A North American System of Nomenclature for *Puccinia recondita* f. sp. *tritici*

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ABSTRACT

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A nomenclature system for designating virulence combinations of cultures of *Puccinia recondita* f. sp. *tritici* in North America is proposed by the North American Wheat Leaf Rust Research Workers Committee. Host seedling resistance genes *Lr*1, 2a, 2c, 3, 3ka, 9, 11, 16, 17, 24, 26, and 30 occur singly in each of the primary differentials. Host lines are grouped into sets of four, and infection types are recorded for each line. Avirulence and virulence of cultures are determined by low and high infection types, respectively. Virulence combinations are to be designated by a three-letter code followed by a hyphen and a listing of ineffective host genes in any supplemental differential host set used. Additionally, a current leaf rust resistance series that consists of host genes *Lr*19, 21, 25, 29, 32, and RL6059 (*Lr*33 + 34) is recommended for evaluating bulk collections or composites of individual cultures. A supplemental series of *Lr*12, 13, 22a, 22b, and 34 adult-plant resistance genes is recommended for evaluating virulence to adult-plant resistance to leaf rust.

Additional keywords: physiologic specialization, rust races, wheat leaf rust.

Distinct physiologic races of *Puccinia recondita* Rob. ex. Desm. f. sp. *tritici* were first reported by Mains and Jackson in 1921 (19). Isolates of the fungus were separated on the basis of their ability to infect the wheat cultivars Kanred and Malakof. These authors later described 12 physiologic races using a differential series of 11 cultivars of wheat (20). The differential cultivars were Malakof, Hussar, Democrat, Webster, Norka, Turkey 47, Mediterranean, Carina, Brevit, Similis, and Loros. Infection types 0, 1, and 2 indicated host resistance, and infection types 3 and 4 indicated host susceptibility (20). Physiologic races were identified by a dichotomous key of resistant and susceptible host reactions.

Johnston and Mains (14) dropped the cultivar Turkey 47 from the differential series because of seed impurity, and they dropped the cultivars Norka and Similis because their resistance pattern was similar to that of Malakof. The remaining eight differential cultivars formed the basis for what later became known as the International Register of Physiologic Races of *Puccinia recondita* f. sp. *tritici* (11) (Table 1), and 26 additional physiologic races were described (14). The register was revised several times by the addition of newly described physiologic races (11,13). By 1966, 228 International Standard races of *P. r. tritici* had been described (11).

Of the eight differential cultivars, Carina, Brevit, and Hussar were temperature sensitive for infection type and difficult to evaluate. Johnston (10) and Basile (2) proposed removing these three differentials from the keys and combining the International Standard races into 27 Unified Numeration races. International Standard races that were grouped together produced identical or similar infection types on the five remaining differentials: Malakof, Webster, Loros, Mediterranean, and Democrat (Table 1). Solimon et al (30) subsequently showed that in North America the resistance provided by both Mediterranean and Democrat is conditioned by the single gene *Lr*3; thus for North American virulence identification, one cultivar may be omitted.

Supplemental differential cultivars for North America were proposed in 1961 (16) and 1965 (34). The supplemental cultivars Thew (*Lr*20) (31), Gaza (32), Spica, and Kenya 1483 (33) were added to identify Australian and New Zealand races of leaf rust.

Genetic studies led to the identification of individual genes for leaf rust resistance. Designation of these genes by *Lr* number was initiated by Ausemus et al in 1946 (1). Browder (3) summarized the information on designated *Lr* genes through *Lr*29. The gene-for-gene concept as developed by Flor (9) and expanded by Person (21) showed the value of using single-gene host resistance in the classification of cereal rust fungi. Near-isogenic lines of wheat differing by single genes for resistance to leaf rust were developed by Johnston and Heyne (12) in a Wichita genotype and by Dyck

and Samborski (7) in a Thatcher genotype. Genetic studies of Samborski and Dyck (27,28) and Dyck and Samborski (7,8) identified the resistance genes present in the eight original differential cultivars and other sources of resistance (Table 2) and confirmed a gene-for-gene relationship in the *Triticum aestivum-P. r. tritici* pathosystem.

