

## Leaf rust (*Puccinia triticina*) resistance in wheat (*Triticum aestivum*) cultivars grown in Northern Europe 1992–2002

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Diversity of resistance to leaf rust caused by *Puccinia triticina* can be enhanced in wheat (*Triticum aestivum*) cultivars through a better knowledge of resistance genes that are present in important cultivars and germplasm. Multi-pathotype tests on 84 wheat cultivars grown in Denmark, Finland, Norway and Sweden during 1992–2002 and 39 differential testers enabled the postulation of nine known genes for seedling resistance to leaf rust. Genes *Lr1*, *Lr2a*, *Lr3*, *Lr10*, *Lr13*, *Lr14a*, *Lr17*, *Lr23* and *Lr26* were found singly or in combination in 47 of the cultivars (55.9%). The most frequently occurring genes in cultivars grown in Sweden were *Lr13* (20.4%), *Lr14a* (14.8%) and *Lr26* (14.8%). *Lr14a* was the most common gene in cultivars grown in Norway (18.7%), *Lr13* in Denmark (35.5%) and *Lr10* in Finland (20.0%). Although 28 cultivars (33.3%) exhibited a response pattern that could not be assigned to resistance genes or combinations present in the tester lines, several pathotypes carried virulence and hence these genes or combinations are of limited use. Nine cultivars (10.7%) lacked detectable seedling resistance. One cultivar was resistant to all pathotypes used in the study.

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Leaf or brown rust, caused by the fungus *Puccinia triticina* Eriks., is one of the most common diseases of bread wheat (*Triticum aestivum* L.) in the world. Yield losses in Mexico can vary from 6.6% in resistant cultivars to 62.7% in susceptible cultivars under high disease pressure (SAYRE et al. 1998). Quality losses due to leaf rust include reduced protein levels and softness equivalent scores (EVERTS et al. 2001). In the North European countries Denmark, Finland, Norway and Sweden, the disease generally appears late in the crop season. Yield losses are rarely severe but can be substantial during years when susceptible cultivars are used, winters are mild and conditions for development of leaf rust continue to be favorable throughout the season (WIIK 1991). In Sweden, yield losses of up to 10% have been noted in field trials (SANDNES and WAERN 1991; WIIK 1991).

Genetic resistance is one of the most effective, environmentally sound and economic means of control of diseases on wheat (PINK 2002). Knowledge of the identity and diversity of leaf rust resistance genes in cultivars and commonly used germplasm in breeding programs can improve the efficiency of developing new resistant cultivars. More than 50 resistance genes to leaf rust have been identified in wheat (MCINTOSH et al. 2003, 2004). However, new pathogen races

rapidly overcome most race-specific resistance genes. For example in Australia the release of cultivars with single genes for resistance to *Puccinia triticina* during 1938–1964 was followed by increased frequencies of pathotypes with matching virulence (PARK et al. 2001). There is a continuous need to identify and incorporate effective resistance genes into cultivars of wheat.

The distribution of leaf rust resistance genes has been investigated for cultivars grown in Western and Eastern Europe (BARTOŠ and VALKOUN 1988; WARZECHA 1992; BROERS and DE HAAN 1994; BARTOŠ et al. 1996; MESTERHÁZY et al. 2000; WINZELER et al. 2000; PARK et al. 2001; SINGH et al. 2001) but only for a few cultivars grown in Northern Europe (BROERS and DE HAAN 1994; WINZELER et al. 2000; HERRERA FOESSEL 2001).

The objective of the present study was to investigate the occurrence and distribution of genes for seedling resistance to leaf rust in 84 bread wheat cultivars commonly grown in Denmark, Finland, Norway and Sweden during 1992–2002. Information on the genetic basis of resistance could contribute to a better understanding of the durability of resistance and facilitate the accumulation of effective resistance genes into cultivars.

## MATERIAL AND METHODS

### Host material

The host material represents 84 of the most widely cultivated spring and winter wheat cultivars in Denmark (31 cultivars), Finland (25 cultivars), Norway (16 cultivars) and Sweden (54 cultivars) between 1992 and 2002 (Table 1). Cultivars with the highest quantity of certified seed were selected based on figures obtained from the following seed control agencies or plant breeding companies: Plantedirektoratet in Denmark, Statens utsädeskontroll in Sweden, Landbrukstilsynet in Norway and Boreal PB in Finland. Svalöf-Weibull AB in Sweden, Graminor A/S in Norway and Boreal PB in Finland kindly provided seed. Information on pedigrees and year of release was provided by plant breeding companies, The Nordic Gene Bank or obtained from the Wheat Pedigree and Identified Alleles of Genes On Line database (<http://genbank.vurv.cz/wheat/pedigree/>).

A set of differential tester lines that carry known leaf rust (*Lr*) resistance genes were also included (Table 2). The tester lines, mostly developed by P.L. Dyck, Agriculture Canada, Winnipeg, Man., Canada, are maintained at CIMMYT (International Wheat and Maize Improvement Center) in Mexico.

### Pathogen material

Twelve Mexican pathotypes of *Puccinia triticina* were used to evaluate the testers and cultivars. The nomenclature of the pathotypes follows the system of LONG and KOLMER (1989), with two additional supplementary sets (SINGH 1991). The pathotypes used were the following: BBB/BN, BBG/BN, CBJ/QB, CBJ/QL, CCJ/SP, MBJ/SP, MCJ/QM, MCJ/SP, MFB/SP, NCJ/BN, TBD/TM and TCB/TD (Table 3).

### Inoculation, disease assessment and gene postulation

A set of 6–8 seeds per cultivar and tester line was used in the test with each pathotype. Ten-day-old seedlings were inoculated by spraying with urediniospores suspended in a light-weight mineral oil (2–3 mg ml<sup>-1</sup>). Inoculated plants were placed in a dew chamber overnight at 18–20°C and then transferred to greenhouse chambers at 18–22°C. (SINGH and RAJARAM 1991). For pathotype NCJ/BN, avirulent to *Lr13*, seedlings of cultivars and tester lines were inoculated after 14 days since expression of *Lr13* is known to be clearer when older seedlings are inoculated (SINGH and RAJARAM 1991). Infection types (IT) were recorded 9 to 12 days after inoculation according to the 0 to 4 scale described by STAKMAN et al. (1962) and ROELFS (1984) where 0 = no macroscopic symptoms, ; = hypersensitive necrotic or chloro-

tic flecks, 1 = small uredinia surrounded by necrosis, 2 = small to medium uredinia often surrounded by necrosis or chlorosis, X = random distribution of variable-sized uredinia on single leaf, 3 = medium-sized uredinia that may be associated with chlorosis, 4 = large uredinia without chlorosis, + = uredinia somewhat larger than normal for the infection type, – = uredinia somewhat smaller than normal, C = more chlorosis than normal, N = more than usual degree of necrosis. Discrete infection types on different plants of the same line were separated by a comma (e.g. 4, or 1,3). A range of infection types on a single leaf, not adequately described by X, was recorded using more than one infection type with the predominant infection type listed first (e.g. 3C3, 12<sup>-</sup>). Infection types 3 and 4 (susceptible host/virulent pathotype) were considered high and 0–2 were considered low (resistant host/avirulent pathotype).

The presence of leaf rust resistance genes in the cultivars was postulated by comparing the high and low infection types displayed by a cultivar with the infection type of known *Lr* genes in the tester lines. Based on the gene-for-gene concept, lines susceptible to a pathotype cannot have an *Lr* gene for which the pathotype is avirulent. *Lr* genes were considered present if the low infection type produced on a cultivar by one or more pathotypes, matched the infection type of the corresponding tester line. If the low infection type produced on a cultivar was lower than the corresponding tester lines, then the cultivar was considered to have one or more unidentified *Lr* genes (STATLER 1984; MODAWI et al. 1985; McVEY 1989).

