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Analysis of durable resistance to stem rust in barley

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Summary

Since the mid-1940's, barley cultivars grown in the northern Great Plains of the USA and Canada have been resistant to stem rust caused by *Puccinia graminis* f. sp. *tritici.* This durable resistance is largely conferred by a single gene, *Rpg*1, derived from a single plant selection of the cultivar Wisconsin 37 and an unimproved Swiss cultivar. At the seedling stage, barley genotypes with *Rpg*1 generally exhibit low mesothetic reactions at 16–20° C and slightly higher mesothetic reactions at 24–28° C to many stem rust pathotypes. This resistance is manifested by a low level of rust infection and mostly incompatible type uredia on adult plants. *Rpg*1 reacts in a pathotype-specific manner since some genotypes of *P. g.* f. sp. *tritici* are virulent on cultivars carrying this gene in the field. Several factors may have contributed to the longevity of stem rust resistance in barley, a) since barley is planted early and matures early, it can sometimes escape damage from stem rust inoculum carried from the south; b) one or more minor genes may augment the level of resistance already provided by *Rpg*1; c) the cultivation of resistant wheat cultivars and eradication of barberry have reduced the effective population size and number of potential new pathotypes of *P. g.* f. sp. *tritici,* respectively; and d) virulent pathotypes of *P. g.* f. sp. *tritici* and *P. g.* f. sp. *secalis* have not become established. This situation changed in 1989 when a virulent pathotype (Pgt-QCC) of *P. g.* f. sp. *tritici* became widely distributed over the Great Plains. However, *Rpg*1 may still confer some degree of resistance to pathotype QCC because stem rust severities have been low to moderate and yield losses light on barley cultivars carrying the gene during the last four seasons (1989–1992). Several sources of incomplete resistance to pathotype QCC have been identified in barley. To facilitate the transfer of resistance genes from these sources into advanced breeding lines, molecular marker assisted selection is being employed.

Introduction

The stem rust (or black rust) fungus, *Puccinia graminis,* is one of the most devastating pathogens of cereals worldwide. In the northern Great Plains of the USA and Canada, the wheat stem rust pathogen (*P. g.* f. sp. *tritici*) has caused a number of spectacular epidemics on both wheat (*Triticum aestivum* and *T. turgidum* var. *durum*) and barley (*Hordeum vulgare*) resulting in catastrophic yield losses (Stakman & Harrar, 1957). These epidemics were the impetus for the initiation of cereal breeding programmes. With wheat, breeding programmes for stem rust resistance began in earnest after the widespread and destructive epidemic of 1904 (Stakman & Harrar, 1957). Before any resistant cultivars were developed, the Canadian cultivar, Marquis, was widely grown because it matured early and largely escaped damage by stem rust. Marquis was heavily rusted during the 1916 epidemic, but was still grown over large areas until 1936. The release of Ceres in 1926 marked the

beginning of the 'boom and bust' cycles of plant breeding since it was the first major cultivar bred for stem rust resistance in the region (Dyck & Kerber, 1985). Ceres was heavily damaged in the 1935 and 1937 epidemics caused by pathotype (race) 56 of *P.g.*f.sp. *tritici* (Stakman & Harrar, 1957). Cultivars with other genes for stem rust resistance supplanted Ceres from 1938 to 1950. During this period, only traces of stem rust were observed on the durum and bread wheats. However, in the early 1950's, a dangerous pathotype (15B) with virulence on most of the durum and bread wheats became widely distributed. Pathotype 15B was responsible for the destruction of the durum wheats and nearly one quarter of the bread wheats during the epidemics of 1953 and 1954 (Stakman & Harrar, 1957). Since the mid-1950's, there has not been a serious outbreak of stem rust on wheat in the northern Great Plains. This success is due primarily to the development of wheat cultivars that possess a number of stem rust resistance genes (Dyck & Kerber, 1985; Roelfs, 1985), the diligent monitoring of pathotypes of *P. g.* f. sp. *tritici* in the USA and Canada, and the eradication of the barberry (*Berberis vulgaris*) (Roelfs, 1982).

A different sequence of events has taken place with regard to stem rust on barley during the same era (1904 to the present) and in the same area of production (the northern Great Plains). The Red River Valley of northwestern Minnesota, eastern North Dakota, northeastern South Dakota, and southern Manitoba is one of the most productive cereal-growing regions in the northern Great Plains (Fig. 1). However, stem rust is present every year in this area and is capable of causing serious damage on barley and wheat. Prior to 1940, yield losses in barley from stem rust were nearly as common as they were in wheat during epidemic years, although never as severe (Table 1). In 1942, the first barley cultivar with stem rust resistance (Kindred) was released to US farmers in the southern Red River Valley region. Since this time, there have been no significant losses due to stem rust in barley, even during the 1953 and 1954 epidemics when the wheat crop was devastated (Table 1). During the 1954 epidemic, barley in the northern Red River Valley region of Manitoba, Canada suffered serious damage (total losses exceeded $9 million) because over 90% of the hectarage was still being sown to stem rust susceptible cultivars (McDonald, 1970). The hectarage of resistant barley cultivars increased in Manitoba after the 1954 epidemic, and losses to stem rust have been minimal ever since.

The resistance of barley to stem rust is durable (Steffenson, 1989) according to the definition of Johnson (1984). This resistance has remained effective for 50 years in different cultivars that have been widely grown. The hectarage and range of these resistant cultivars is immense; in the USA, between 1.4 and 1.8 m ha are planted annually across the northern tier of states from Wisconsin in the east to Washington in the west and south to Wyoming and Colorado. The plantings of resistant cultivars are concentrated in the Red River Valley states of Minnesota, North Dakota, and South Dakota. Large areas of barley with the same resistance are also cultivated in Canada, mainly in the province of Manitoba. In the Red River Valley region alone, over 1 m ha of resistant barley are planted each year. Stem rust is particularly severe on cereal crops grown in the Red River Valley due, primarily, to the region's location along the main

Table 1. Estimated percent yield loss of barley and wheat to stem rust during several epidemics in North Dakota and Minnesota from 1916–55[a]

Year of epidemic	North Dakota		Minnesota	
	Barley	Wheat	Barley	Wheat
1916	–[b]	70.0	–[b]	61.0
1923	3.0	12.0	1.5	15.0
1925	0.8	5.0	0.5	11.0
1935	15.0	56.5	15.0	51.6
1937	8.0	25.0	5.0	10.0
1952	Trace	5.6	Trace	2.3
1953	Trace	37.7	Trace	13.4
1954	Trace	42.9	Trace	18.0
1955	Trace	8.0	Trace	2.4

[a] From Roelfs, A.P., 1978. Estimated losses caused by rust in small grain cereals in the United States – 1918–76. U.S. Dept. Agri., Misc. Pub. # 1363.

[b] Data not available for barley. The data for wheat in 1916 were provided by M.E. Hughes, USDA-ARS Cereal Rust Laboratory, St. Paul.