Near-isogenic lines were used in Canada (24) and the United States (17) to identify races of *P. r. tritici*. A modified Unified Numeration (UN) nomenclature was proposed with four single gene lines substituted for the five previous differential cultivars (17). Avirulence/virulence formulae were used to describe physiologic specialization in Canada (24,25). Virulence formulae, combined with the modified UN system, were used in the United States (17,18). Loegering and Browder (15) suggested a nomenclatural system in which each differential line was assigned a sequential number (SN). These numbers then were used in avirulence/virulence combinations, and each combination was assigned a code number.

The lack of a fully accepted nomenclatural system, other than the detailed avirulence/virulence formulae, in describing races of *P. r. tritici* has limited communications among North American researchers and consequently has hindered epidemiological and evolutionary studies. This paper describes a nomenclatural system agreed upon by the North American Leaf Rust Workers Committee in April 1986, in St. Paul, MN, that should enhance communication among scientists and encourage studies of population genetics and evolutionary development of *P. r. tritici* in North America. This system is by design similar to the nomenclatural system recently described for *P. graminis* (Pers.) f. sp. *tritici* (23).

MATERIALS AND METHODS

The 12 differential isolines selected for use in the nomenclature (designated as Prt [for *P. r. tritici*] code) are *Lr*1, 2a, 2c, 3, 3ka, 9, 11, 16, 17, 24, 26, and 30 (Table 2). The cultivar Thatcher was used as the common background because leaf rust resistance genes are strongly expressed in this cultivar (8). Differential hosts were chosen in part because of a clear distinction between low and high infection types in the environments normally used for evaluation. Thatcher, the background host parent, is used as a check for determining a high infection type. Host resistance genes *Lr*1, 2a, 2c, and 3 were chosen to provide historical continuity because they were in the International Standard differential set and comprise the modified UN set (17) (Table 1). These differentials also account for the majority of the variation in the North American wheat leaf rust population. Resistance genes *Lr*1, 2a, and 3 have been used in commercially grown cultivars in the north central United States. Cultures virulent to *Lr*2a are invariably virulent to *Lr*2c; however, cultures avirulent to *Lr*2a may be either virulent or avirulent to *Lr*2c (8). Isolates virulent on *Lr*2c and avirulent to *Lr*2a are commonly found in the eastern and Pacific regions of Canada and the United States. Isolates from the prairie regions of North America generally produce similar infection types on *Lr*2a and *Lr*2c. These four differentials thus distinguish 12 races in North America (17), generally corresponding to 12 of Basile's UN races (2).

Host resistance genes *Lr*9, 16, 24, and 26 are important sources of resistance in North America. Virulence to these genes in North America is currently less than 10% in most areas (18,26). *Lr*9 has been used in soft red winter wheat cultivars (3) widely grown in the southern and eastern United States. *Lr*16 was used in the extensively grown Canadian cultivar Selkirk and more recently in the Canadian cultivar Columbus and U.S. hard red winter cultivars. Numerous hard red winter cultivars have *Lr*24. The *Lr*26 resistance is found in many cultivars worldwide and more recently in one U.S. cultivar (29). Virulence to the gene combination *Lr*24 and 26 is currently present in less than 1% of the population (18). Resistance genes *Lr*3ka, 11, 17, and 30 are commonly used in virulence surveys but are difficult to evaluate because of their temperature sensitivity (6). Intermediate levels of virulence to *Lr*3ka and *Lr*11 have been reported in eastern regions of Canada and the United States.

Additional single-gene resistance lines may be used to supplement the 12 chosen for the North American leaf rust differential series (Table 3). Intermediate frequencies of virulences to *Lr*B and 18 are characteristic of the leaf rust population found in eastern Canada (26). These genes are not known to have been used in commercial cultivars. The *Lr*10 gene has been used as a differential. Currently most of the leaf rust population in the Great Plains area of the United States is virulent to this resistance (18), whereas in the eastern United States the frequency of virulence is

TABLE 1. Differential hosts and *Lr* genes used in the International Register of Physiologic Races and the Unified Numeration system for *Puccinia recondita* f. sp. *tritici* (Prt)

International Standard differential host[x]	*Lr* gene(s)[y]	Unified Numeration differential host[z]	Comments
Malakof	1	+	*Lr*1 included in Prt set
Webster	2a	+	*Lr*2a included in Prt set
Carina	2b, B		Temperature sensitive
Brevit	2c, B		Temperature sensitive
Loros	2c	+	*Lr*2c included in Prt set
Mediterranean	3	+	*Lr*3 included in Prt set
Hussar	11		Temperature sensitive, included in Prt set.
Democrat	3	+	Duplicates Mediterranean in North America

[x] Mains and Jackson (20).
[y] Samborski and Dyck (27).
[z] Basile (2).

