+	4	1+
*Lr*14b	4	4–	4	4–	3	4	4–	3–	4	4	2+	4	3	4	3
*Lr*15	4	1	1	1–	4	2–	1–	3	2–	4	4	4	3	3+	1
*Lr*16	2	4	3–	4	3–	4–	3–	2+	4	2+	2+	2+	3–	2+	4
*Lr*17	4	3	3–	3–	4	3	2+	4	2+	4-	4	3	4–	4–	3
*Lr*18	3–	4	3+	3	3+	4–	3–	3+	3	3+	3+	3	3	3	3–
*Lr*19	;	0	0;	;	;	;	0;	;	0;	;	;	;	;	;	;
*Lr*20	4	2	4	;	4	4	4	4	4	4	3+	4	4	4	;
*Lr*21	3	4	3+	3+	3–	4–	4–	4	4–	4	3	4–	3+	3–	4
*Lr*22	3–	4	4	4–	3+	3	4	3+	4–	4–	3	4	3–	3	4
*Lr*23	3–	4	4	2+	4	3+	4	2+	4	2+	2+	2+	3	3	2+
*Lr*24	;	1	;	1+	;	1+	;1	;	;	1	;	;	2–	1–	1
*Lr*25	2	4	;	;	1	1	2–	1–	2	1	;	;	2+	1+	1
*Lr*26	2+	0	0	1	2+	0	0	;	0	;	1	;	2	2–	0
*Lr*27+31	4–	3–	2+	3–	3	3–	2–	1–	2+	;	1	;	3	3	4
*Lr*28	2+	;	0	;	2+	;	0	1	0;	4	1	3	2+	1	4
*Lr*29	1	;	;	;	2–	1	2	1–	1+	1	1–	;	1	1	1+
*Lr*30	3–	2+	2+	1	3	2+	2+	1	2+	2	2–	;	3	3	2+
*Lr*32	3	4	2+	3+	3	3	3	2	3	3	3–	3–	2+	3–	4
*Lr*33	4–	4	4–	3	4–	4	4–	4	4	4	3+	4–	3–	3–	4
*Lr*34	4–	4	4	4	4–	4–	4	3–	4–	4	4–	4	3	4	4
*Lr*35	3+	4	4	4	4–	4	4	4	4	4	3+	4	3+	4	4
*Lr*37	4	3	3	2+	4–	3	3–	2	4	3–	2+	2+	3–	4	2+
*Lr*38	1–	1–	;	;	2+	;	;1	;	;1	1	2–	2–	;	1	;
*Lr*44	3+	4	4–	4–	4	4–	3+	1+	3+	2	2	2+	4	3+	4–
*Lr*B	4	4	4	4	4	4	3	4	4–	3	4	3+	3+	4	4
*Lr*W	2–	2–	1–	1–	2–	2	2	2+	1	2–	2+	1	2–	1	1
*Lr*Tc	4	4	4	4	4	4	4	4	4	4–	3+	4	4	4	4

†ITs: 0 = immune; ";" = hypersensitive fleck with no sporulation; 1 = small uredinia with necrosis; 2 = small uredinia with chlorosis; 3 = moderate size uredinia without chlorosis or necrosis; 4 = large uredinia without chlorosis or necrosis; "+" = slightly larger uredinia; and "–" = slightly smaller uredinia; ITs with two symbols indicate a range in ITs.

‡Similar races are separated by Arabic numerals.

LGKTQ, SBJPQ-3, SBJPL, SBJPQ-4, BGGQJ, BGGTK, BGGSG, and BFJSG and high ITs to all other isolates studied. Similarly, the genes *Lr*23 and *Lr*37 in combination had similar low ITs to all the isolates listed above and high ITs to the rest of the isolates tested. Therefore, cultivars Galama and K-6295-4A were postulated as having the genes *Lr*23 and *Lr*37. Cultivar Sirbo had low ITs to isolates FGKTJ, FGJTJ-1, BFJTG-1, FGJTJ-2, FGJTJ-3, FGGTJ, BGJRH, BGJRH, BGJTG-2, CGJTJ, FGKPK, CGKPJ, BGGTJ, DBJTT, SBJPL, BGGQJ, BGGTK, BGGSG, BJJKJ, and BGJSG and high ITs to all other isolates tested. The genes *Lr*1 and *Lr*21 in combination also had low ITs to these isolates and high ITs to the rest of the isolates. Hence, cultivar Sirbo was postulated as having

Table 3. Continued.