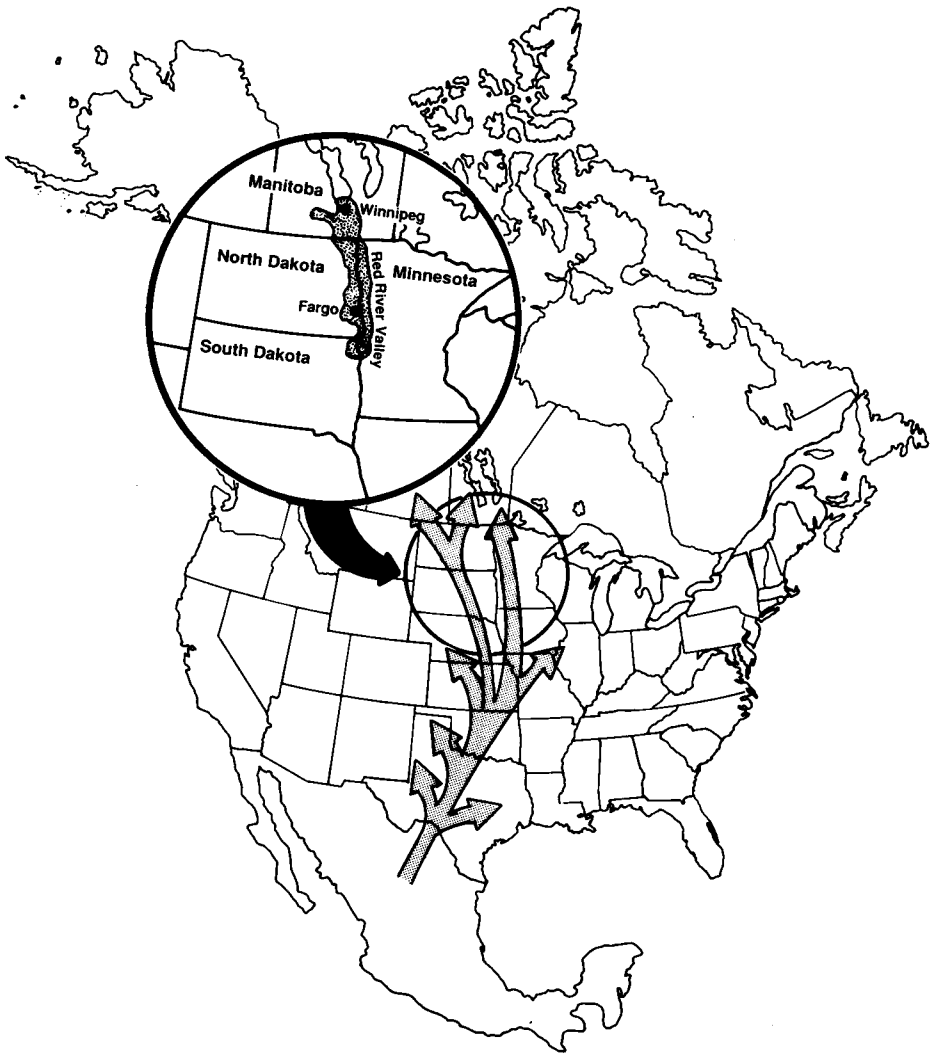

Fig. 1. The Red River Valley of Minnesota, North Dakota, and South Dakota in the USA and Manitoba in Canada. Stippled arrows represent the generalized movement of stem rust urediospores (*Puccinia graminis*) during the spring season.

pathway of stem rust inoculum (Fig. 1) and a favourable environment for disease development. The severity of stem rust in a given year will depend on the date of urediospore arrival, the amount of inoculum transported from the south, and the weather conditions. In this paper, only the Red River Valley and surrounding regions will be considered since stem rust is a continual threat to barley in this area.

Durable resistance was defined by Johnson (1984) as a type of resistance that remains effective for a long time in cultivars that are widely grown. This definition was made without reference to any underlying genetic mechanisms or associated characters of resistance. The unrestrictive nature of this definition is appropriate since some researchers have presumptuously assumed certain unifying mechanisms and principles for the terms they have used to describe host resistance. These underlying mechanisms or principles have not proven universal. In order to gain an understanding as to the range of characteristics and possible mechanisms of durable resistance, we must dissect and analyse each example of resistance that proves durable.

Table 2. CI or PI number, use, origin, year of introduction or release, pedigree, reaction to stem rust, probable source(s) of stem rust resistance, and period of peak hectarage of major barley cultivars grown in the tri-state region of Minnesota, North Dakota, and South Dakota in the USA and Manitoba in Canada from 1945 to the present[a]

Cultivar	CI or PI number	Use	Origin	Year introduced or released	Pedigree	Reaction to stem rust	Probable source(s) of stem rust resistance	Period of peak hectarage
Tri-state region of Minnesota, North Dakota, and South Dakota								
Kindred	6969	Malting	S. Lykken, Kindred, ND	1942	Single plant selection from Wisc. 37	Resistant	unknown	1945–58
Traill	9538	Malting	N. Dakota Agr. Expt. Station, Fargo, ND	1956	Kindred/Titan	Resistant	Kindred	1959–62
Trophy	10647	Malting	N. Dakota Agr. Expt. Station, Fargo, ND	1961	Traill/White aleurone UM570	Resistant	Kindred + Peatland	1963–64
Larker	10648	Malting	N. Dakota Agr. Expt. Station, Fargo, ND	1961	Traill/White aleurone UM570	Resistant	Kindred + Peatland	1965–79
Dickson	10968	Malting	N. Dakota Agr. Expt. Station, Fargo, ND	1964	Traill/Kindred/CI 7117–77	Resistant	Kindred	1967–72
Beacon	15480	Malting	N. Dakota Agr. Expt. Station, Fargo, ND	1973	Conquest/Dickson	Resistant	Kindred + Peatland	1975–78
Morex	15773	Malting	Minnesota Agr. Expt. Station, St. Paul, MN	1978	Cree/Bonanza	Resistant	Kindred + Peatland	1980–84
Glenn	15769	Malting	N. Dakota Agr. Expt. Station, Fargo, ND	1978	Br5755–3/Trophy//ND B138	Resistant	Kindred + Peatland	1981–83
Azure	15865	Malting	N. Dakota Agr. Expt. Station, Fargo, ND	1982	Bonanza/Nordic/ND B130	Resistant	Kindred + Peatland	1984–89
Robust	476976	Malting	Minnesota Agr. Expt. Station, St. Paul, MN	1983	Morex/Manker	Resistant	Kindred + Peatland	1985–present
Excel	542047	Malting	Minnesota Agr. Expt. Station, St. Paul, MN	1990	Cree/Bonanza//Manker/Robust	Resistant	Kindred + Peatland	released 1990
Manitoba, Canada								
O.A.C. 21[b]	1470	Malting	Ontario Agricultural College, Guelph, Ont.	1910	Single plant selection from Manscheuri	Susceptible	–	pre-1945–49
Gartons	7016	Feed	Farmer, Portage la Prairie, Man.	1930	Selection of barley from John Garton Company, England	Moderately resistant	unknown	pre-1945–49 and 1955
Plush	6093	Feed	Dominion Experimental Farm, Brandon, Man.	1939	Lion/Bearer	Susceptible	–	pre-1945–48
Montcalm	7149	Malting	MacDonald College Quebec, Que.	1945	Michigan 31604/Common 6-rowed 4307 M.C./Mandscheuri 1807 M.C.	Susceptible	–	1950–57
Vantage	7324	Feed	Dominion Experimental Farm, Brandon, Man.	1947	Newal/Peatland/Plush	Resistant	Peatland	1954–55
Husky	9537	Feed	University of Saskatchewan, Saskatoon, Sask.	1953	Peatland/Regal/O.A.C. 21/Newal	Resistant	Peatland	1955–57
Herta	8097	Feed	Plant Breeding Inst. Weibullsholm, Landskrona, Sweden	1956	Kenia/Isaria	Moderately Susceptible	–	1969–71
Parkland	10001	Malting	Dominion Experimental Farm, Brandon, Man.	1956	Newal/Peatland/O.A.C. 21/Olli/Montcalm	Resistant	Peatland	1958–1966
Keystone	10877	Feed	Dominion Experimental Farm, Brandon, Man.	1961	Vantage/Jet/Vantmore	Resistant	Peatland	1964–65
Conquest	11638	Malting	Canada Dept. of Agriculture Expt. Farm, Brandon, Man.	1965	Vantage/Jet/Vantmore/Br4635/Swan/ Parkland	Resistant	Peatland	1967–72
Fergus	13797	Feed	University of Guelph, Guelph, Ont.	1968	Selection from Firlbecks III	Susceptible	–	1972–77
Bonanza	14003	Malting	Canada Dept. of Agriculture Expt. Farm, Brandon, Man.	1970	Vantage/Jet/Vantmore/Parkland/Conquest	Resistant	Peatland	1975–87
Bedford	15774	Feed	Agriculture Canada Res. Sta., Brandon, Man.	1979	Keystone/Vantage/Jet/Vantmore/Husky/ Cree	Resistant	Peatland	1984–present
Norbert	452125	Malting	Agriculture Canada Res. Sta., Winnipeg, Man.	1980	CI 5791/Parkland/Betzes/Piroline/Akka/ Centennial/Klages	Resistant	Peatland	1984–86
Argyle	496255	Malting	University of Manitoba, Winnipeg, Man.	1981	Bonanza/UM67–907	Resistant	Peatland	1988–present