TABLE 2. Range of low infection types produced when wheat cultivar Thatcher lines with *Lr* genes used in the *Puccinia recondita* f. sp. *tritici* (Prt) differential set were inoculated with cultures of *P. r. tritici* that are avirulent with respect to these genes

Lr gene	Source	Low infection types[a]	Test line	Comments
1	Centenario	0;	TcLr1, RL6003	Used in hard red spring (HRS), hard red winter (HRW), and soft red winter (SRW) wheat breeding
2a	Webster	;	TcLr2a, RL6000 RL6016	Used in HRS
2c	Brevit	;1	TcLr2c, RL6047	
3	Democrat	;C	TcLr3, RL6002	Used in spring and winter wheat
3ka	Klein Anversario	12	TcLr3ka, RL6007	
9	*Aegilops umbellulata*	0;	TcLr9, RL6010	Used in SRW
11	Hussar	2;	TcLr11, RL6053	Used in SRW
16	Exchange	;1N	TcLr16, RL6005	Linked to *Sr*23
17	Klein Lucero	;12	TcLr17, RL6008	Used in HRW and SRW
24	*Agropyron elongatum*	;	TcLr24, RL6064	Linked to *Sr*24 Used in HRW
26	St 1.25	;	TcLr26, RL6078	Linked to *Sr*31 Used in HRW
30	Terenzio	2	TcLr30, RL6049	

[a] Expected low infection type may vary slightly depending on the entire host or pathogen genotype or with changes in environment. 0 = no uredia or other macroscopic signs of infection; ; = no uredia, but hypersensitive necrotic or chlorotic flecks of varying size present; 1 = small uredia often surrounded by necrosis; 2 = small to medium uredia often surrounded by chlorosis or necrosis; C = more chlorosis than normal for infection type; N = more necrosis than normal for infection type (23).

less. Many cultivars grown in the Great Plains have *Lr*10 as all or part of their resistance (3). *Lr*14a and 14b have been used to differentiate leaf rust cultures originating in the prairie region of western Canada from those in the intermountain region and eastern Canada (26).

Host resistance genes *Lr*19, 21, 25, 29, 32, and RL6059 (*Lr*33 + 34) are currently resistant to almost all isolates of leaf rust in North America and are recommended for evaluating virulence of bulk collections or composites of individual cultures (Table 4). This will facilitate the isolation of rare virulence characteristics in the leaf rust population. Newly found resistance genes which may be effective against all current isolates of leaf rust also should be added to this series. Genes *Lr*12, 13, 22a, 22b, and 34 may be used in tests to determine the frequency of virulence to cultivars with adult-plant resistance (Table 3).

A modified system of nomenclature was chosen from the available systems (22). The 12 differential isolines were arranged in three sets of four, and a letter was assigned to each of the 16 combinations of infection types possible for each of the three sets (Table 5). The consonants B through T were used to designate the 16 virulence combinations available for each of the three four-gene groups. The resulting three-letter code (Prt designation) can be followed by a hyphen, which separates the Prt code from that designating local supplemental differentials.

TABLE 3. Low infection types of other known leaf rust resistances that could serve as supplemental differential hosts for *Puccinia recondita* f. sp. *tritici*