NIL	Race‡															
	BGJTG-2	CGJTJ	FGKPK	CGKPJ	BGGTJ	DBJTT	LGKTQ	SBJPQ-3	SBJMQ	SBJPL	SBJPQ-4	BGGQJ	BGGTK	BGGSG	BJJKJ	BGJSG
*Lr*1	;	;	0	0;	0	0	4	4	4–	3	4	;	0	;	0;	;
*Lr*2a	;	;1	1	;	;	1	;	3+	4	3	4	;	0	;	;	;
*Lr*2b	;	;	;	0	;	3–	2+	4–	3+	3	4	;	0	1+	;	1
*Lr*2c	1	2+	3	2+	;	4	2–	3+	4	3+	4	;	;	1	;	1–
*Lr*3	1	3–	4	4	;	;	1	;	;	1–	;	;	2	1–	;	1
*Lr*3bg	;	3+	3	3–	;	;	1	;	;	1	;	;	;	1;	;	1+
*Lr*3ka	;	2–	;	;	;	2–	1	0;	2	1	;0	2	;	;	;	2
*Lr*9	0	0	0	0	0	0	;0	0;	0;	;	1	0	0	;	0	;
*Lr*10	4	3	2+	2+	4	4	4	1+	2+	1	2+	4	4	4	4	3+
*Lr*11	4	4	4–	4–	4	4	4	4	4	3–	4	4	4	4	4	4
*Lr*12	4	4	4	4	4	4	4	4	4–	3	4	4	4	4	4	4
*Lr*13	4	4	4	4	4–	4	4	3+	4	3–	4	4	4	4	4	4
*Lr*14a	4	4	3+	4	3+	4	4	4	2+	3+	4	2	4	4	3	4
*Lr*14b	3	4	4–	4–	4	4	4	3–	4	2+	3–	4	4	3–	4–	3+
*Lr*15	2+	1	1	1+	;	4	4	4	4	3+	4	;	;	2	1	2
*Lr*16	4	4	4–	3–	3+	2	3–	2+	2+	2+	2+	4	4	3+	4–	3+
*Lr*17	3+	3–	3	3	2–	3–	4	4–	3+	3	4	2+	1	2+	3+	4
*Lr*18	3+	4	4	4	3–	4–	3–	3–	3	3–	3+	1	4	2+	3	2+
*Lr*19	;	0	0	0	0;	0;	;	;	0;	;	;	0;	;	;	;	;
*Lr*20	1	4	2+	;	4–	;	1–	4	4–	3+	4–	3+	2–	1	3–	1
*Lr*21	4	4–	4	4–	4–	4	3+	3–	3–	2+	3–	3–	4	3–	3	3+
*Lr*22	3+	4	4	3	4	4–	4	3+	3	3	4–	3	4	4	4	3–
*Lr*23	2+	4	4	4	4–	3	2+	2–	3–	2	2+	4	3+	2–	3	2+
*Lr*24	;	1	;	;	;	1	1–	1	1	1–	2	;	1	1	2+	2–
*Lr*25	;	4	;	0	4	1	1+	1–	;	1	2–	0	4	1+	;	1
*Lr*26	0	0	0	0	0	0	2+	;	;	;	;	0	0	0;	0	;
*Lr*27+31	4	2+	3–	2+	3–	2+	4	1+	1	1	2	3	3	3+	3	3+
*Lr*28	1	0	4	0	;	3	1	;	;	1–	;	0;	4	2	;	1
*Lr*29	1–	0	;	;	;	2	;	;	;	;	1–	0;	;	1	1	1–
*Lr*30	2	2	3–	3–	;	1+	3–	1+	2	1+	2	0;	;	2	2–	1
*Lr*32	3	3–	3–	;2+	3+	4	3–	3–	4	2+	3	3–	3+	2+	3	2+
*Lr*33	4	3	4	4–	3	3+	3+	3	3+	3–	3+	3–	4	3+	4–	4–
*Lr*34	4–	3+	4–	4	4	4–	4	4–	4	3	4	4–	4	4	4	4
*Lr*35	3+	4	4	3	4	4	4	4	4	3+	4	4	4	3+	4	3+
*Lr*37	2+	3	4	3–	2	3+	4	3–	3	2+	2+	2+	2	2	3–	2+
*Lr*38	;	;	0;	;	;	1	2	1	2+	1	2	;	;	;	;	;
*Lr*44	4	3+	3+	3	3+	3	3+	2–	2+	1–	2	3+	4	4–	4	4
*Lr*B	4–	4	4–	3+	4	4	4	4	3+	3–	3+	4–	4	3–	4–	4
*Lr*W	2	2+	2	;	;	2–	2+	1+	2	1+	2	;	;	2–	1	2–
*Lr*Tc	4	4	4	4	4	4	3+	4	4	4	4	4	4	4–	4–	4