[a] Data on the CI or PI number, use, origin, year of introduction or release, pedigree, and reaction to stem rust of most entries were obtained from the Barley Variety Dictionary published by the American Malting Barley Association, Inc., Milwaukee, Wisconsin (Anonymous, 1990). Hectarages of major barley cultivars grown in the USA and Canada were provided by Mr. S.E. Heisel, American Malting Barley Association, Inc., and Dr. N.T. Kendall, Brewing and Malting Barley Research Institute, Winnipeg, Manitoba, respectively. The probable source(s) of stem rust resistance in cultivars is based on published pedigrees.

[b] O.A.C. 21 was reported to possess some resistance to stem rust (Jedel et al., 1989).

Some of the features that should be considered with regard to resistance are the sources, genetics, pathotype-specificity, ontogenetic expression, components, and effect of environmental factors. The objectives of this paper are to describe and analyse what is known about the durable resistance to stem rust in barley and to discuss possible breeding strategies for the lasting control of this disease.

Important features of stem rust resistance in barley

Sources of resistance. The origin of the first stem rust resistant barley cultivar is unusual since it was produced by an astute farmer rather than a scientific breeding programme. During the severe epidemic of 1935, a farmer named Sam Lykken of Kindred, North Dakota identified a single green (rust-free) plant in his heavily infected field of Wisconsin 37 barley (Lejeune, 1951). This plant was probably the result of an admixture rather than a mutation because it was distinctly different from Wisconsin 37 for a number of characters (Wiebe & Reid, 1961). Thinking this plant may possess some useful resistance to stem rust, Lykken harvested all 18 seeds and increased them for six consecutive seasons. The stem rust resistance of this genotype was later confirmed by researchers at the North Dakota Agricultural Experiment Station. In 1942, Lykken's single plant selection was released as the commercial cultivar, Kindred (Lejeune, 1951). In addition to being resistant to stem rust, Kindred also passed the stringent industry requirements for classification as a malting barley cultivar. Kindred and cultivars derived from it have dominated the barley hectarage in the north central region of the USA from 1942 to the present (Table 2). Indeed, Lykken's single plant selection was probably the most important factor contributing to stable barley production in the southern Red River Valley area during the early post-World War II era.

Another source of stem rust resistance in barley was derived from an umimproved cultivar from the Canton of Lucerne in Switzerland. This germplasm was brought to the United States Department of Agriculture (USDA) in 1914. Two selections from this bulk seed lot, Chevron and Peatland, proved to be highly resistant during the pathotype 56 epidemics of 1935 and 1937 (Shands, 1939). Peatland was the source of stem rust resistance in most Canadian barleys starting with the release of Vantage in 1947 (Table 2). Larker and Trophy, released to growers in 1961, were the first major US malting barley cultivars with Peatland in their pedigree.

Selections from the cultivar Gartons were reported to possess resistance to stem rust in Canada (Lejeune, 1947). The original seed lot of Gartons traces to a Manitoba farmer who procured a barley sample from the John Garton Company in England during the early 1930's (Anonymous, 1990). The stem rust resistant selections of Gartons were cultivated under the same name from the 1930's to the early 1960's, mainly in Manitoba (N.T. Kendall, personal communication). No studies have been advanced to determine the genetics of stem rust resistance in Gartons or the relation of this resistance to other known sources.

Genetics of resistance. The inheritance of resistance in barley to *P. g.* f. sp. *tritici* was first studied by Powers & Hines (1933) who found that resistance in Peatland was governed by a single dominant gene. This gene was designated 'T' since it conferred resistance to the *tritici* forma specialis of *P. graminis* (Powers & Hines, 1933). The current locus designation for the *T* gene is *Rpg*1 (Søgaard & von Wettstein-Knowles, 1987). A number of other studies have been completed on the genetics of resistance in Peatland, Chevron, or their derivatives to several different pathotypes of the wheat stem rust fungus. Some of these studies corroborated the original findings of Powers & Hines (1933) that a single dominant gene confers stem rust resistance (Andrews, 1956; Brookins, 1940; Jedel et al., 1989; Shands, 1939). However, other studies documented the presence of genes with minor effects in addition to *Rpg*1 (Lejeune, 1946; Miller & Lambert, 1955; Patterson, 1950).

In a cross between Kindred and Minn. 615 (a derivative of Peatland), no obvious segregation was observed to pathotype 15B of *P. g.* f. sp. *tritici* (Miller & Lambert, 1955). Similar results were obtained with a cross between Kindred and Peatland to pathotype 56 (S. Fox, personal communication).

These data indicate that the resistance factor in Kindred is allelic to that found in Peatland, namely *Rpg*1. Thus, the durable resistance of North American barley cultivars to *P. g.* f. sp. *tritici* is oligogenic.