## RESULTS

The 84 selected cultivars, estimated to be the most commonly grown in Northern Europe 1992–2002 based on quantities certified seed, are presented in Table 1. Several cultivars were grown in more than one country. A few of the most popular cultivars were not available to the present study: ‘Ebi’ and ‘Lars’ in Sweden; ‘Stakado Abed’, ‘Sleipner’ and ‘Hereward’ in Denmark; ‘Folke’, ‘Portal’, ‘Kalle’, ‘Rida’, ‘Rubin’, ‘Lars’ and ‘Skjaldar’ in Norway; ‘Ramiro’ and ‘Gunbo’ in Finland. According to literature, ‘Sleipner’ carries *Lr26* (McINTOSH et al. 1995) and ‘Hereward’ has *Lr13* (GOYEAU and PARK 1997).

The infection types produced on the tester lines with known *Lr* genes after inoculation with twelve Mexican leaf rust pathotypes are presented in Table 2. The low infection types of the tester lines were in accordance with low infection types reported by McINTOSH et al. (1995). The presence of genes *Lr3ka*, *Lr9*, *Lr14b*, *Lr16*, *Lr19*, *Lr20*, *Lr22b*, *Lr25*, *Lr29*, *Lr30*, *Lr34*,

Table 1. Cultivars grown in Denmark, Finland, Norway and Sweden 1992–2002 and postulated genes for seedling resistance after inoculation with twelve pathotypes of *Puccinia triticina*.

Cultivar	Pedigree <sup>1</sup>	Year <sup>2</sup>	Locality <sup>3</sup>	Postulated <i>Lr</i> gene(s) <sup>4</sup>
<i>Winter wheat</i>				
Aura	Ertus/Vakka	1975	F*	<i>u</i>
Ballad	Sv85297/Sv85568	2000	S	<i>u</i>
Bill	(DH) Multicross	n/a	D/S*	<i>Lr3 + Lr17 + Lr23 + u</i>
Bjørke	SvU75630/Rida	1998	N*	<i>u</i>
Brigadier	Squadron/Rendezvous	1992	D/S	<i>Lr26 + u</i>
Citadel	Composite cross of 24 cvs with main cv Tadorna	1983	D	<i>Lr13</i>
Dirigent	Ritmo/Reaper	n/a	D	<i>u</i>
Flair	Ares/Marabu; Ares/3/Rabe/Jubilar//Armada	1996	D/S	<i>u</i>
Florida	Caribo/Disponent	1985	D/S	<i>Lr26</i>
Grommit	Apostle/Torfrida//Hereward	n/a	D/S	<i>Lr3 + Lr10 + Lr17 + u</i>
Haven	Hedgehog/Norman//Moulin	1988	D*/S	<i>Lr26 + u</i>
Holme	Starke/WW-1014-55	1972	S	<i>u</i>
Hurtig	Severin M8B8/Sperber//Urban/3/Konsul	2003	S	<i>u</i>
Hussar	Squadron/Rendezvous	1991	D*/S	<i>Lr26 + u</i>
Ilves	Hja b356/Vakka	1984	F*	<i>none</i>
Kamerat	Rida/Moulin//Disponent/2*Rida	n/a	N	<i>Lr26</i>
Kartesch	Severin M8B8/Sperber//Urban/3/Konsul	2003	S	<i>u</i>
Konsul	Ertus/Norre//Holme-M/3/Cerc.Res	1990	D/S	<i>Lr13 + u</i>
Kosack	Mironovskaya-808/Starke-M//Holme-M	1984	D/N*/S*	<i>u</i>
Kris	Hereward/Rendezvous//Torfrida	1999	D*/S*	<i>Lr10 + Lr13 + u</i>
Linna	Panu/Hja04519/Virtus	1976	F	<i>none</i>
Lynx	Rendezvous/CWW-4442-64	1992	D*	<i>Lr17 + Lr26 + u</i>
Magnifik	Composite cross of German and Swedish lines	2004	N/S	<i>Lr1</i>
Marabu	LP-6077-71/Monopol//Kronjuwel	1988	D/S	<i>Lr26 + u</i>
Marshal	Kontiki/Brigadier	2001	S	<i>Lr26 + u</i>
Meridien	Starke/Norre/3/2*Ertus/Norre//Holme/4/Wampum/5/Moisson	1993	D/S*	<i>Lr13 + u</i>
Mjølner	TL340/Starke/W25458	1996	N*/S	<i>Lr10 + u</i>
Nova	Angela/TJB-330-1491//Arminda	1993	D/S	<i>Lr14a + u</i>
Otso	Elo/Vakka	1995	F	<i>u</i>
Pagode	Composite cross of 36 cultivars	1986	S	<i>Lr13</i>
Pepital	ROC/VDH-040-71-B; ROC-109-751/VDH-040-71-B; ROC/VDH-1040-71-B	1989	D*/S	<i>Lr10 + Lr13</i>
Pitko	Ta 05901/Vakka	1985	F*	<i>u</i>
Rental	Sv70355/M. Huntsman	1993	S	<i>u</i>
Residence	Obelisk//Cebeco-8451/Arminda	1998	S	<i>Lr13 + u</i>
Revelj	Kanzler M15M28	2000	D/S	<i>Lr13 + u</i>
Rialto	Haven (sib)/Fresco (sib)	1993	D	<i>Lr13 + Lr26 + u</i>
Ritmo	Hobbit//Line-1320/Wizard/3/Marksman/4/Virtue	1990	D*/S*	<i>Lr13 + u</i>
Stava	Helge-M7D1/Helge-M7D2//WW-31254	1995	D/S*	<i>u</i>
SW Gnejs	KosackMB/3*Kraka/4/Kurier	2001	S	<i>Lr1</i>
SW Harnessk	WD-linje/Konsul	2001	S	<i>Lr13 + u</i>
Tarso	Taras/Hadmerslebener 13313-80	1992	D*/F/S*	<i>Lr26 + u</i>
Terra	Kraka/TJB730-3637	1992	D*/N/S	<i>Lr13</i>
Tjelvar	Sture D/4/StureM3bM5M7	1984	S	<i>Lr26</i>
Toronto	Disponent/Weihestephaner 616–67//Kronjuwel	1990	D	<i>Lr26</i>
Trintella	CB-239/VDH-256-81//RPB-48-75-A/Moulin	1994	D	<i>Lr13</i>
Tryggve	Riley/Holme//18614/3/Helge	1990	F/S	<i>u</i>
Urban	Kranich/Diplomat	1981	S*	<i>none</i>
Urho	Nisu/Tsitsin	1999	F	<i>u</i>
Vakka	Varma/Kehra	1960	F	<i>u</i>
Virke	n/a	1999	S	<i>none</i>
<i>Spring wheat</i>				
Anniina	Satu/Polkka	2001	F*	<i>u</i>
Avle	22279M15/20299M12//Canon	1996	N*/S	<i>Lr14a</i>
Bajas	Bastian/Sport	n/a	N/S	<i>u</i>

Table 1 (Continued)