†ITs: 0 = immune; ";" = hypersensitive fleck with no sporulation; 1 = small uredinia with necrosis; 2 = small uredinia with chlorosis; 3 = moderate size uredinia without chlorosis or necrosis; 4 = large uredinia without chlorosis or necrosis; "+" = slightly larger uredinia; and "–" = slightly smaller uredinia; ITs with two symbols indicate a range in ITs.

‡Similar races are separated by Arabic numerals.

genes *Lr*1 and *Lr*21. Cultivar Shinna had low ITs to isolates SBJPQ-1, SBJPR-1, SBJPQ-2, SBJPR-2, FGKPK, CGKPJ, SBJPQ-3, SBJMQ, SBJPL, and SBJPQ-4 and high ITs to all other isolates tested. The genes *Lr*10 and *Lr*44 also had similar pattern of ITs with cultivar Shinna, which led to the postulation that this cultivar had the genes *Lr*10 and *Lr*44.

In general, a total of 18 seedling leaf rust resistance genes were postulated to be present in the 36 bread wheat cultivars tested (Table 4). The 23 Ethiopian bread wheat cultivars tested were postulated as having leaf rust resistance genes *Lr*1, 2c, 3, 3ka, 9, 10, 14a, 14b, 13, 16, 18, 21, 23, 27+31, 30, 37, and 44, while the 13 German bread wheat cultivars were postulated as having *Lr*9, 18, 20, and 21.

Table 4. Postulated genes and virulence of 31 *Puccinia triticina* isolates against wheat cultivars of Ethiopian and German origins tested at seedling stage.†