Specificity to pathotypes of Puccinia graminis. When the cultivar Kindred and those derived from Peatland became widely grown in the late 1940's, it appeared that their resistance was effective against a number of pathotypes of the wheat stem rust pathogen, including 15B, a pathotype known to be virulent on many wheat cultivars (Lejeune, 1947). However, in 1950, large, compatible type uredia were observed on barley breeding lines known to carry *Rpg*1 at St. Paul, Minnesota (Miller & Lambert, 1956). Subsequent experiments confirmed the virulence of this rust, identified as pathotype 59A, on Peatland, Chevron, Kindred and their derivatives (Ali, 1954; Miller & Lambert, 1956). This was not the only report of stem rust on barley genotypes carrying *Rpg*1 since Canadian researchers found that Peatland and its derivatives were completely susceptible to strains of pathotype 11 identified in Winnipeg in 1952 (Johnson, 1954; Johnson, 1961). In 1959 and again in 1981, compatible type uredia were isolated from barley cultivars carrying *Rpg*1 in the Red River Valley region. This rust was identified as pathotype 23 (E.E. Banttari, personal communication) and 151 (Franckowiak & Miller, 1983), respectively.

The resistance of selected barley genotypes was studied to a composite of four pathotypes, Pgt-RTQ[a] (113-RTQ); -QTH (151-QSH); -TPL (15-TNM); and -HTC (29-HJC), and to the single pathotype -QFC (151-QFB) in isolated rust nurseries in 1989. The four pathotypes used in the composite were previously considered the most common or virulent pathotypes occurring on barley in the northern Great Plains (Steffenson et al., 1985). Pathotype QFC was studied to determine its virulence on adult plants carrying *Rpg*1 in the field. Genotypes with *Rpg*1 could be easily distinguished from those without the gene to the pathotype composite of *P. g.* f. sp. *tritici:* genotypes with *Rpg*1 had low to moderate levels of rust infection (7.5–20%) and low to moderately low infection responses (primarily resistant [R] to moderately resistant [MR] responses), whereas those without the gene had high levels of rust infection (52.5–90%) and high to moderately high infection responses (primarily susceptible [S] to moderately susceptible [MS] responses) (Table 3). Some differences also were noted among genotypes with *Rpg*1 as the level of rust infection on Chevron was significantly lower than on Azure, 80-TT-29, and Morex. When infected with pathotype QFC, genotypes with *Rpg*1 exhibited high terminal rust severities (77.5–90%) and high to moderately high infection responses (Table 3). Thus, it was not possible to differentiate genotypes with and without *Rpg*1 to pathotype QFC.

The specificity of *Rpg*1 to various pathotypes of *P. g.* f. sp. *tritici* also was documented in a number of greenhouse studies (Ali, 1954; Immer et al., 1943; Jedel et al., 1989; Johnson, 1954; Patterson et al., 1957; Steffenson et al., 1985).

In addition to the wheat stem rust pathogen, barley also can be attacked by the rye stem rust pathogen, *P. graminis* f. sp. *secalis*. Some pathotypes of the rye stem rust fungus are highly virulent on adult barley genotypes possessing *Rpg*1 at the field (Johnson, 1954; Johnson & Buchannon, 1954; Steffenson et al., 1985); however, in the seedling stage, many of these same genotypes exhibit low infection types (Immer et al., 1943; Johnson & Buchannon, 1954; Patterson et al., 1957; Steffenson et al., 1985).

Expression of resistance at the seedling stage. At the seedling stage, most barley genotypes, including those known to be very susceptible in the field, exhibit uredia that are associated with some degree of chlorosis (Patterson et al., 1957; Miller & Lambert, 1955; Waterhouse, 1948). This type of reaction makes it difficult to assess infection types using the conventional stem rust scale developed for wheat by Stakman et al. (1962). To overcome this difficulty, Miller & Lambert (1955) devised a scale

[a] Pathotype (race) designations for *P.g.*f.sp. *tritici* are based on the nomenclatural system of Roelfs & Martens (1988). The number and letter codes in parentheses represent the previous pathotype designations under the Stakman (Stakman et al., 1962) and Cereal Rust Laboratory (CRL) (Roelfs & McVey, 1973) nomenclatural systems, respectively.

for barley that was based primarily on uredium size.

Barley seedlings also commonly display mesothetic reactions (a mixture of different infection types on the same plant) to many pathotypes of the stem rust pathogen, especially at lower temperatures (Jedel et al., 1989; Miller & Lambert, 1955; Patterson et al., 1957; Steffenson et al., 1985). It is difficult to differentiate barley genotypes on the basis of the infection type when most exhibit a mesothetic response. A weighted infection type, based on the relative frequency of each infection type present (Steffenson et al., 1985), has been useful in separating some genotypes (e.g. with or without *Rpg*1) that display mesothetic responses (Jedel et al., 1989; Steffenson et al., 1985); however, this analysis is cumbersome and time-consuming.

Recently, Steffenson et al. (1991) found that pathotypes MCC (56-MBC) and HPH (29-HNH) could clearly differentiate genotypes with *Rpg*1 from those without the gene at the seedling stage. When infected with these pathotypes, barley genotypes with *Rpg*1 commonly exhibited infection types ranging from 0; to 10;, whereas those without the gene gave 23− to 33+ (Table 4). The reactions exhibited by the barley genotypes to pathotype TPM (15-TNM) are typical of those exhibited to other pathotypes in that similar infection types are sometimes observed on genotypes with (80-TT-29 and Hector) and without (80-tt-30, Steptoe, Harrington, Hietpas 5, and PI 382313) the gene, *Rpg*1. Some of these genotypes can be differentiated by the frequency of individual infection types (e.g. 23- vs 3-2) which was the basis of the weighted infection type described earlier.

Expression of resistance at the adult plant stage.

Table 3. Terminal rust severity (in percent) and infection response of selected barley genotypes inoculated with a composite of pathotypes (Pgt-HTC, QTH, RTQ, and TPL) and with the single pathotype Pgt-QFC of *Puccinia graminis* f. sp. *tritici* in isolated nurseries at Fargo and Casselton, North Dakota, respectively, in 1989

Genotype	Recognized allele for stem rust reaction[a]	Pathotype composite (HTC, QTH, RTQ, TPL)		Pathotype QFC	
		Terminal stem rust severity[b]	Infection response[c]	Terminal stem rust severity	Infection response
Chevron	*Rpg*1	7.5 a[d]	R-MR	77.5 ab	MS-S(MR)
Peatland	*Rpg*1	13.0 ab	R-MR	80.0 abc	MS-S(MR)
Kindred	*Rpg*1	14.3 ab	MR-R(MS)	80.0 abc	MS-S
Azure	*Rpg*1	18.8 b	MR-R(MS)	90.0 cd	S-MS
80-TT-29	*Rpg*1	18.8 b	R-MR	80.0 abc	S-MS
Morex	*Rpg*1	20.0 b	R-MR	85.0 bc	S-MS
Hietpas 5	*Rpg*2	52.5 c	MS-S	75.0 ab	S-MS
Black Hulless	*rpg*BH	57.5 cd	S-MS	80.0 abc	MS-S
80-tt-30	*rpg*1	62.5 d	MS-S(MR)	72.5 a	S-MS(MR)
Steptoe	*rpg*1	65.0 d	S-MS	80.0 abc	S-MS
Hiproly	*rpg*1	90.0 e	S	95.8 d	S-MS

[a] *Rpg*1 denotes the dominant homozygous resistant condition for the *T* gene and *Rpg*2 for *T*2. *rpg*1 denotes the recessive homozygous susceptible condition for the *T* gene. *rpg*BH denotes the recessive homozygous resistant condition for a gene (previously designated, *s*; Steffenson et al., 1984) that confers resistance to *Puccinia graminis* f. sp. *secalis*. Genotypes 80-TT-29 (*Rpg*1) and 80-tt-30 (*rpg*1) are near-isogenic (Steffenson et al., 1985).