Cultivar	Pedigree <sup>1</sup>	Year <sup>2</sup>	Locality <sup>3</sup>	Postulated <i>Lr</i> gene(s) <sup>4</sup>
Bastian	Bajio-66/Runar/4/Yaktana/Norin10/Brevor/3/Moystad/5/Rollo/Magnif/4/Sonora/Tezanos-Pintos-Precoz//Nainari/3/Moystad	1989	F*/N*	<i>none</i>
Bjarne	SvB87293/Bastian	2002	N	<i>Lr1</i>
Canon	Sicco/2*WW-12502//2*Sappo/3/Kadett	1990	S	<i>Lr14a</i>
Curry	Canon s/Nemares//Kadett Mp1	1994	S*	<i>Lr14a+u</i>
Dacke	P18/17269//19151	1990	S	<i>none</i>
Drabant	CI-12633/6*Ring	1973	S	<i>Lr14a</i>
Dragon	Sicco/WW-12502//Sappo/5*Kadett	1988	D*/S*	<i>Lr14a+u</i>
Hanno	Banjo/Hermes	n/a	D/N	<i>u</i>
Heta	Hja a1105/Hja a4431	1988	F*	<i>Lr10</i>
Hugin	Dragon (sib)/Nemares	1996	D/S	<i>Lr13+u</i>
Jondolar	Sicco/Tilly//VDH-1166-76-M	1990	D	<i>Lr14a</i>
Kadett	Kolibri/WW 439-66/Pompe-M	1981	F*/S	<i>u</i>
Kruunu	Mahti/Hja23471	2001	F*	<i>Lr10</i>
Laari	Villa Glofi/Tuoko	1990	F	<i>u</i>
Lavett	WW118466/Kadett//Dragon	1992	S	<i>u</i>
Leguan	ST-324-84/ST-174-83	1997	D*	<i>Lr14a+u</i>
Luja	Svenno//Hopea/Tammi	1981	F*	<i>u</i>
Mahti	Cebeco/Hja20519	1995	F*	<i>Lr10</i>
Manu	Ruso/Runar	1992	F*	<i>u</i>
Polkka	Sv70415/Snabbe//Norrena/Karn-2/3/Snabbe	1992	F*/N*/S	<i>u</i>
Runar	Els/Rollo; Els/7*Rollo	1972	N	<i>u</i>
Ruso	Reward/Pika	1967	F	<i>Lr10</i>
Satu	Snabbe/Drabant//T-106/Snabbe	1990	F/S	<i>none</i>
Sport	P18/17269//19151	1991	S	<i>u</i>
SW Vals	Can.M12 M14 M18 B9 B10/ Can.M14 M15 B9	2001	S	<i>Lr2a+u</i>
Tapio	Hja c3929/Kolibri	1980	F	<i>Lr10+u</i>
Thasos	Miron.808/ Bastion// Minaret; Max /Ze73.1331.2/Minaret	1994	S	<i>none</i>
Tjalve	Reno/KolibriM//15432	1981	F/N*/S	<i>none</i>
Triso	SaxoArgan/Kadett	1996	S	<i>u</i>
Vinjett	Tjalve M14/Tjalve M15//Canon	1998	D*/F/N*/S*	<i>Lr14a</i>
Zebra	Ralle/Dragon	2001	F/N/S	<i>Lr14a</i>

<sup>1</sup> Alternative pedigrees are separated by a semi-colon (;); n/a = not available.

<sup>2</sup> n/a = not available.

<sup>3</sup> D = Denmark, F = Finland, N = Norway, S = Sweden; \* = total quantity certified seed 1992-2002 was among the ten highest for the country and cultivar.

<sup>4</sup> *u* = unidentified gene(s).

*Lr36*, *Lr37* and *LrB* could not be determined with the twelve pathotypes used in the study because all were avirulent or virulent to these genes.

The results of the gene-postulations for different cultivars are presented in Table 1. A summary of the identified and unidentified genes in the material is presented in Table 4. Comparisons of infection types displayed by the cultivars and tester lines allowed the postulation of nine known leaf rust genes in the material: *Lr1*, *Lr2a*, *Lr3*, *Lr10*, *Lr13*, *Lr14a*, *Lr17*, *Lr23* and *Lr26*. Of the 84 cultivars tested, 9 had no detectable seedling resistance; 47 lines had one or more known *Lr* genes including 26 cultivars that had one or more known *Lr* genes and one or more unidentified *Lr* genes. The infection types of the 28 cultivars exhibiting only a response pattern not corresponding to the tester lines and postulated to

carry only unidentified *Lr* genes are presented in Table 5. Eleven different combinations of known and unknown *Lr* genes were detected in the material. Ten cultivars were resistant to more than eight pathotypes including one cultivar ('Lavett') that was resistant to all pathotypes used in the study (Table 5).

The results for the 54 cultivars commonly grown in Sweden 1992–2002 are presented in Tables 1 and 4. The cultivar 'Kosack' (*u*) was released in 1984 and has dominated the seed market to the present day. The winter wheat cultivars 'Ritmo' (*Lr13+u*), 'Stava' (*u*), 'Tarso' (*Lr26+u*), 'Kris' (*Lr10+Lr13+u*), 'Meridien' (*Lr13+u*), 'Urban' (*none*), 'Bill' (*Lr3+Lr17+Lr23+u*), 'Ebi' and 'Lars' and spring wheat cultivars 'Dragon' (*Lr14a+u*), 'Curry' (*Lr14a+u*) and 'Vinjett' (*Lr14a*) were the most extensively grown during 1992–2002 estimated from quantities certified seed

Table 2. Seedling infection types<sup>1</sup> displayed by tester varieties with known *Lr* genes when tested with 12 different pathotypes of *Puccinia triticina*.

<i>Lr</i> gene (s)	Tester	Pathotype											
		BBB/BN	BBG/BN	CBJ/QB	CBJ/QL	CCJ/SP	MFB/SP	TBD/TM	TCB/TD	MCJ/QM	MCJ/SP	MBJ/SP	NCJ/BN
1	R.L.6003	0;	0;	0;	0;	0;	3+	3+	3+	3+	3+	3+	3+
2a	R.L.6016	0;	1	;	0;	0;	0;	3+	3+	0;	0;	0;	1
2b	R.L.6019	;	1+	1-	0;	;	;	3+	3+	0;	0;	;	1+
2c	R.L.6025	;1	3C3	1+3C	;1-	;	1-	3+	3+	;	0;	;	3
3	R.L.6002	12	;1-	3+	23-	3	3+	3+	3+	23C	23C	3+	;
3bg	R.L.6042	;1	;	23C	3+	;12	3C3	3+	3+	3C3	;1-	3+	;
3ka	R.L.6007	;1	;1-	23C	;1-	;12-	12-	12	;12	;12	3C	23C	12
9	R.L.6010	0;	0;	0;	;	0;	0;	0;	0;	0;	0;	;	0;
10	R.L.6004	3+	3+	;1	3+	3+	3+	3+	;1-	3+	3+	3+	3+
11	R.L.6053	13C	4	4	4	3+	3C3	1+3C	1+3	3+	3+	3+	3+
12	R.L.6011	X+, 3+	3C	3+	4	3+	3+	3+	X+3	3+	3+	3+	XX+
13	Manitou	X	1, 1+	3+	3+	3+	3+	3+	3+	3+	3+	3+	11+
14a	R.L.6013	X	X	3+	4	3+	3+	3+	3+	3+	3+	3+	3+
14b	R.L.6006	3+	3+	3+	4	3+	3+	3+	3+	3+	3+	3+	3+
15	R.L.6052	;1-	;1-	0;	;	3+	3+	3+	3+	;	3+	3+	;1-
16	R.L.6005	1	1	1	1+	1+3C	1	1	1	1	1+3C	1+3C	11+
17	R.L.6008	;	;	3+	X+	3+	;1-	3+	;1-	3+	3+	3+	2+3C
18	R.L.6009	23C	23C	3+	3+	23C	22+	3+	3+	23C	3C	12	2
19	R.L.6040	;	;	0;	0;	;	0;	;	;	0;	;	;	0;
20	W.203	3+	3+	3+	3+	3+	4	3+	3+	3+	3+	3+	3+
21	R.L.6043	12	;1	12	12	12	;12-	;1	;12	12	23C	12	3+
22a	R.L.6044	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	12
22b	C.I.10003	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+
23	R.L.6012	3+	3+	;1	;1	3+	3+	23C	3+	;1	3+	3+	3+
24	R.L.6064	;	;	;1-	;1-	;	23C	0;	;	0;	;	;	;1-
25	R.L.6084	0;	0;	0;	;	0;	0;	0;	0;	0;	0;	0;	0;
26	R.L.6078	23C	0;	1+3C	;1-	3+	3+	;1-	3+	3+	3+	11+	3+
27+31	Baviacora 92	X-	;1	X	X-	X+	3	3+	X-	3+	3+	3+	X
27+31+10	Gatcher	X-	;1-	;	X-	X+	3+	3+	;	3+	3+	3+	;1
28	R.L.6079	X+	;1-	0;	0;	0;	3+	3+	X+	0;	0;	0;	3C3+
29	R.L.6080	;1-	;1-	;1	;1-	;1-	1	;1	;1	;1	;1-	;1-	1
30	R.L.6049	2-	12	23C	;12	;12	12	23C	23	23C	;12-	23-	12-
32	R.L.5497-1	;1	;1-	3C3	3+	23	;12-	3	;1	3C3	12	12	12-
33	R.L.6057	3	3+	23	3+	23	3C	12	;23	3	12	23	23-
34	R.L.6058	3+	3+	3+	3+	3	3	3	3+	3+	;23=	3	3
35	R.L.5711	3+	3C3	3+	3+	3	3	3	3+	1+3C	3C	3+	3+
36	E.84018	;1	;1	;1-	12	X	;	;1	;1	1	12	13C	;1-
37	R.L.6081	3+	3C3+	3+	3+	3+	3+	X+3	3+	3+	3+	3+	2+3C
B	R.L.6051	3+	3+	3+	3+	3+	3+	3	3+	3+	3+	3+	3+