Lr gene	Source	Low infection type[a]	Test line	Comments
2b	Carina	01C	TcLr2b, RL6019	
3bg	Bage	;C,23	TcLr3bg, RL6042	
10	Lee	;,2C	TcLr10, RL6004	
12	Exchange	APR[b]	TcLr12, RL6011	
13	Frontana	APR	TcLr13, CT263	
14a	Hope	X	TcLr14a, RL6013	
14b	Bowie	X	TcLr14b, RL6006	
15	Kenya 1-12-E-19-J	;C	TcLr15, RL6052	
18	Africa 43	2	TcLr18, RL6009	
20	Thew	0;	Thew	Linked to *Sr*15
22a	*Aegilops squarrosa*	APR	TcLr22a, RL6044	
22b	Thatcher	APR	Thatcher	
23	Gabo	0;	TcLr23, RL6012	
27	Gatcher	0;	Gatcher	Functions with *Lr*31
28	*Aegilops speltoides*	0;	TcLr28	
31	Gatcher	23	Gatcher	Functions with *Lr*27
33	PI58548	1+	TcLr33, RL6057	More effective with *Lr*34
34	Terenzio	APR	TcLr34, RL6058	
B	Brevit	;1	RL6047	

[a] 0 = no uredia or other macroscopic sign of infection; ; = no uredia, but hypersensitive necrotic or chlorotic flecks of varying size present; 1 = small uredia often surrounded by a necrosis; 2 = small to medium uredia often surrounded by necrosis or chlorosis; C = more chlorosis than expected for infection type; X = random distribution of variable-sized uredia on single leaf with a pure culture; + = uredia somewhat larger than normal for the infection type (23).
[b] Adult plant resistance.

TABLE 4. Source of the leaf resistance genes, the expressed low infection type, and the host lines recommended for inclusion in the resistant series

Lr gene	Source	Low infection type[a]	Test line	Comments
19	*Agropyron elongatum*	0	TcLr19, RL6040	Linked to *Sr*25
21	*Aegilops squarrosa*	0	TcLr21, RL6043	
25	*Secale cereal*	;N	Transec, RL6084	
29	*Agropyron elongatum*	0;	TcLr29, RL6080	
32	*Aegilops squarrosa*	;1+	TcLr32, RL5494-1	
33 + 34	PI58548	0;	RL6059	Effective combination

[a] Low infection type expressed may depend on the pathogen phenotype as well as changes in environment. 0 = no uredia or other macroscopic sign of infection; ; = no uredia, but hypersensitive necrotic or chlorotic flecks of varying size present; 1 = small uredia often surrounded by a necrosis; N = more necrosis than normal for infection type; + = uredia somewhat larger than normal for infection type (23).

RESULTS AND DISCUSSION

Of the genes found in the International Standard differential cultivars, two, *Lr*B (Carina and Brevit) and *Lr*2b (Carina), are not used in the new differential set. These genes were among those deleted by Basile (2) and Johnston (10) when they proposed the Unified Numeration system. The more recently identified genes *Lr*3ka, 9, 16, 17, 24, 26, and 30 have been added to the five remaining genes that were used to distinguish the International Standard races of *P. r. tritici*.

The infection types and Prt designations of current races of *P. r. tritici* from North America are presented in Table 6. The first four genes in the Prt nomenclature are those of the modified (UN) system. The Prt nomenclature differential series does not provide a complete phenotypic description of virulence because only selected host resistance genes are evaluated. Host genes such as *Lr*B, 10, 14a, 14b, and 18 can be used in addition to further differentiate virulences in *P. r. tritici*.

We propose that the North American virulence combination designation be reported with a Prt notation, followed by a hyphen and a listing of the *Lr* genes in the supplemental series on which the culture is virulent. Workers also should indicate which host genes in the supplemental series were used to evaluate the isolate collection. Host genes in the resistant series can be evaluated for resistance by using bulk collections of the leaf rust fungus. Cultures of the fungus isolated from high infection type pustules on host genes in the resistant series should be characterized for virulence using the Prt differentials and supplemental differentials.

The mean range of the low infection types produced with the selected host genotypes is shown in Table 2. All low infection types produced by these genes are treated as equivalent for the purposes of race designation. This will help avoid the subdividing of races on the basis of small environmental differences rather than genetic differences in the rust fungus.