Cultivar	Race‡															Postulated genes
	MBTTS-1	FGKTJ	FGJTJ-1	BGJTG-1	MGTTS	FGJTJ-2	FGJTJ-3	SBJPQ-1	FGGTJ	SBJPR-1	SBJPQ-2	SBJPR-2	MGKTS	MBTTS-2	BGJRH	
Bobitcho	1+	0	0	;0	2+	;	;	;	0	;	;	;	1–	2–	0	*Lr*9
Galama	3	4	4	;0	4	4	0	;	4	;	2+	2+	3+	4–	;2	*Lr*23, 37
Tussie	;	0	0	0	2	0	0	;	0	0	;	;	1	;	0	*Lr*9
Shinna	4	4	4	4–	4	4	4–	1–	4–	2	2	2	3+	4	4	*Lr*10, 44
Dereselign	4	4–	4	;	4	4–	4	2+	4	;	;	0	4–	4	;	*Lr*3
ET-13A2	4	3	4	1	4	3–	4–	1	3+	2–	1	;	3+	4–	2+	*Lr*14a, 23
Sirbo	4–	;	0	;	4	0;	;	3–	0	4–	3–	4–	3–	4–	0	*Lr*1, 21
K6295-4A	3–	4	4	2	4	4–	4	1+	4	1+	1	;	4–	4–	2+	*Lr*23, 37
Hawi	1	4	0	0	2+	3	0	;	0	;	1	;	2	1+	0	*Lr*2c, 23, 27+31
Katar	4	4	4	;	4	4	4	;	4	;	;	0;	3+	4–	0	*Lr*3
Abola	2+	1+	0	;0	1+	0;	1	;	2–	;	;	0	2	2+	0	*Lr*2c, 30
Wabe	4	0	0	0	4	;	0	1	0	;	1	;	4	4–	0	*Lr*1, 10
Dashen	2	0	0	0	4	0	0	1	0	;	;	;	1	2–	0	*Lr*3ka, 16
Pavon-76	4	0	0	0;	4	0;	0	1	0	1–	1	;	4	4–	0	*Lr*1, 10, 13
Dodotta	4–	4	4	3	4	4	4–	3–	4	3–	2+	4	3+	4–	4–	*Lr*14b, 18
Kubsa	4	4	4	3	4	4	4	2+	4	2+	2	2+	4	3+	4	*Lr*44
Granny	4	4	4	4	4	4	4	3+	4	4	4–	3+	4	4	3+	*Lr*21
Fasan	4–	2	4	;	4	4–	4	3+	4	4	3–	3–	3+	4–	;	*Lr*20
Epos	4	2	3+	;	4	4	4	4	4	4	4	4	4	4	;	*Lr*20
Triso	4	1+	4–	;	4–	4	4–	4	4	4	3+	4–	4	4–	;	*Lr*18, 20
Quattro	3+	2+	4	;	4	4	3+	4	4	4	4	4	4	4	;	*Lr*20
Tybalt	;	;	;	;	1	;	1	1–	;	;	;	;	;	;	;	*Lr*9

†Infection types (ITs): 0 = immune; ";" = hypersensitive fleck with no sporulation; 1 = small uredinia with necrosis; 2 = small uredinia with chlorosis; 3 = moderate size uredinia without chlorosis or necrosis; 4 = large uredinia without chlorosis or necrosis; "+" = slightly larger uredinia; and "–" = slightly smaller uredinia; ITs with two symbols indicate a range in ITs.

‡Similar races are separated by Arabic numerals.

Cultivars Galama, Shinna, ET-13A2, Sirbo, K6295–4A, Hawi, Abola, Wabe, Dashen, Pavon-76, and Dodota from Ethiopia and cultivar Triso from Germany were postulated as having more than one gene for leaf rust resistance. Cultivars Hawi and Pavon-76 were postulated as having a combination of three leaf rust resistance genes, whereas cultivars Galama, Shinna, ET-13A2, Sirbo, K6295-4A, Abola, Wabe, Dashen, Dodota, and Triso were assumed to contain two leaf rust resistance genes. On the other hand, cultivars Bobitcho, Tussie, Dereselign, Katar, and Kubsa from Ethiopia and cultivars Granny, Fasan, Epos, Quattro, and Tybalt from Germany have a single gene for leaf rust resistance. As indicated in Table 4, the most commonly detected leaf rust resistance genes in the German and Ethiopian wheat cultivars tested were *Lr*20 and *Lr*23, respectively. Both leaf rust resistance genes occurred in four wheat cultivars from each of the two countries.

The leaf rust resistance genes present in cultivars Mitike, Simba, Wetera, K6290 Bulk, Magal, Morocco, Tura, Lavett, Monsun, and Naxos could not be postulated because of nonmatching IT patterns with any of the NILs tested (Table 5). It was also not possible to postulate gene(s) that may be present in cultivars Munk, Perdix, Monopol, and Thasos because these cultivars were susceptible to all isolates of *P. triticina* tested (Table 5).