<sup>1</sup> 0=No uredinia or other macroscopic signs of infections;;=no uredinia, but hypersensitive necrotic or chlorotic flecks of varying size present; 1=small uredinia often surrounded by necrosis; 2=small to medium uredinia often surrounded by chlorosis or necrosis; 3=medium-sized uredinia that may be associated with chlorosis or rarely necrosis; 4=large uredinia without surrounding chlorosis; X=random distribution of variable-sized uredia on single leaf; +=uredinia somewhat larger than normal for the infection type; -=uredinia somewhat smaller than normal; C=more chlorosis than normal; N=more necrosis than normal. Discrete infection types on plants of the same line are separated by a comma. A range of infection types on a single leaf is described using more than one infection type with the predominant infection type listed first.

Table 3. Avirulence/virulence formulae for leaf rust genes based on seedling reactions for 12 *Puccinia triticina* pathotypes used in the study<sup>1</sup>.

Pathotype	Avirulence to <i>Lr</i> genes	Virulence to <i>Lr</i> genes
BBB/BN	1,1c,2a,2b,2c,3,3bg,11,13,14a,15,17,18,21,24,26,27+31	10,22a,23,28
BBG/BN	1,1c,2a,2b,2c,3,3bg,11,13,14a,15,17,18,21,24,26,27+31,28	10,22a,23
CBJ/QB	1,1c,2a,2b,2c,10,15,18,21,23,24,26,27+31,28	3,3bg,11,13,14a,17,22a
CBJ/QL	1,2a,2b,2c,15,18,21,23,24,26,27+31,28	3,3bg,10,11,13,14a,17,22a
CCJ/SP	1,1c,2a,2b,2c,18,21,24,28	3,3bg,10,11,13,14a,15,17,18,22a,23,26,27+31
MFB/SP	2a,2b,2c,11,17,18,21	1,3,3bg,10,13,14a,15,22a,23,24,26,27+31,28
TBD/TM	1c,11,21,23,24,26	1,2a,2b,2c,3,3bg,10,13,14a,15,17,18,22a,27+31,28
TCB/TD	1c,10,11,17,21,24,27+31,29	1,2a,2b,2c,3,3bg,13,14a,15,18,22a,23,26,28
MCJ/QM	1c,2a,2b,2c,15,18,21,23,24,28	1,3,3bg,10,11,13,14a,17,22a,26,27+31
MCJ/SP	1c,2a,2b,2c,21,24,28	1,3,3bg,10,11,13,14a,15,17,18,22a,23,26,27+31
MBJ/SP	1c,2a,2b,2c,21,24,26,28	1,3,3bg,10,11,13,14a,15,17,18,22a,23,27+31
NCJ/BN	2a,2b,3,3bg,10,13,15,18,22a,24,27+31	1,2c,10,11,14a,17,21,23,26,28

<sup>1</sup>All pathotypes were avirulent in seedling stage for genes *Lr3ka*, *Lr9*, *Lr16*, *Lr19*, *Lr25*, *Lr29*, *Lr30*, *Lr36*; and were virulent for genes *Lr14b*, *Lr20*, *Lr22b*, *Lr34*, *Lr37*, *LrB*.

(NILSSON and ANDERSSON 1998; ANDERSSON et al. 2002). Of the cultivars tested, 11.1% were susceptible; 61.1% were postulated to carry one or more known *Lr* genes with or without additional unidentified genes. 68.5% showed infection types not corresponding to the tester lines and were postulated to have one or more unidentified *Lr* genes with or without known *Lr* genes. The most commonly occurring genes were *Lr13* (20.4%), *Lr14a* (14.8%) and *Lr26* (14.8%) while *Lr2a*, *Lr3*, *Lr10*, *Lr17* and *Lr23* occurred in less than 10% of the cultivars.

The results for the 31 cultivars commonly grown in Denmark are presented in Tables 1 and 4. Wheat is mainly of winter type in Denmark and there is a rapid change in cultivar distribution. The two most commonly grown cultivars typically account for more than 50% of the area under cultivation e.g. 'Ritmo' was grown on more than 50% of the wheat area 1998 and 1999 (HOVMØLLER 2001). 'Pepital' (*Lr10+Lr13*), 'Haven' (*Lr26+u*), 'Hussar' (*Lr26+u*), 'Ritmo' (*Lr13+u*), 'Lynx' (*Lr17+Lr26+u*), 'Kris' (*Lr10+Lr13+u*), 'Terra' (*Lr13*), 'Sleipner' and 'Hereward' have been the most common winter wheat cultivars during 1992–2002. 'Dragon' (*Lr14a+u*), 'Leguan' (*Lr14a+u*) and 'Vinjett' (*Lr14a*) have been the most popular spring wheat cultivars (PLANTEDIREKTORATET 1992–2002). The infection response patterns of the selected cultivars and tester lines enabled postulation of *Lr* genes in 83.9% of the material while a total of 77.4% displayed a resistance response not matching the testers. *Lr13* occurred in 35.5%; *Lr26* in 29.0%; *Lr14a* in 16.1%; *Lr10* and *Lr17* in 9.7%; *Lr3* in 6.4% and *Lr23* in 3.2% of the material.

The results for the 16 cultivars commonly grown in Norway are presented in Tables 1 and 4. Cultivars 'Avle' (*Lr14a*), 'Zebra' (*Lr14a*), 'Bjarne' (*Lr1*), 'Tjalve'

(*none*), 'Bastian' (*none*), 'Polkka' (*u*), 'Mjølner' (*Lr10+u*), 'Terra' (*Lr13*), 'Bjørke' (*u*), 'Magnifik' (*Lr1*) and 'Folke' have been the most commonly grown during 1992–2002 (ÅSSVEEN et al. 2003). Of the 16 cultivars grown in Norway, 50.0% contained one or more of genes *Lr14a* (18.7%), *Lr1* (12.5%); *Lr10*, *Lr13* or *Lr26* (6.2%) while 37.5% had an infection type pattern not matching the tester lines and 12.5% were susceptible.