[b] Terminal rust severity was assessed using the modified Cobb scale (Stubbs et al., 1986) when the plants were in the mid-dough stage of development.

[c] Infection responses were assessed using the criteria of Stubbs et al. (1986) where R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible. Infection responses given in parenthesis were observed infrequently.

[d] Values are the means of four replicates. Means with different letters within a column are significantly different according to Duncan's Multiple Range Test (P = 0.05).

Adult plants with *Rpg*1 generally exhibit small (incompatible type) uredia and low percentages of stem rust infection to many of the common pathotypes of *P. g.* f. sp. *tritici* (Jedel et al., 1989; Lejeune, 1947; Shands, 1939; Steffenson & Wilcoxson, 1987; Steffenson et al., 1985) (Table 3). In some cases, a small percentage of compatible type uredia will develop on the stems or leaf sheaths to these same pathotypes (Brookins, 1940; Jedel et al., 1989; Steffenson et al., 1985). Jedel et al. (1989) found distinct differences with regard to the expression of *Rpg*1 in several two- versus six-rowed barleys; the former commonly exhibited higher infection levels than the latter. Virulent pathotypes of *P. graminis* have been isolated from barley in the past as described previously. When these virulent pathotypes (e.g. QFC) are inoculated onto genotypes with *Rpg*1, fully susceptible reactions are expressed (Table 3). The degree of association between the stem rust reaction at the seedling stage and that expressed at the adult plant stage is an important factor to consider, especially in the development of greenhouse screening techniques. In general, the seedling reaction to *P. g.* f. sp. *tritici* corresponds to that observed on adult plants in the field (Brookins, 1940; Immer et al., 1943; Miller & Lambert, 1955; Shands, 1939; Steffenson et al., 1985).

Components of resistance. Quantitative or rate-reducing components of resistance have been described in a number of cereal rust pathosystems (Parlevliet, 1979). In the barley:stem rust pathosystem, few studies have been made to determine if *Rpg*1 is involved in conferring any quantitative components of resistance to *P. g.* f. sp. *tritici*. Sellam & Wilcoxson (1976) studied the development of the stem rust fungus in barley cultivars with and without *Rpg*1. Urediospore germination, appressorium formation, and penetration by the fungus were similar in the two groups of barley; however, the number of uredia forming on leaves was lower and the growth of the pathogen restricted in genotypes with *Rpg*1 (Sellam & Wilcoxson, 1976). Low receptivity was closely associated with the presence of *Rpg*1 in barley genotypes infected with pathotypes RTQ and QTH in the field and also with the latter pathotype in the greenhouse (Steffenson & Wilcoxson, 1987). This was not the case with pathotype RTQ in the greenhouse, since the near-isogenic lines for *Rpg*1 did not differ significantly in numbers of uredia/cm^2 in either the seedling or adult plant stage. Thus, in addition to qualitative characters of resistance, *Rpg*1 also may be involved in reducing the number of successful infections that occur on barley; however, this quantitative component of resistance may vary with pathotype.

Effect of the environment. The effect of various environmental factors on the resistance conferred by *Rpg*1 has not adequately been studied. Temperature is known to affect the stem rust reaction in barley. At the seedling stage, barley genotypes with *Rpg*1 generally exhibit low mesothetic reac-

Table 4. Infection types of barley seedlings to pathotypes Pgt-MCC, HPH, and TPM of *Puccinia graminis* f. sp. *tritici* at 25–28° C

Genotype	Recognized allele for stem rust reaction[a]	Seedling infection type		
		Pathotypes		
		MCC	HPH	TPM
Chevron	*Rpg*1	0;1[b]	0;1	21
Kindred	*Rpg*1	0;1	0;1	12
Glenn	*Rpg*1	0;1	0;1	21
Excel	*Rpg*1	0;	0;1	21
Bowman	*Rpg*1	0;1	0;1	21
Hector	*Rpg*1	0;1	10;	23–
80-TT-29	*Rpg*1	0;1	0;1	23–
80-tt–30	*rpg*1	3–3	33+	3-2
Steptoe	*rpg*1	3–3	3–3	3-2
Harrington	*rpg*1	3–3	3–3	3-2
Hietpas 5	*Rpg*2	23–	3–3	23–
PI 382313	*Rpg*3	23–	3–3	23–
Black Hulless	*rpg*BH	3–2	3–3	3–3

[a] See Table 3. *Rpg*3 denotes the dominant homozygous condition for the *T*3 gene.

[b] Data are the two most common infection types (most prevalent type listed first) observed on individual genotypes from five replicates. Infection types were assessed 12 days after inoculation using the system of Miller & Lambert (1955). Infection types 0;, 1, and 2 are indicative of resistance (low infection response), whereas infection types 3 and 4 are indicative of susceptibility (high infection response). The '+' and '–' symbols were used to denote more or less sporulation, respectively.

tions at low temperature (16–20° C) and slightly higher mesothetic reactions at high temperature (24–28° C) (Miller & Lambert, 1955; Steffenson et al., 1985). Infection type differences between genotypes known to be resistant or susceptible in the field are most distinct at high incubation temperatures because genotypes that lack *Rpg*1 generally exhibit high infection types (Andrews, 1956; Jedel et al., 1989; Miller & Lambert, 1955; Patterson et al., 1957; Steffenson et al., 1985). For this reason, most researchers have used incubation temperatures above 24° C when evaluating barley seedlings to *P. g.* f. sp. *tritici*. It is possible that higher ambient temperatures during the growing season could reduce the effectiveness of *Rpg*1 in adult barley plants in the field, but this aspect has not been investigated.

In another study, Patterson et al. (1957) examined the effect of pre-inoculation temperature and different combinations of post-inoculation daylength and light intensity treatments on the infection type of cultivar Valentine (possesses *Rpg*1). The infection type of this cultivar did not change appreciably in any of the different treatments.

Factors contributing to the longevity of stem rust resistance in barley.

The durability of the *Rpg*1 resistance in barley is remarkable considering the potential variability of *P. g.* f. sp. *tritici* and the vast hectarages of cultivars that are genetically uniform for stem rust resistance. Few single resistance genes have performed as well and as long as *Rpg*1 in a cereal rust pathosystem. However, the longevity of stem rust resistance in barley was undoubtedly aided by a number of factors.

First, because most of the barley is planted early in the spring and matures in a relatively short time, stem rust inoculum carried from the south will sometimes reach the crop in the north (Fig. 1) when it is nearly mature and cannot be seriously damaged. In the northern Great Plains, barley is a 88–90 day crop and matures approximately 7–12 days before many of the common wheat cultivars. Thus, like the early-maturing wheat cultivar, Marquis, barley can sometimes escape severe stem rust infection (Green, 1971). Barley will not escape rust infection by this means in all years. Cool, wet weather during the spring season can delay the seeding of barley providing additional time for the stem rust pathogen to reach and reproduce on the crop.