The identification of virulence combinations in *P. r. tritici* has been and will remain an integral part of resistance breeding

TABLE 5. Code for the 12 North American differential hosts for *Puccinia recondita* f. sp. *tritici* (Prt) in ordered sets of four

Prt code[a]		Infection type[b] produced on near isogenic *Lr* lines:			
	Host set 1:	1	2a	2c	3
	Host set 2:	9	16	24	26
	Host set 3:	3ka	11	17	30
B		L	L	L	L
C		L	L	L	H
D		L	L	H	L
F		L	L	H	H
G		L	H	L	L
H		L	H	L	H
J		L	H	H	L
K		L	H	H	H
L		H	L	L	L
M		H	L	L	H
N		H	L	H	L
P		H	L	H	H
Q		H	H	L	L
R		H	H	L	H
S		H	H	H	L
T		H	H	H	H

[a] Prt code consists of the designation for set 1 followed by that for set 2, etc. For example, race MGB: set 1 (M)—virulent to *Lr*1, 3; set 2 (G)—virulent to *Lr*16; set 3 (B)—avirulent.
[b] L = low infection type (avirulent pathogen); H = high infection type (virulent pathogen).

TABLE 6. Infection types[a] produced by selected races of *Puccinia recondita* f. sp. *tritici* (Prt) from North America on resistance genes in the Prt differential set

Prt code	*Lr* genes												Previous race designations[b]	
	1	2a	2c	3	9	16	24	26	3ka	11	17	30	UN	International Standard
BBB	L	L	L	L	L	L	L	L	L	L	L	L	1	1,16,63,123
CBB	L	L	L	H	L	L	L	L	L	L	L	L	2	15,25,34,59,127
CBG	L	L	L	H	L	L	L	L	L	H	L	L	2	2,62,151,153
CBM	L	L	L	H	L	L	L	L	H	L	L	H	2	15,25,34,59,127
CCB	L	L	L	H	L	L	L	H	L	L	L	L	2	15,25,34,59,127
DBB	L	L	H	L	L	L	L	L	L	L	L	L	10	11,38,74,131,132,154,227
DBD	L	L	H	L	L	L	L	L	L	L	H	L	10	11,38,74,131,132,154,227
FBB	L	L	H	H	L	L	L	L	L	L	L	L	3	3,32,44,58,61,84,111,161,226
FLM	L	L	H	H	H	L	L	L	H	L	L	H	3	3,32,44,58,61,84,111,161,226
JBB	L	H	H	L	L	L	L	L	L	L	L	L	12	68,96,97,106,134,139,168, 190,195,215
JCB	L	H	H	L	L	L	L	H	L	L	L	L	12	68,96,97,106,134,139,168, 190,195,215
KBB	L	H	H	H	L	L	L	L	L	L	L	L	17	45,76,81,87,88,90,140,142, 143,176,185,212
KBG	L	H	H	H	L	L	L	L	L	H	L	L	17	57,67,85,136,162,167,188, 189,203,204,207,208,209
KDB	L	H	H	H	L	L	H	L	L	L	L	L	17	45,76,81,87,88,90,140,142, 143,176,185,212
KFB	L	H	H	H	L	L	H	H	L	L	L	L	17	45,76,81,87,88,90,140,142, 143,176,185,212
LBB	H	L	L	L	L	L	L	L	L	L	L	L	11	36,93
LDB	H	L	L	L	L	L	H	L	L	L	L	L	11	36,93
MBB	H	L	L	H	L	L	L	L	L	L	L	L	5	5
MBD	H	L	L	H	L	L	L	L	L	L	H	L	5	5
MBF	H	L	L	H	L	L	L	L	L	L	H	H	5	5
MBG	H	L	L	H	L	L	L	L	L	H	L	L	5	52,100
MBL	H	L	L	H	L	L	L	L	H	L	L	L	5	5
MBM	H	L	L	H	L	L	L	L	H	L	L	H	5	5
MBR	H	L	L	H	L	L	L	L	H	H	L	H	5	52,100
MCB	H	L	L	H	L	L	L	H	L	L	L	L	5	5
MCC	H	L	L	H	L	L	L	H	L	L	L	H	5	5
MDB	H	L	L	H	L	L	H	L	L	L	L	L	5	5
MDG	H	L	L	H	L	L	H	L	L	H	L	L	5	52,100
MFB	H	L	L	H	L	L	H	H	L	L	L	L	5	5
MGB	H	L	L	H	L	H	L	L	L	L	L	L	5	5
NBB	H	L	H	L	L	L	L	L	L	L	L	L	14	22,37,43,50,110
NBC	H	L	H	L	L	L	L	L	L	L	L	H	14	22,37,43,50,110
NBG	H	L	H	L	L	L	L	L	L	H	L	L	14	49,64,69,128,182
PBB	H	L	H	H	L	L	L	L	L	L	L	L	6	39,83,103,105,126
PBC	H	L	H	H	L	L	L	L	L	L	L	H	6	39,83,103,105,126
PBD	H	L	H	H	L	L	L	L	L	L	H	L	6	39,83,103,105,126
PBG	H	L	H	H	L	L	L	L	L	H	L	L	6	6,28,40,144
PBJ	H	L	H	H	L	L	L	L	L	H	H	L	6	6,28,40,144
PBL	H	L	H	H	L	L	L	L	H	L	L	L	6	39,83,103,105,126
PBM	H	L	H	H	L	L	L	L	H	L	L	H	6	39,83,103,105,126
PBQ	H	L	H	H	L	L	L	L	H	H	L	L	6	6,28,40,144
PBR	H	L	H	H	L	L	L	L	H	H	L	H	6	6,28,40,144
PGD	H	L	H	H	L	H	L	L	L	L	H	L	6	39,83,103,105,126
PLM	H	L	H	H	H	L	L	L	H	L	L	H	6	39,83,103,105,126
PLR	H	L	H	H	H	L	L	L	H	H	L	H	6	6,28,40,144
SBB	H	H	H	L	L	L	L	L	L	L	L	L	9	9,10,19,70
SBD	H	H	H	L	L	L	L	L	L	L	H	L	9	9,10,19,70
SBJ	H	H	H	L	L	L	L	L	L	H	H	L	9	13,20,23,29,31,108,146, 147,148
TBB	H	H	H	H	L	L	L	L	L	L	L	L	13	30,35,54,65,82,113,114,122
TBD	H	H	H	H	L	L	L	L	L	L	H	L	13	30,35,54,65,82,113,114,122
TBG	H	H	H	H	L	L	L	L	L	H	L	L	13	21,42,77,80,89,94,101,104, 112,115,116,130,145,149, 150,186,196,210
TCB	H	H	H	H	L	L	L	H	L	L	L	L	13	30,35,54,65,82,113,114,122
TDB	H	H	H	H	L	L	H	L	L	L	L	L	13	30,35,54,65,82,113,114,122
TFM	H	H	H	H	L	L	H	H	H	L	L	H	13	30,35,54,65,82,113,114,122
TGB	H	H	H	H	L	H	L	L	L	L	L	L	13	30,35,54,65,82,113,114,122
THB	H	H	H	H	L	H	L	H	L	L	L	L	13	30,35,54,65,82,113,114,122
TLG	H	H	H	H	H	L	L	L	L	H	L	L	13	21,42,77,80,89,94,101,104, 112,115,116,130,145,149, 150,186,196,210