The results for the 25 selected cultivars grown in Finland are presented in Tables 1 and 4. In Finland, the cultivars 'Tjalve' (*none*), 'Mahti' (*Lr10*), 'Vinjett' (*Lr14a*), 'Kruunu' (*Lr10*), 'Bastian' (*none*), 'Zebra' (*Lr14a*), 'Manu' (*u*) and 'Anniina' (*u*) have dominated the spring wheat market. The most common winter wheat cultivars during 1992–2002 were 'Tryggve' (*u*), 'Urho' (*u*), 'Tarso' (*Lr26+u*), 'Aura' (*u*), 'Ilves' (*none*), 'Gunbo' and 'Ramiro' (M. Jalli, pers. comm). Gene-postulation showed the presence of *Lr10* (20.0%); *Lr14a* (8.0%) and *Lr26* (4.0%) in 32.0% of the material while 48% displayed only a resistance reaction different from that of the tester lines and 20.0% were susceptible to all twelve leaf rust pathotypes.

## DISCUSSION

The results of the present study showed that infection types corresponding to nine known and several unidentified *Lr* resistance genes, either singly or in combination, conditioned race-specific seedling resistance in 75 of the 84 investigated wheat cultivars commonly grown in Northern Europe between 1992 and 2002. Genes masked by gene suppression, not expressed in the seedling stage or under the given environmental conditions could remain undetected

Table 4. Number and percentage of cultivars (cvs) found susceptible, with unidentified resistance (u) and with postulated Lr gene(s) after testing with 12 *Puccinia triticina*<sup>1</sup>.

Country	No cvs	susceptible	unidentified – only	Single Lr genes					Lr genes in combinations										Single Lr genes and combinations								
				Lr1	Lr10	Lr13	Lr14a	Lr26	Lr2a/u	Lr3/Lr10/Lr17/u	Lr3/Lr17/Lr23/u	Lr10/u	Lr10/Lr13	Lr10/Lr13/u	Lr13/u	Lr13/Lr26/u	Lr14a/u	Lr17/Lr26/u	Lr26/u	Lr1+	Lr2a+	Lr3+	Lr10+	Lr13+	Lr14a+	Lr17+	Lr23+
Sweden	54	6	15	2	–	2	5	2	1	1	1	1	1	7	–	3	–	6	2	1	2	4	11	8	2	1	8
%		11.1	27.8	3.7	–	3.7	<b>9.2</b>	3.7	1.8	1.8	1.8	1.8	1.8	<b>13.0</b>	–	5.5	–	11.1	3.7	1.8	3.7	7.4	<b>20.4</b>	14.8	3.7	1.8	14.8
Denmark	31	–	5	–	–	3	2	2	–	1	1	–	1	5	1	3	1	5	–	–	2	3	11	5	3	1	9
%		–	16.1	–	–	<b>9.7</b>	6.4	6.4	–	3.2	3.2	–	3.2	<b>16.1</b>	3.2	9.7	3.2	<b>16.1</b>	–	–	6.4	9.7	<b>35.5</b>	16.1	9.7	3.2	29.0
Finland	25	5	12	–	4	–	2	–	–	–	–	1	–	–	–	–	–	1	–	–	–	5	–	2	–	–	1
%		20.0	48.0	–	<b>16.0</b>	–	8.0	–	–	–	–	<b>4.0</b>	–	–	–	–	–	<b>4.0</b>	–	–	–	<b>20.0</b>	–	8.0	–	–	4.0
Norway	16	2	6	2	–	1	3	1	–	–	–	1	–	–	–	–	–	–	2	–	–	1	1	3	–	–	1
%		12.5	37.5	12.5	–	6.2	<b>18.7</b>	6.2	–	–	–	<b>6.2</b>	–	–	–	–	–	–	12.5	–	–	6.2	6.2	<b>18.7</b>	–	–	6.2
Total	84	9	28	3	4	4	6	4	1	1	1	2	1	7	1	4	1	6	3	1	2	9	14	10	3	1	12
%		10.7	33.3	3.6	4.8	4.8	<b>7.1</b>	4.8	1.2	1.2	1.2	2.4	1.2	<b>8.3</b>	1.2	4.8	1.2	7.1	3.6	1.2	2.3	10.7	<b>16.7</b>	11.9	3.6	1.2	14.3

<sup>1</sup>some cultivars were grown in more than one country, percentages are therefore presented as cultivars/country and total represents the total number/percentage of cultivars within the material. The highest percentage are shown in bold type in different sections of the table.

Table 5. Infection type<sup>1</sup> response patterns of cultivars grown in northern Europe 1992–2002 with only unidentified genes (*u*) for seedling resistance and/or resistance to more than eight pathotypes after inoculation with twelve pathotypes of *Puccinia triticina*.

Cultivar	Pathotype												Postulated
	BBB/BN	BBG/BN	CBJ/QB	CBJ/QL	CCJ/SP	MFB/SP	TBD/TM	TCB/TD	MCI/QM	MBJ/SP	MCJ/SP	NCJ/BN	<i>Lr</i> gene(s)
Anniina	3+	3+	4	2+	3	3+	3+	3+	3+	3+	3+	4	<i>u</i>
Aura	3+	3+	3+	2+3	3+	4	3+	3+	3+	3+	3+	4	<i>u</i>
Bajas	3+	3+	;23C	* <sup>2</sup>	3+	3	3	3+	3	3+	3+	3+	<i>u</i>
Ballad	3+	3+	3+	4	3+	3+	3+	3+	3+	3+	3+	2+	<i>u</i>
Bill	;1–	;1	;	;	3+	12	12	;1–	;1	3+	3+	1	<i>Lr3+Lr17+Lr23+u</i>
Bjørke	3+	;	;	; 3+	3+	3	3+	4	3+	3+	3+	3+	<i>u</i>
Brigadier	;	0;	;1–	;	X	;12–	;	;1–	;11–	;1	3+	;	<i>Lr26+37+u</i>
Dirigent	;	0;	;	0;	3+	2+	;	1+2	;1	12	3C3	12	<i>u</i>
Flair	3+	3+	23C	;	3+	3+	3+	3+	3+	3+	3+	3+	<i>u</i>
Grommit	;1–	0;	0;	;23	3+	;	;1–	0;	;1	;23C	;23	0;	<i>Lr3+Lr10+Lr17+u</i>
Hanno	3+	23C	3+	1+3C	3+	3+C	3+	3+4	3+	3+	3C3	2+3C	<i>u</i>
Haven	X	0;	0;	0;	3+	2+3	;	;1–	23C	X	3C3	2+3C	<i>Lr26+u</i>
Holme	3+	X	;12	;	3+	4	4	3+	3	3+	3+	3+	<i>u</i>
Hurtig	3+	3+	3+	2+3C	3+	2+3C	3+	3+	3+	3+	3+	12–	<i>u</i>
Hussar	;	0;	0;	0;	X+	;1–	;	;	;1–	;1	3C3+	;	<i>Lr26+u</i>
Kadett	3+	4	23C	;	3+	4	4	3+	3+	3+	3+	3+	<i>u</i>
Kartesch	3	1+3C	3+	4	3+	2+3C	3+	3+	3+	3+	3+	;1–	<i>u</i>
Kosack	3+	3C3	;1	0;	3+	3+	4	3+	3+	3+	3+	2+3C	<i>u</i>
Kris	;1–	;1	;	3+	3+	2+3C	12	0;	;12	3+	3+	1+2	<i>Lr10+Lr13+u</i>
Laari	3+	3+	3+	2+3C	3+	3+	3+	3+	3+	3+	3+	3+	<i>u</i>
Lavett	;1+	;1	1+	1+	1+3C	1–	;	;1	1	1+	1+2	12	<i>u</i>
Luja	3+	X	4	23C	3+	4	3+	3+	3+	3+	3+	3+	<i>u</i>
Lynx	;	0;	0;	0;	23	;1–	;	;	;	;1	3+	;	<i>Lr17+Lr26+u</i>
Manu	3+	X	3+	22+	3+	3+	3+	3+	3+	3+	3+	2+3C	<i>u</i>
Marshal	;1–	0;	;1	;1C	X+	23C	;	1+3C	1+2	23C	3+	12	<i>Lr26+u</i>
Otso	3+	X	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	<i>u</i>
Pitko	3+	X	4	4	3+	4	3+	3+	3+	3+	3+	4	<i>u</i>
Polkka	3+	3+	3+	23C	3+	3+	;1–	3+	3+	3+	3+	4	<i>u</i>
Rental	3+	3C3+	4	4	3+	3+	4	3+	3+	3+	3+	4	<i>u</i>
Rialto	;11+	0;	;	;1–	X+	23C	;	; 3+	23C	23C	3+	X, 3+	<i>Lr13+u</i>
Runar	3+	4	3+	2+3	3+	3+	3+	3+	3+	3+	3+	4	<i>u</i>
Sport	3+	3+	23C	;1–	3+	3+	3+	3+	3+	3+	3+	4	<i>u</i>
Stava	3+	3+	;1	0;	X+3	23C	2+	2+3	3C3	3+	3+	1+	<i>u</i>
SW Vals	0;	;	;1–	0;	0;	;	3+	3+	0;	;	;	X	<i>Lr2a+u</i>
Triso	3+	3+	3+	4	3+	3+	3+	3+	3+	2+3C	3+	3+	<i>u</i>
Tryggve	3+	3+	13C	;	3+	3+	3+	3+	3+	3+	3+	3+	<i>u</i>
Urho	3+	2+3C	3+	2+3C	3+	3+	3+	3+	3+	3+	3+	4	<i>u</i>
Vakka	3+	2+3C	4	2+3C	3+	3+	4	3+	3+	3+	3+	4	<i>u</i>