DISCUSSION

The leaf rust–causing pathogen, *Puccinia triticina* Eriks., occurs almost everywhere wheat is grown. The disease is also one of the most important diseases of wheat in Ethiopia, and its recurrent outbreaks have threatened wheat production in the past (Assefa, 2001; Badebo, 2002). For instance, out of the 26 wheat cultivars released in the period 1970 to 1993, only three retained their resistance to leaf rust (Geleta and Tanner, 1995). Use of host resistance is the most economical and environmentally friendly method of controlling leaf rust on wheat. In Ethiopia, wheat production is characterized by high biodiversity in crops and low-input systems, and the control of rust diseases largely relies on genetic resistance. In Germany, in contrast, production systems with high input of fertilizers, narrow genetic diversity of cultivars and high yield potential favor the use of fungicides for the control of leaf diseases in wheat. Since the significance of genetic resistance largely differs in these production systems, seedling leaf rust resistance of wheat from both countries was investigated in parallel.

Table 4. Continued.†

Cultivar	Race‡																Postulated genes
	BGJTG-2	CGJTJ	FGKPK	CGKPJ	BGGTJ	DBJTT	LGKTQ	SBJPQ-3	SBJMQ	SBJPL	SBJPQ-4	BGGQJ	BGGTK	BGGSG	BJJKJ	BGJSG	
Bobitcho	0	0	0	0	0	0	1+	;	;2	;	;	0	0	0	2–	;	*Lr*9
Galama	2	4	4	4–	;	4	2+	2	3	1	;	2+	0	;	3	;	*Lr*23, 37
Tussie	0	0	0	0	0	0	;	1–	;	;	0	0	0	0	0	;	*Lr*9
Shinna	4	3–	0	0	4–	4	4	2–	;	1	1	3	4	4	4–	4–	*Lr*10, 44
Dereselign	;	4–	4–	3+	;	;	1	;	;	1–	;	;	;	1–	;	1	*Lr*3
ET-13A2	;	4	4	4	3+	3	2+	2	1+	2–	1	;	3	;	3	2	*Lr*14a, 23
Sirbo	1	0	0	0	0	0	3+	3–	3–	2+	3	0	0	0	0;	;	*Lr*1, 21
K6295-4A	1–	4	4–	4–	2–	4	2+	2	3–	1	1	;	2+	2	3	1	*Lr*23, 37
Hawi	0	0	4	0	0	0	2+	2	;	;	;	0	0	0	0	;0	*Lr*2c, 23, 27+31
Katar	;	4	4	4–	;	;	;	1	;	;	;	;	;	;	;	1	*Lr*3
Abola	;	0	4	2+	0	0	;	;	0	;	;	0;	0	;	;	;	*Lr*2c, 30
Wabe	;0	0	2+	0	2+	0	3+	;	1	1–	;	0	0	0	0	0	*Lr*1, 10
Dashen	1	0	0	0	0	0	2	0;	;	;	;	0	0	;	0	;0	*Lr*3ka, 16
Pavon-76	0	0	0	0;	0	0	4	1	;1	1–	2–	0	0	0	0	0	*Lr*1, 10, 13
Dodotta	3–	4–	4	4–	3–	4	3+	3–	3+	2	3–	;	4	2+	3	2+	*Lr*14b, 18
Kubsa	4	4	4–	4	4	4	4	2+	2+	1+	2+	3+	4	4–	4	4	*Lr*44
Granny	4	4	4	4	3+	4	3+	3+	3+	2+	4	3+	3	4	3+	4	*Lr*21
Fasan	1	3+	2	1	4–	;	1	4	4	3	4–	4–	2–	;	3	2	*Lr*20
Epos	;	4	2+	2+	4	;	1–	4	4	4	4	4	2+	1–	3	2+	*Lr*20
Triso	;	4	1	1	3–	;	1	4	4	3+	4	1	1	;	3	1	*Lr*18, 20
Quattro	;	4	2+	1	4	;	2+	4	4	3	4	4–	1+	;	3	1	*Lr*20
Tybalt	;	1	0	;	;	;	;	;1	;	1	1–	;	1+	;	;	1–	*Lr*9

†Infection types (ITs): 0 = immune; ";" = hypersensitive fleck with no sporulation; 1 = small uredinia with necrosis; 2 = small uredinia with chlorosis; 3 = moderate size uredinia without chlorosis or necrosis; 4 = large uredinia without chlorosis or necrosis; "+" = slightly larger uredinia; and "–" = slightly smaller uredinia; ITs with two symbols indicate a range in ITs.