Second, one or more minor genes may augment the level of resistance provided by *Rpg*1 in barley cultivars. Additional genes for stem rust resistance have been documented in several genetic studies (Miller & Lambert, 1955; Lejeune, 1946; Patterson, 1950) as previously described, but their effect in suppressing stem rust development is not fully understood. Barley genotypes commonly exhibit chlorosis around uredia at the seedling stage. The ubiquitousness of this chlorotic reaction led Patterson et al. (1957) to conclude that many barley genotypes possess at least some level of resistance to *P. graminis*. It is not known whether this seedling resistance is effective in the later stages of plant development; however, in recent greenhouse and field experiments, we have not been able to achieve high levels of rust infection on some barley genotypes (with or without *Rpg*1) with virulent pathotypes of *P. g.* f. sp. *tritici* prior to anthesis (B.J. Steffenson & Y. Jin, unpublished data). Thus, some barleys may possess resistance genes that protect them from severe stem rust infection up to the stage of anthesis. According to Green (1971), the *H. vulgare:P. graminis* pathosystem exhibits the primitive host:parasite characteristics of low specialization and low parasite aggressiveness. He suggested that slow rusting resistance may have protected barley from stem rust damage in western Canada. If this is true, the genetic basis of this resistance is unknown.

Third, the cultivation of stem rust resistant wheats in the northern Great Plains has prevented local outbreaks of stem rust (Steffenson et al., 1985) and reduced the effective population size of *P. g.* f. sp. *tritici* in North America (Schafer & Roelfs, 1985). The reduced population size of *P. g.* f. sp. *tritici* may not be highly significant in contributing to the longevity of stem rust resistance in barley since the potential number of mutant spores

produced on wheat that possess virulence on single resistance genes is great (Schafer & Roelfs, 1985).

Fourth, the eradication of the barberry in the Great Plains has greatly contributed to the stability of stem rust resistance in wheat (Roelfs, 1982) and certainly in barley as well even though this alternate host was essentially eliminated before cultivars with *Rpg*1 were released to growers.

Fifth, virulent pathotypes of *P. g.* f. sp. *secalis* have not increased to damaging levels in the Great Plains (Green, 1971). The reason for this may be due to the limited hectarage of the pathogen's primary host, rye, and eradication of the alternate host, barberry, especially in the USA. However, a number of wild grass species can harbour *P. g.* f. sp. *secalis* and are common in the region (Roelfs, 1985).

Finally, although virulent pathotypes of *P. g.* f. sp. *tritici* have been detected on barley periodically in the past, they have not increased and become established. The reasons for this are unclear. In the northern Great Plains, stem rust infections are initiated every spring by inoculum from the south (Fig. 1) since the fungus rarely overwinters north of Oklahoma. If virulent pathotypes are to survive each year, they must be capable of attacking winter wheats or wild grass species because the hectarage of barley is very small in the southern and central Great Plains. It is possible that virulent pathotypes were simply 'filtered-out' on different wheat genotypes in the south during the winter and decreased in frequency (Vanderplank, 1968) – that is, until the appearance of pathotype Pgt-QCC.

Pathotype QCC. In 1989, compatible stem rust uredia were observed on barley cultivars carrying *Rpg*1 in many fields throughout the northern areas of production in the USA (B.J. Steffenson, unpublished data). Subsequent pathotype determinations of these field collections by the Cereal Rust Laboratory in St. Paul revealed that the rust was pathotype QCC of *P. g.* f. sp. *tritici* – a pathotype new to the Great Plains of the USA (Roelfs et al., 1991a). Pathotype QCC was first detected in the Great Plains region one year earlier by Martens et al. (1989) in Canada. In identifying this pathotype in Saskatchewan and Manitoba, Martens et al. (1989) noted that, 'it is unusual to obtain virulence in the prairie region that is characteristic of the Pacific region.' This early discovery was significant because pathotype QCC was detected in nearly every barley field surveyed in the southern Red River Valley region during the following three seasons (1989–1991). It is likely that pathotype QCC originated in the Pacific Northwest because isolates with the same virulence pattern were described from that region prior to 1989 (Martens et al., 1989; Roelfs et al., 1990a). Additionally, it is possible that this pathotype arose from barberry since this sexual host is known to occur in the Pacific Northwest region. Regardless of whether this pathotype originated from a sexual or asexual host, this incident demonstrates the importance of periodic inoculum exchanges from the western to the central stem rust population.

Minor stem rust epidemics were recorded on barley in the northern Great Plains in 1990 and 1991. The severity of stem rust on barley in eastern North Dakota, northeastern South Dakota, and northwestern Minnesota ranged from trace to 60% (Roelfs et al., 1990b). Not since the late 1930's has barley stem rust been as prevalent and severe in this region. Fortunately, overall yield losses in barley cultivars with *Rpg*1 were light, ranging from 1–3% (Roelfs et al., 1990b; Roelfs et al., 1991b). Late planted crops, however, suffered higher yield losses (Harder & Dunsmore, 1991). The actual dollar loss from stem rust was greater than the yield loss estimates would predict since many growers did not receive the premium afforded malting barley due to a low percentage of plump kernels in their grain. This reduction in kernel size was likely due to stem rust infection (Dill-Macky et al., 1990).

Pathotype QCC is virulent on several winter wheat cultivars and wild grass species in the south and is now well established in the Great Plains. During the past four years, QCC has become one of the most prevalent pathotypes of *P. g.* f. sp. *tritici* on barley and wheat in North America (D.E. Harder & A.P. Roelfs, personal communication). This recent change in the frequency of wheat stem rust pathotypes is due primarily to the susceptibility of cultivated barley. The effect of barley on the pathotype composition of the wheat stem rust pop-

ulation should not be understated as indicated by Luig (1985). Indeed, Fox & Harder (1991) detected significant changes in the frequency of *P. g.* f. sp. *tritici* pathotypes on different barley genotypes grown in the field. It is possible that pathotypes with virulence on northern spring wheat cultivars (both bread and durum types) could arise from stem rust infected barley plants. This could result in stem rust epidemics on wheat because barley would provide an early and local source of inoculum. The potential vulnerability of spring wheat highlights the urgency of identifying and incorporating additional stem rust resistance genes into new barley cultivars.

Table 5. Reaction of selected barley genotypes to pathotype QCC of *Puccinia graminis* f. sp. *tritici* as seedlings in the greenhouse and adult plants in the field[a]

Genotype[b]	Seedling infection type[c]		Field reaction	
	Mode	Range	Average terminal rust severity[d]	Infection response[e]
Q21861	0;1	0;/23–	6.1 a[f]	MR-MS
Diamond	21	12/23–	7.1 a	MR
PI 452421	23–	12/3–2	9.4 ab	MS-S
PC11	123–	12/33–	10.0 ab	MR-R-MS
PC84	23–1	12/23–	10.1 ab	MR-MS
Hietpas 5	23–	23/3–2	13.9 b	MS-S
Robust	21	12/23–	25.0 c	S-MS

[a] Data from Jin et al., 1992.