<sup>1</sup> 0 = No uredinia or other macroscopic signs of infections; ; = no uredinia, but hypersensitive necrotic or chlorotic flecks of varying size; 1 = small uredinia often surrounded by necrosis; 2 = small to medium uredinia often surrounded by chlorosis or necrosis; 3 = medium-sized uredinia that may be associated with chlorosis or rarely necrosis; 4 = large uredinia without surrounding chlorosis; X = random distribution of variable-sized uredinia; + = uredinia somewhat larger than normal for the infection type; – = uredinia somewhat smaller than normal; C = more chlorosis than normal; N = more necrosis than normal. Discrete infection types on different plants of the same line are separated by a comma. A range of infection types on a single leaf is described using more than one infection type with the predominant infection type listed first.

<sup>2</sup> \* = missing data.



but may still have an effect on the disease resistance in the field.

Genes *Lr13*, *Lr26*, *Lr14a* and *Lr10* were postulated in more than 10% of the material followed by *Lr1*, *Lr17*, *Lr3*, *Lr23* and *Lr2a*. Twenty-eight cultivars displayed infection type patterns that could not be attributed to known *Lr* genes in the tester lines. Lines with identical infection types to the same pathotypes may or may not have the same unidentified *Lr* gene(s). The unidentified genes could be known *Lr* genes that could not be postulated with the leaf rust pathotypes in the present study, adult-plant resistance genes that are expressed slightly in the seedling stage, undescribed *Lr* genes or alleles of known *Lr* genes. Inclusion of additional testers, pathotypes and adult plant tests would possibly have allowed some of these *Lr* genes to be identified.

In order to understand the usefulness of the genes postulated in the material grown in Northern Europe, it is necessary to compare the presence of postulated *Lr* genes with virulence data for *Puccinia triticina* populations. Pathogenicity surveys carried out in Sweden in 1957 (GUSTAVSSON 1958), 1958 (BJÖRKMAN 1959), 1959 (LEIJERSTAM 1960) and 1960 (HERMANSEN 1962) showed five predominating pathotypes often occurring in mixtures. However, the virulence composition of the pathotypes was difficult to determine due to the method of analysis. In the absence of recent virulence data, virulence surveys in neighboring countries and comparisons of the results from the present study with annual disease severity ratings of leaf rust in Sweden and Norway may indicate presence of virulence to the postulated genes in the material grown in Northern Europe.

Surveys in Western and Central Europe 1996–1999 have shown that countries have few pathotypes in common, indicating a great genetic diversity within the pathogen (MESTERHÁZY et al. 2000). Virulence surveys in Western Europe 1995 (PARK and FELSENSTEIN 1998) detected 53 pathotypes, including 4 predominating pathotypes with virulence to *Lr3*, *Lr10*, *Lr17b* and *Lr26*. Based on these surveys, cultivars with *Lr9*, *Lr12*, *Lr19*, *Lr22a*, *Lr24*, *Lr25*, *Lr28*, *Lr29*, *Lr34*, *Lr35* and *Lr37* should provide some protection against leaf rust also in Northern Europe, particularly if combined with other efficient resistance genes.

The gene *Lr13* was the most common resistance gene that could be postulated in the material and is probably the most widely distributed *Lr* gene in the world (MCINTOSH et al. 1995). WINZELER et al. (2000) found that 58% of the European wheat genotypes tested carried *Lr13* alone or in combination. The gene was once considered to confer durable

adult plant resistance (SINGH et al. 2001) but is now ineffective in several countries including Mexico (SINGH 1991). *Lr13* is still considered effective in combinations with other race-specific genes in Australia as the *Lr13*-virulent pathotype was avirulent on many other resistance genes (SINGH et al. 2001). However, in Mexico, pathotypes contain virulence to *Lr13* in combination with virulence on several important resistance genes (SINGH 1991) and many cultivars that carry *Lr13* alone or in combination with other genes were susceptible in field trials (SINGH and RAJARAM 1991). In Europe 1996–1999, virulence to cultivars with *Lr13* varied with genotype suggesting that either the frequency of virulence to *Lr13* varied across Europe or that additional genes are present in cultivars displaying higher field resistance (WINZELER et al. 2000). In North America, cultivar ‘Era’ with *Lr10*, *Lr13* and *Lr34* has remained highly resistant to moderately resistant since the 1970s (OELKE and KOLMER 2004). Effective resistance in the North American cultivars ‘Alsen’ and ‘Norm’ were found to be due to the interaction of *Lr13* and *Lr23*, with *Lr34*; and *Lr13*, *Lr16*, *Lr23* with *Lr34* (OELKE and KOLMER 2005). In the present study, *Lr13* was found together with *Lr10*, *Lr26* and/or unidentified genes. According to annual surveys of disease severity in Sweden, cultivar ‘Revelj’ (*Lr13+u*) had an average of 25% diseased leaf area 1997–2001 (LARSSON et al. 2002) indicating that *Lr13* and the unidentified gene(s) have been overcome in Sweden. Diseased leaf area for ‘Ritmo’, ‘Konsul’ and ‘Pagode’ was 1% 1993–1997 (LARSSON et al. 1997); ‘Meridien’ 5% and ‘Residence’ 4% 1997–2001 (LARSSON et al. 2002); ‘SW Harnesk’ 5% 1998–2002 (LARSSON et al. 2003) and ‘Trintella’ 4% leaf rust 1995–1999 (LARSSON et al. 2000). It is thus likely that these cultivars contain additional resistance genes more effective than those of ‘Revelj’. ‘Kris’ (*Lr10+Lr13+u*) had 2% diseased leaf area 1998–2002 (LARSSON et al. 2003) while ‘Pepital’ (*Lr10+Lr13*) had 1% diseased leaf area 1993–1997 (LARSSON et al. 1997). Although disease severity varies between years and cultivars, it seems that virulence exists to *Lr13* and the combinations of *Lr13* with *Lr10* and unidentified genes in northern Europe.