‡Similar races are separated by Arabic numerals.

Sources of disease resistance from areas with high biodiversity in wheat may be used in other areas in breeding programs to reduce the frequency of fungicide applications as well as for organic production systems.

Postulation of the leaf rust resistance genes effective at the seedling stage was performed on the basis of the gene-for-gene specificity concept described by Flor (1971). Gene postulation allows one to quickly determine the genes present in wheat cultivars of diverse genetic backgrounds (Kolmer, 2003). In this study, 18 leaf rust resistance genes were postulated to be present in the 36 wheat cultivars of Ethiopian and German origins. The genes *Lr*1, 2c, 3, 3ka, 9, 10, 13, 14a, 14b, 16, 18, 21, 23, 27+31, 30, 37, and 44 were postulated to be present in the Ethiopian wheat cultivars tested, while the German bread wheat cultivars were postulated to have *Lr*9, 18, 20, and 21. Cultivar Pavon-76 was postulated to have *Lr*1, 10, and 13, the same way as postulated by Singh and Rajaram (1991), demonstrating the validity of the gene postulation practice in this study. However, the genes present in cultivars K6290 Bulk, Lavett, Magal, Mitike, Monsun, Morocco, Naxos, Simba, Tura, and Wetera could not be postulated because of the nonmatching virulence patterns with any of the NILs tested. In a previous study, the leaf rust resistance gene(s) present in cultivar Lavett could not be postulated (Hysing et al., 2006). The genes present in cultivars Munk, Perdix, and Thasos could not be postulated because these cultivars were susceptible to all isolates tested. It may be necessary to use more isolates of diverse virulence phenotypes and/or NILs with other resistance genes to postulate the genes in these cultivars. Cultivar Thasos may lack effective leaf rust resistance genes as our results are in agreement with the conclusion of Hysing et al. (2006) using other leaf rust isolates. Cultivar Monopol was also susceptible to infection by all isolates tested. This cultivar is not known to have a leaf rust resistance gene and is mostly used as a susceptible check in various studies.

The leaf rust resistance genes *Lr*9, *Lr*19, *Lr*24, *Lr*26, *Lr*29, *Lr*38, and *Lr*W were effective against all *P. triticina* isolates tested, making it difficult to postulate these genes in cultivars Bobitcho, Tussie, and Tybalt, which also had resistance genes effective against all isolates tested. The genes *Lr*19, *Lr*29, and *Lr*38 had not been exploited in agriculture (McIntosh et al., 1995) and hence may not be present in cultivars Bobitcho, Tussie or Tybalt. Therefore, *Lr*9, *Lr*24, and *Lr*26 are the practical candidate genes that may be present in the three wheat cultivars. McVeh and

Table 5. Seedling leaf rust resistance genes that could not be postulated as they were tested against the 31 *Puccinia triticina* isolates.†

Cultivar	Race‡															Postulated genes§
	MBTTS-1	FGKTJ	FGJTJ-1	BGJTG-1	MGTTS	FGJTJ-2	FGJTJ-3	SBJPQ-1	FGGTJ	SBJPR-1	SBJPQ-2	SBJPR-2	MGKTS	MBTTS-2	BGJRH	
Mitike	4	3+	4	3	3+	4	4	2+	4	2+	2+	3	3	3+	3	U
Simba	4	4	4	;	4	4	4	;	4	;	;	0;	3+	4–	0	U
Wetera	4–	3+	3	3	3+	3	2	4	4	4	4–	4	4–	4	4	U
K6290 Bulk	2+	1+	0	;0	1+	0;	1	;	2–	;	;	0	2	2+	0	U
Magal	2	4	0	0	3	;	0	;	0	0;	;	0	2+	2	0	U
Morocco	4–	1+	;	3–	2	1	4	3	;	2	3	3	1	4	4–	U
Tura	3–	;	3+	;	2–	2+	0;	;	0	;	;	0	1–	2	0;	U
Munk	4	4	4	4	4	4	4	3+	4	4–	3+	4	4	4–	4	NG
Lavett	2+	2+	2+	1	3+	3+	3+	2	2+	2–	2–	1	2+	2+	;	U
Monsun	4	4	4	4	4	4	4	4	4	4	4	4	3+	4	4	U
Perdix	4	4	4	4	4	4	4	4	4	4	4	4	3+	4	4	NG
Monopol	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	NG
Thasos	4–	4	4	4	4	4	4	3	4	4	4	3	3–	4	3	NG
Naxos	4	4	2	4	4	4	3+	3	4	4	3	4–	2+	4–	;	U