[b] Diamond, PI 452421, and Hietpas 5 were selected as being resistant to pathotype QCC by B.J. Steffenson and coworkers at North Dakota State University; PC11 and PC84 by S. Fox at the University of Manitoba; and Q21861 by Dr. A.P. Roelfs, USDA-ARS Cereal Rust Laboratory, St. Paul. The resistance of Q21861 and Diamond was independently verified by B.J. Steffenson and S. Fox, respectively. Robust is a widely grown cultivar that is susceptible to pathotype QCC.

[c] Infection types were assessed 12 days after inoculation using the system of Miller & Lambert (1955). The seedlings were incubated in a greenhouse at 21–25° C. Mode = most commonly observed infection types and range = lowest/highest observed infection types.

[d] Terminal rust severity was assessed using the modified Cobb scale (Stubbs et al., 1986) when the plants were in the mid-dough stage of development. Average terminal severity is based on four replications at each of the following 1991 rust nurseries: Fargo, North Dakota and St. Paul, Minnesota.

[e] See Table 3.

[f] Values are the means of eight replicates. Means with different letters within a column are significantly different according to Duncan's Multiple Range Test (P = 0.05).

Identification of resistance to pathotype QCC. In 1989, a cooperative project was initiated among researchers at North Dakota State University, University of Minnesota, USDA, Agriculture Canada, and Busch Agricultural Resources, Inc. to identify resistance in barley to pathotype QCC. Disease evaluations were made mainly on accessions from the USDA National Small Grains Collection (NSGC) in the greenhouse and at several field nurseries in the USA and Canada. Resistance to pathotype QCC is rare in barley as fewer than 10 genotypes were selected as possessing adequate resistance from over 17,000 entries evaluated.

At North Dakota State University, detailed studies are being conducted on six selected genotypes: Q21861, PC11, and PC84, genotypes originating from the CIMMYT barley breeding programme; Hietpas 5, a selection from Oderbrucker that possesses the *Rpg2* (*T2*) gene for stem rust resistance (Patterson et al., 1957); and PI 452421, and PI 491573, selections from the USDA NSGC (Table 5). PI 491573 is the cultivar Diamond which was produced by the Agriculture Canada Research Station at Lacombe. None of these six genotypes possesses complete resistance to pathotype QCC. At the seedling stage, the infection types on these lines can be quite variable, ranging from 0; to 33–. Differences in resistance between the selected lines and common cultivars like Robust are detectable in the field after heading; the former exhibit relatively low terminal rust severities and numbers of compatible type uredia (moderately susceptible or susceptible types) and the latter higher terminal rust severities and numbers of compatible type uredia (Table 5). The incomplete resistance of Diamond may be due to a reduction in receptivity and uredium size (Steffenson et al., 1990).

Q21861 possesses the highest level of resistance among the six selections under study. This line was one of several hundred originally selected by Dr. W.J.R. Boyd from a CIMMYT barley nursery established by Dr. H. Vivar (R.G. Rees, personal communication). In Australia, Q21861 possesses

resistance to pathotype Pgt-LSH in the field (Dill-Macky et al., 1992). The resistance of this line to pathotype QCC was first described by Dr. A.P. Roelfs at St. Paul and was independently confirmed by our research group at Fargo. At the seedling stage, Q21861 commonly exhibits infection types ranging from 0; to 21, although higher reactions are sometimes observed at elevated temperatures (> 24° C) (J.D. Miller, personal communication). Adult plants exhibit small to minute uredia with chlorosis; however, large compatible uredia are often present near the top node and on the peduncle – a common occurrence on many other barley genotypes. Preliminary genetic studies indicate that the resistance of Q21861 to pathotype QCC is governed by one or possibly two recessive genes. Additionally, the reaction of PC11, PC84, Diamond, and Hietpas 5 to pathotype QCC appears to be simply inherited with resistance dominant (Y. Jin & B.J. Steffenson, unpublished data).

Breeding for resistance to stem rust in barley

The appearance of pathotype QCC in the Great Plains has forced barley pathologists and breeders to reevaluate their strategies for the control of stem rust. The resistance gene, *Rpg*1, was effective for nearly 50 years in barley cultivars that were widely grown, but it is not realistic to expect such longevity from another resistance gene. Several gene deployment strategies have proven effective in a number of cereal pathosystems over the past three decades. Two of these strategies, the deployment of genetically diverse cultivars and gene pyramiding, may prove useful in the barley production areas of the northern Great Plains.

Deployment of cultivars that are genetically diverse for stem rust resistance. Strategies that increase the diversity of disease resistance have been used with some success in several cereal pathosystems (Mundt & Browning 1985; Wolfe & Barrett, 1980). These schemes may vary according to the level of diversity within a unit of area. For example, the cultivation of a genotype mixture (with the individual components of the mixture differing in the resistance genes they possess) within a single field comprises an intra-field diversity scheme. Inter-field diversity can be achieved by the planned deployment of genotypes over different fields or farms (Mundt & Browning, 1985). The exploitation of an intra-field diversity scheme may not be possible for malting barley in the Red River Valley region due to the rigid cultivar identity requirements of the malting and brewing industries in the USA and Canada. Furthermore, it is unlikely that a planned inter-field diversity scheme would be acceptable to most producers in the area. However, some action should be taken to reduce the extreme genetic uniformity that exists for stem rust resistance in barley today. There are six major breeding programmes that develop barley cultivars for the Red River Valley and surrounding areas. A modest level of inter-field diversity could be achieved if the future cultivars from these programmes were bred with different resistance genes. Unfortunately, the effectiveness of this strategy may be limited since a single cultivar usually becomes dominant in the area and remains so for several years (Wych & Rasmusson, 1983).

Pyramiding stem rust resistance genes in barley. The strategy of gene pyramiding has been effective against stem rust in wheat for over 37 years in North America and Australia (Dyck & Kerber, 1985). This same strategy will likely provide control of *P. g.* f. sp. *tritici* in barley for a long time. The malting and brewing industries dictate, to some extent, the strategy used in barley breeding programmes. The decision by industry to accept a barley cultivar for malting and brewing is based on about 25 different quality traits (Wych & Rasmusson, 1983). These stringent requirements have forced breeders to narrow their germplasm base. To obtain acceptable malting types, it is often necessary to cross closely related parents that already possess superior malting characteristics (Wych & Rasmusson, 1983). Prior to the appearance of pathotype QCC in 1989, breeding for stem rust resistance was easy because it required the incorporation of just one dominant gene (*Rpg*1) which was already present in many superior malting types. To control stem rust in the future, breeders may have

to combine *Rpg*1 and gene(s) for resistance to pathotype QCC in new barley cultivars. The retention of *Rpg*1 in advanced breeding lines is essential since this gene has proven durable to many pathotypes of *P. g.* f. sp. *tritici* in the Great Plains.