The resistance gene *Lr26* is present on the rye segment in a T1BL.1RS wheat-rye translocation. The translocation was spread mainly through wheat derivatives produced in Germany during the 1930s (RABINOVICH 1998). In the present study, cultivars ‘Brigadier’, ‘Florida’, ‘Haven’, ‘Hussar’, ‘Marabu’, ‘Rialto’, ‘Tjelvar’, ‘Tarso’ and ‘Toronto’ showed infection types corresponding to *Lr26* and carry

the T1BL.1RS translocation (SCHLEGEL et al. 1994; KAZMAN and LEIN 1996). The cultivars 'Kamerat' and 'Marshal' also displayed *Lr26*, most likely derived from 'Disponent' and 'Brigadier' in the pedigrees. Pathotypes virulent to *Lr26* exist in most areas (MCINTOSH et al. 1995). In annual disease surveys in Sweden, cultivars 'Florida' (*Lr26*) had an average of 3% leaf rust 1986–1995 (LARSSON and MAGNÉT 1995); 'Tjelvar' (*Lr26*) 3% 1983–1992 (CARLSSON et al. 1992); 'Toronto' (*Lr26*) and 'Tarso' (*Lr26+u*) 5%, 'Haven' (*Lr26+u*) 1% and 'Hussar' (*Lr26+u*) 2% infected leaf area 1993–1997 (LARSSON et al. 1997) and 'Marshal' (*Lr26+u*) showed 3% 1998–2002 (LARSSON et al. 2003). It is thus clear that virulence to *Lr26* and combinations with unidentified genes exists in Northern Europe.

The gene *Lr14a* originates from *Triticum dicoccum* (MCINTOSH et al. 1995). The cultivar 'Canon', displaying *Lr14a*, is the likely donor of this gene to 'Curry', 'Avle', 'Zebra' and 'Vinjett'. Seedling tests with 20 Australian leaf rust pathotypes have shown *Lr20* in 'Canon' but not *Lr14a* (SINGH et al. 2001). *Lr20* could not be detected with the pathotypes used in the present study because all were virulent to this gene. Expression of *Lr14a* can be variable and difficult to interpret due to host genetic background, virulent pathotypes, epistatic genes or intermediate infection types. The gene *Lr14a* is linked to powdery mildew resistance gene *Pm5* (MCINTOSH et al. 1995). Adult plant studies and powdery mildew tests may yield additional information on the presence or absence of *Lr14a* and *Lr20* in 'Canon' used in the present study. The difference could also be due to heterogeneity in the material. Annual disease surveys in Sweden have shown 11% diseased leaf area on 'Curry', 8% on 'Dragon' and 3% on 'Vinjett' 1998–2002 (LARSSON et al. 2003); 16% on 'Drabant' 1985–1992 (CARLSSON et al. 1992); 1% on 'Nova' 1993–1997 (LARSSON et al. 1997) and 10% leaf rust on 'Zebra' 2000–2001 (LARSSON et al. 2002). This indicates that 'Vinjett' and 'Nova' may have additional adult plant and/or additive minor genes that may have contributed to resistance in the field compared to 'Curry' and 'Dragon'. In a province of Norway in 2002, the cultivar 'Zebra' had 50% diseased leaf area, 'Avle' around 20% and 'Vinjett' about 15% (ABRAHAMSEN et al. 2003). This indicates that resistance gene *Lr14a* has been overcome in Sweden and this region in Norway. These cultivars have been widely used in Northern Europe and it is likely that *Lr14a* has been overcome also in other areas.

Resistance gene *Lr10* originates from bread wheat and may have some effect in combinations with other genes in parts of the world (MCINTOSH et al. 1995).

*Lr10* occurred singly or with unidentified gene(s) in the Finnish cultivars 'Ruso', 'Kruunu', 'Mahti', 'Heta' and 'Tapiro'. The source was not apparent from the pedigrees. No information regarding virulence to leaf rust in Finland could be obtained for the present study. In Sweden, annual disease surveys showed 4% diseased leaf area on 'Grommit' and 2% on 'Kris' 1998–2002 (LARSSON et al. 2003) compared to 1% on 'Pepital' 1993–1997 (LARSSON et al. 1997) that all have *Lr10* in combination with other *Lr* genes. Virulence to *Lr10* thus seems to be present in Northern Europe.

The genes *Lr1*, *Lr2a*, *Lr3*, *Lr17* and *Lr23* occurred in less than 5% of the material. Annual disease surveys in Sweden have shown 3% leaf rust on 'SW Gnejs' (*Lr1*) 1998–2002; 4% leaf rust on 'SW Vals' (*Lr2a+u*); 4% on 'Grommit' (*Lr3+Lr10+Lr17+u*) and 3% on 'Bill' (*Lr3+Lr17+Lr23+u*) 1998–2002 (LARSSON et al. 2003). It seems likely that the low incidence of leaf rust on these cultivars could be due to combinations of effective *Lr* genes and adult plant genes and/or additive minor genes.

Several cultivars displayed infection type patterns that did not correspond to known *Lr* genes in the tester lines. In the present material, similar infection types not corresponding to the tester lines were found in 'Hussar', 'Kris', 'Lynx', 'Marshal' and 'Brigadier'. It is possible that these cultivars contain *Lr37*, supported by the presence of 'Rendezvous' in their pedigrees, in addition to unidentified seedling resistance genes. 'Rendezvous' was selected for resistance to eye spot disease and stripe rust from VPM1 and inherited gene *Lr37* from *Triticum ventricosum* (MCINTOSH et al. 1995). Gene *Lr37* confers mainly adult plant resistance and is difficult to detect in seedling tests. Adult plant tests of 'Hussar', 'Kris', 'Lynx', 'Marshal' and 'Brigadier' could confirm the presence or absence of *Lr37*. SINGH et al. (2001) postulated *Lr37* in 'Hussar', 'Lynx' and 'Brigadier'. WINZELER et al. (2000) reported that two cultivars that seemed to carry *Lr37* singly, provided low seedling resistance and full adult plant resistance in western Europe in 1996–1999. Differential tester lines with *Lr37* have shown variable levels of moderate susceptibility to resistance to leaf rust in field trials in Romania, Hungary, Czech Republic, Great Britain and Poland 1998–1999. Virulence to *Lr37* varied between locations although the gene was identified as the most effective of the resistance genes currently used in European wheat cultivars (MESTERHAZY et al. 2000). In Sweden, annual disease surveys showed 2% diseased leaf area on 'Hussar' 1993–1997 (LARSSON et al. 1997) and 4% on 'Kris' and 'Marshal' 1995–1999 (LARSSON et al. 2000). If these cultivars carry *Lr37*, it

appears that virulence exists in Northern Europe to *Lr37* in these cultivars. 'Brigadier' had 0% leaf rust during 1993–1997 (LARSSON et al. 1997). It is probable that this cultivar has additional *Lr* resistance genes and/or additive minor genes that are effective in Sweden.