[a] L = low; H = high.

[b] Unified Numeration scheme (2) and International Standard races (11) may or may not have similar infection types on *Lr*9, 16, 24, 26, 3ka, 17, 30.

programs and studies concerning the epidemiology and evolution of virulence in the pathogen population. The designation of physiologic races in wheat leaf rust has come under criticism (4) for not placing emphasis on individual virulence frequencies. The subject has been reviewed recently by Caten (5). The North American wheat leaf rust population reproduces asexually and therefore is unlikely to be in a state of linkage equilibria. Analysis of virulence combinations based solely on frequencies of individual virulences can result in an incomplete representation of the frequency of phenotypes actually present. The identification and designation of virulence combinations provides a more complete representation of asexual pathogen populations than would data on individual frequencies alone. The proposed Prt nomenclature should simplify the designation of important virulence combinations. Selective changes in the leaf rust population eventually may require the replacement of certain differentials that are no longer useful in distinguishing virulence combinations (25). The new nomenclature also should facilitate the study of evolutionary trends in the leaf rust populations. The previous use of avirulence/virulence frequencies for one or few genes made it difficult to follow trends involving complex combinations. The proposed nomenclature permits the calculation of individual and any tested combination of virulence frequencies and enables the determination of certain virulence combinations in the leaf rust population.

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