†Infection types (ITs): 0 = immune, with no visible necrosis or uredinia; ";" = hypersensitive fleck with no sporulation; 1 = small uredinia surrounded by necrosis; 2 = small uredinia surrounded by chlorosis; 3 = moderate size uredinia without chlorosis or necrosis; 4 = large uredinia without chlorosis or necrosis; "+" = slightly larger uredinia; "–" = slightly smaller uredinia; ITs with two symbols indicate a range in ITs.

‡Similar races are separated by Arabic numerals.

§U: unidentified gene(s) present; NG: no effective gene detected.

Long (1993) and Singh (1993) took the lowest number of genes required to explain a phenotype. Hence, *Lr*9 was taken as the most likely leaf rust resistance gene present in the three wheat cultivars. However, it is recommended that more isolates with different virulence formulae on these *Lr* genes and wheat cultivars should be used for more accurate gene postulation.

The most commonly occurring *Lr* genes in the German and Ethiopian wheat cultivars tested were *Lr*20 and *Lr*23, respectively. Virulence for these genes was found frequently, and the two genes were not considered important components of the genetic base for leaf rust resistance in wheat (McIntosh et al., 1995; Wamishe and Milus, 2004). *Lr*13, probably the most widely distributed *Lr* gene in the world (McIntosh et al., 1995), was postulated only for Ethiopian cultivars. According to Winzeler et al. (2000) and Hysing et al. (2006), this gene, once considered to confer durable adult plant resistance (APR), is present in up to 58% of the European wheat genotypes. The lack of detection in the German cultivars may also be due to the limited number of genotypes tested.

Out of the 18 leaf rust resistance genes detected in this study, 17 were postulated to be present in the Ethiopian wheat cultivars, while the German wheat cultivars were postulated to have only 4 leaf rust resistance genes. For all Ethiopian cultivars tested, at least one resistance gene could be postulated; in contrast, 4 out of 13 German cultivars were susceptible to all *P. triticina* genotypes. That the German wheat cultivars had relatively fewer number of leaf rust resistance genes than the Ethiopian wheat cultivars may indicate that breeding for leaf rust resistance is not a high-priority practice among wheat breeders in the country as farmers can afford to apply fungicides against the disease. On the other hand, host resistance is the only practical means of controlling wheat leaf rust in Ethiopia because resource-poor farmers cannot afford to apply fungicides against wheat diseases. Hence, wheat breeders in Ethiopia incorporated more leaf rust resistance genes into the existing wheat cultivars, which resulted in wheat cultivars with relatively wider genetic base for leaf rust resistance.

Cultivars in our material with no postulated *Lr* seedling resistance genes may have additional APR or additive minor genes that contribute to low disease pressure in the field (Hysing et al., 2006). Adult plant resistance is of high importance in field resistance to leaf rust. For example, *Lr*11, *Lr*12, *Lr*13, *Lr*22b, *Lr*34, *Lr*35, and *Lr*37 have been reported as APR genes (Mishra et al., 2005; McCallum and Seto-Goh, 2006; Kolmer et al., 2007). Winzeler et al. (2000) reported that 55% of European wheat cultivars had APR resulting from the activity of quantitative trait loci (QTL) and/or *Lr*34 that enhances resistance. Sixty out of 105 European wheat cultivars tested showed APR in the field (Pathan and Park, 2006). These genes could be detected by growing adult plants under controlled conditions and testing them by inoculation or by growing the genotypes in the field and monitoring disease severity in the growth period. Although information about the molecular principles of APR to *P. triticina* is limited, QTL studies in segregating populations have been initiated to characterize APR genes for leaf and stripe rust (*P. strii-*