The cultivar 'Kosack' displayed resistance to four pathotypes used in this study but the results did not correspond to any known *Lr* genes in the tester lines. According to the pedigree, the line Mironovskaya 808 contains *Lr3a* (MCINTOSH et al. 1995) but this does not appear to have been transferred to 'Kosack'. The source of the resistance remains unknown. The unidentified resistance in the Finnish cultivar 'Vakka' is the likely origin of the resistance pattern displayed by 'Aura', 'Otso', 'Pitko' and 'Urho' that contain 'Vakka' directly or indirectly in their pedigrees. The Finnish cultivars 'Laari' and 'Luja' also displayed infection types similar to 'Vakka' although this cultivar is not included in their pedigrees and the source of resistance is unknown. The resistance in 'Anniina' to pathotype CBJ/QL was most likely inherited from 'Polkka'. The source of resistance in 'Polkka', 'Runar' and many other cultivars could not be deduced from their pedigrees. In Sweden, annual disease surveys detected 11% leaf rust on 'Kosack' 1995–1999 (LARSSON et al. 2000); 4% on 'Ballad' 1996–2000 (LARSSON et al. 2001); 4% on 'Dirigent' and 5% on 'Hurtig' 1998–2002 (LARSSON et al. 2002); 9% on 'Flair' 1995–1999 (LARSSON et al. 2000); 8% on 'Rental' 1985–1994 (LARSSON et al. 1994); 9% on 'Sport' and 7% on 'Tryggve' 1983–1992 (CARLSSON et al. 1992); 16% on 'Kadett' 1985–1991 (BENGTSSON et al. 1991); 10% on 'Kartesch' 1998–2002 (LARSSON et al. 2003); 10% on 'Stava' 1992–1996 (LARSSON and MAGNÉT 1996) and 11% on 'Triso' 1998–2002 (LARSSON et al. 2003). Virulence seems to exist to the unidentified seedling resistance genes in these cultivars though some genes may be more effective than others, singly or in combination with adult plant or additive minor genes. It is difficult to estimate the virulence on genes that only occur in combinations and further field studies including cultivars or lines with single *Lr* genes are needed to assess the effectiveness of such genes in the present material.

In the material grown in Northern Europe, a total of 9 cultivars were found without seedling resistance to the twelve leaf rust pathotypes used in the study. WINZELER et al. (2000) found that 55% of European wheat cultivars had adult plant resistance, contributed to by quantitative trait loci (QTL) and/or *Lr34* that enhances resistance. In Sweden, diseased leaf area was 3% on 'Urban' 1993–1997 (LARSSON et al. 1997); 8% on 'Virke' 1998–2002 (LARSSON et al. 2003); 2% on

'Thasos' 1992–1996 (LARSSON and MAGNÉT 1996) and 6% on 'Dacke' 1995–1999 (LARSSON et al. 2000). Although a completely susceptible tester line was not included in the annual disease surveys, the percentage leaf rust on these cultivars is low compared to for example 16% on 'Drabant' with *Lr14a* (CARLSSON et al. 1992). Thus, these cultivars with no postulated *Lr* seedling resistance genes may have additional adult plant resistance or additive minor genes that contribute to low disease pressure in the field and may be interesting for further analysis and use in breeding for leaf rust resistance.

The results of the present study and annual disease surveys in Sweden and Norway indicate that virulence exists to most of the known and unidentified seedling *Lr* genes in the cultivars grown in Northern Europe 1992–2002. Variation in virulence is determined by the genotypes of the pathotypes that were originally introduced to a region; over-wintering infected host plants; migration of urediniospores between regions; sexual recombination, mutation and selection pressure by host resistance genes in the region (KOLMER and LIU 2000). The viability of leaf rust urediniospores has been reported to be 1–5% after 24 h exposure to temperatures of  $-4$  to  $-6^{\circ}\text{C}$  (EVERSMAYER and KRAMER 1995). Although information on the virulence and genetic diversity of *Puccinia triticina* populations in northern Europe is at present limited, the pathogen is likely restricted by sub-freezing winter temperatures and the absence of the principal alternate host, *Thalictrum speciosissimum* (ANIKSTER et al. 1997). The epidemiology of leaf rust populations in northern Europe would largely be influenced by migrating spores from neighboring areas and the presence and distribution of resistance genes in the wheat host.

Comparative studies of resistance genes in the wheat host and pathogenicity surveys have illustrated the effects of host selection pressure on the *Puccinia triticina* pathogen population. In regions of Canada, virulence frequencies in leaf rust collections changed almost annually from 1987–1997 because of the introduction of *Lr* genes in winter wheat cultivars grown in the United States (KOLMER 1999). Pathotypes with virulence to *Lr17* increased in a region of Canada from 1996–1998 due to extensive cultivation of one susceptible wheat cultivar with *Lr17* in Kansas (KOLMER 2001). In the US and Canada, pathotypes with virulence to *Lr16* declined in the late 1980s following decreased cultivation of winter wheat with this gene (KOLMER 1999). In Israel, where cultivars with *Lr26* are absent, pathotypes with virulence to *Lr26* have increased due to annual migration of spores from other regions (KOZMAN et al. 2004). However,

studies on leaf rust in former Czechoslovakia since the 1960s concluded that changes of virulence in *Puccinia triticina* could only partially be ascribed to changes of resistance genes in wheat cultivars (BARTOŠ et al. 1996).

The results of the present investigation show that several known and unidentified leaf rust seedling resistance genes have been deployed in Sweden, Norway, Finland and Denmark during 1992–2002 that could have contributed toward host selection on the leaf rust pathogen in the field. The breakdown of the resistance genes present in the material grown in Northern Europe was most likely influenced by the cultivation of a few cultivars on extensive areas. However, information on quantities certified seed was only available as total figures for countries per year and disease severity was available as average percentage diseased leaf area for several years. Area under cultivation and disease severity of a certain cultivar may vary with region and year and from the present information it is thus not possible to conclude how *Lr* genes in wheat hosts may have affected disease severity patterns in Northern Europe. Additional data on disease severity, virulence surveys and adult plant tests in the region are needed to provide evidence of interactions between the *Puccinia triticina* pathogen and *Lr* genes present in the wheat host.

Pyramiding genes, i.e. accumulating several effective resistance genes in the same cultivar, has been suggested as a method to achieve more durable resistance against pathogens with low genetic diversity, high gene flow and an asexual mating system (MESTERHÁZY et al. 2000; McDONALD and LINDE 2002). The combination of several effective (undefeated) resistance genes into a single cultivar should extend the period of resistance since mutations at several avirulence loci would be required to produce a new virulent pathotype (PINK 2002). Molecular markers that could facilitate gene pyramiding have been developed for several effective resistance genes, including *Lr9*, *Lr19*, *Lr24*, *Lr25*, *Lr35*, *Lr37* and *Lr52* (HELGUERA et al. 2003; BLASZCZYK et al. 2004; HIEBERT et al. 2005). Slow-rusting or partial resistance has been reported to be a more durable type of resistance than single seedling resistance genes (SINGH et al. 2001). Cultivars with a combination of the adult plant resistance gene *Lr34* and 3–4 additive partially effective genes have been shown to confer high levels of nonspecific resistance in many areas of the world (SINGH et al. 2000; NAVABI et al. 2005). Quantitative trait loci (QTL) for partial resistance to leaf rust have been identified in several wheat genotypes (MESSMER et al. 2000; XU et al. 2005) that could be used to develop markers necessary for breeding programs.

Future host selection pressure on the pathogen could be further decreased by rotating genes through time and space by mixtures or regional deployment of cultivars with different effective resistance genes (McDONALD and LINDE 2002; PINK 2002). The knowledge of presence of leaf rust seedling resistance genes facilitates future studies and use of adult plant resistance and additive minor genes in these cultivars. A few cultivars have dominated the market and annual disease surveys have shown that many of the most commonly grown cultivars in Northern Europe during 1992–2002 are susceptible to leaf rust (LARSSON et al. 1994–2003; ABRAHAMSEN et al. 2003). It is thus important to continue breeding for leaf rust resistance and monitor the pathogen as part of a management control strategy.

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