Table 5. Continued.[†]

Cultivar	Race[‡]																Postulated genes[§]
	BGJTG-2	CGJTJ	FGKPK	CGKPJ	BGGTJ	DBJTT	LGKTQ	SBJPQ-3	SBJMQ	SBJPL	SBJPQ-4	BGGQJ	BGGTK	BGGSG	BJJKJ	BGJSG	
Mitike	4	0	4	0	0	0	2+	2	;	;	;	0	0	0	0	;0	U
Simba	;	4	4	0	0	0	;	0;	;	;	0	0	0	0	0;	0	U
Wetera	4	0	0	0	0	0	1	;	0	0	;	0	0	;	0	;	U
K6290 Bulk	;	3	3–	3–	3–	4	4	4	4	4	4	3	4	3+	4	4	U
Magal	;	4	4	0	0	0	;	1	0;	;	0;	0	0;	0	0	;	U
Morocco	4	3–	4	4	4	4	3–	4	4	2+	4	;	4	4	4	3–	U
Tura	0	0	0	4	;	0	2+	1	0;	1	2+	0	0	0;	0;	0	U
Munk	4	4	4	4–	4	4	4	4	4	4	4	4–	4	4–	4	4	NG
Lavett	1	3+	1+	1	2	;1	1	2	2–	1	2	2+	2–	1	2+	1	U
Monsun	;	4	4	4	4–	4	2+	4	4	4	4	4	4	4	4	4	U
Perdix	4	4	4–	4	4–	4	3+	4	4	3	4	4	4	4	4	4	NG
Monopol	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	NG
Thasos	4	4–	4–	3	4	4	3+	4	4	3+	4	4	4	4	4	4	NG
Naxos	4	4–	4	3–	4	4	3	4	;	3–	;	;	4	4	;	3–	U

[†]Infection types (ITs): 0 = immune, with no visible necrosis or uredinia; ";" = hypersensitive fleck with no sporulation; 1 = small uredinia surrounded by necrosis; 2 = small uredinia surrounded by chlorosis; 3 = moderate size uredinia without chlorosis or necrosis; 4 = large uredinia without chlorosis or necrosis; "+" = slightly larger uredinia; "–" = slightly smaller uredinia; ITs with two symbols indicate a range in ITs.

[‡]Similar races are separated by Arabic numerals.

[§]U: unidentified gene(s) present; NG: no effective gene detected.

formis) in several wheat genotypes (Messmer et al., 2000; Singh et al., 2005; Xu et al., 2005; William et al., 2006; Leonova et al., 2007).

Durable rust resistance may be achieved by pyramiding, that is, accumulating several effective resistance genes in one cultivar (Mesterhazy et al., 2000; McDonald and Linde, 2002). The combination of *n* (number of genes) undefeated resistance genes should extent the longevity of each resistance since it would require simultaneous mutations in at least *n* avirulence loci to produce a new virulent pathotype (Pink, 2002). Genes like *Lr*13, *Lr*34, and *Lr*46 have been reported to confer durable resistance to *P. triticina*—at least in some regions (Barcellos et al., 2000; Martinez et al., 2001). Molecular markers facilitating gene pyramiding have been developed for several *Lr* genes (Helguera et al., 2003; Blaszczyk et al., 2004; Hiebert et al., 2005). Slow rusting has been shown to be more durable than major seedling resistance (Singh et al., 2001), and a combination of APR gene *Lr*34 and several additional minor genes has resulted in a high level of nonspecific resistance in some cultivars (Singh et al., 2000; Navabi et al., 2005).

The results of the current study show that most of the wheat cultivars do not have an adequate level of resistance for leaf rust, indicating the need for incorporating more effective leaf rust resistance genes into the Ethiopian and German bread wheat cultivars tested.

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