Molecular marker assisted selection of genes for stem rust resistance. The incorporation of multiple stem rust resistance genes in barley will significantly increase the complexity of the breeding process. To aid breeders in this task, a project has been initiated for the molecular marker assisted selection of genes that confer stem rust resistance in barley. This technique is based on the identification of molecular markers (isozymes, restriction fragment length polymorphisms [RFLPs], or random amplified polymorphic DNAs [RAPDs]) that are closely linked to the genes of interest. If a tight linkage is found between a molecular marker and a disease resistance gene, the former can be exploited for the indirect selection of the latter without the need for laborious and sometimes variable pathogen inoculations (Melchinger, 1990). Genome maps of two doubled haploid populations (one derived from Steptoe/Morex and the other from Harrington/TR306) are under construction as part of the North American Barley Genome Mapping Project. These populations will serve as useful models for the molecular marker assisted selection of stem rust resistance in barley since both are polymorphic for *Rpg*1 (Steffenson & Dahleen, 1991; B.J. Steffenson, unpublished data). Two flanking RFLP markers (*Tel*1S [subtelomeric] and *Plc* [barley plastocyanin precursor]) to *Rpg*1 were recently identified in the Steptoe/Morex doubled haploid population (Steffenson et al., 1992). The DNA probe for *Plc* will best facilitate the transfer of *Rpg*1 in breeding programmes because it is closely linked (ca. 3 cM) to the gene and gives a strong, unambiguous hybridization signal.

The bulked segregant analysis procedure (Michelmore et al., 1991) is being used to identify molecular markers (RAPDs) that are closely linked to genes conferring resistance to pathotype QCC in a doubled haploid population derived from the cross, Q21861/SM89010. This population was developed by Drs. B.G. Rossnagel and K. Kao at the University of Saskatchewan and is polymorphic for reaction to the leaf (brown) rust (*Puccinia hordei*) and powdery mildew (*Blumeria* = *Erysiphe graminis* f. sp. *hordei*) pathogens in addition to pathotype QCC of *P. g.* f. sp. *tritici* (B.J. Steffenson & Y. Jin, unpublished data). Bulked segregant analysis is a simple and elegant technique that was first validated with genes for resistance (*Dm* genes) to the downy mildew pathogen (*Bremia lactucae*) in lettuce. Using this procedure, Michelmore et al. (1991) identified three markers that were 6, 8, and 12 cM away from the *Dm*5/8 locus. The use of this procedure on doubled haploid populations offers several advantages over the conventional analysis on F_2 progeny: a) there is no need to verify homozygous resistant plants in the F_3 generation since all the alleles are fixed, and b) replicated inoculations to determine the infection phenotype of individuals can be repeated as often as necessary and with several different pathogens over time since the doubled haploids represent a permanent or 'immortal' population. This latter attribute is valuable when the expression of a resistance gene is significantly altered by environmental factors or if the goal of a molecular marker assisted selection programme is to tag and transfer genes for resistance to more than one pathogen.

Concluding remarks

The durable resistance conferred by *Rpg*1 in barley to stem rust has faltered because a virulent pathotype of *P. g.* f. sp. *tritici* became widely distributed in the Great Plains. However, *Rpg*1 may still confer some degree of resistance to pathotype QCC because stem rust severities have been low and yield losses light on barley cultivars carrying the gene during the last four seasons (1989–1992) in the USA. In Canada, Harder & Dunsmore (1991) reported only light to moderate yield losses on cultivars carrying *Rpg*1 (e.g. Argyle, Leduc, and Bonanza) and heavy losses on the cultivar Tupper which lacks the resistance gene. Genotypes with *Rpg*1 (and some without the gene) appear to possess a level of resistance that prevents severe rust infection by pathotype QCC prior to anthesis in

both greenhouse and field experiments (B.J. Steffenson & Y. Jin, unpublished data). This 'pre-anthesis' resistance, whether conferred by *Rpg*1 or other genes, may protect barley from serious damage by stem rust. Additionally, it is possible that pathotype QCC will decrease to innocuous levels in the wheat stem rust population. This situation apparently occurred four times during the past 42 years with the virulent pathotypes 59A, 11, 23, and 151. Whether pathotype QCC continues to predominate in the Great Plains population of *P. g.* f. sp. *tritici* or not, there are grounds for optimism that durable resistance will continue to be achieved in future barley cultivars by the incorporation of multiple resistance genes using molecular marker assisted selection.

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References

Anonymous, 1990. Barley Variety Dictionary. American Malting Barley Assoc., Inc., Milwaukee.

Ali, S.B., 1954. Behavior of isolates of race 59 of *Puccinia graminis tritici* on certain varieties of wheat and barley. (Abstr.) Phytopathology 44: 481.

Andrews, J.E., 1956. Inheritance of reaction to loose smut, *Ustilago nuda,* and to stem rust, *Puccinia graminis tritici,* in barley. Can. J. Agric. Sci. 36: 356–370.

Brookins, W.W., 1940. Linkage relationship of the genes differentiating stem rust reaction in barley. Ph.D. Thesis. University of Minnesota, St. Paul.

Dill-Macky, R., R.G. Rees & W.J.R. Boyd, 1992. Sources of resistance to stem rust in barley. Plant Dis. 76: 212.

Dill-Macky, R., R.G. Rees & G.J. Platz, 1990. Stem rust epidemics and their effects on grain yield and quality in Australian barley cultivars. Aust. J. Agric. Res. 41: 1057–1063.

Dyck, P.L. & E.R. Kerber, 1985. Resistance of the race-specific type. In: A.P. Roelfs & W.R. Bushnell (Eds.). The Cereal Rusts. Vol. II. Diseases, distribution, epidemiology, and control, pp. 469–500. Academic Press, Inc., New York.

Fox, S. & D. Harder, 1991. Selection pressure of barley genotypes on a stem rust population. (Abstr.) Can. J. Plant Pathol. 13: 276.

Franckowiak, J.D. & J.D. Miller, 1983. Reaction of barley to a culture of wheat stem rust, race 151. Barley Newsl. 27: 52.

Green, G.J., 1971. Hybridization between *Puccinia graminis tritici* and *Puccinia graminis secalis* and its evolutionary implications. Can. J. Bot. 49: 2089–2095.

Harder, D.E. & K.M. Dunsmore, 1991. Incidence and virulence of *Puccinia graminis* f. sp. *tritici* on wheat and barley in Canada in 1990. Can. J. Plant Pathol. 13: 361–364.

Immer, F.R., J.J. Christensen & W.Q. Loegering, 1943. Reaction of strains and varieties of barley to many physiologic races of stem rust. Phytopathology 33: 253–254.

Jedel, P.E., D.R. Metcalfe & J.W. Martens, 1989. Assessment of barley accessions PI 382313, PI 382474, PI 382915, and PI 382976 for stem rust resistance. Crop Sci. 29: 1473–1477.

Jin, Y., B.J. Steffenson & T.G. Fetch, Jr., 1992. Evaluation of barley for resistance to stem rust, 1991. Biol. & Cult. Tests 7: 73.

Johnson, R., 1984. A critical analysis of durable resistance. Ann. Rev. Phytopathol. 22: 309–330.

Johnson, T., 1954. The reaction of barley varieties to certain races of wheat stem rust. Div. of Botany & Plant Pathol., Sci. Serv., Dept. of Agr., Winnipeg. Rept. # 7.

Johnson, T., 1961. Rust research in Canada and related plant-disease investigations. Res. Branch, Canada Dept. Agr., Winnipeg. Publ. # 1098.

Johnson, T. & K.W. Buchannon, 1954. The reaction of barley varieties to rye stem rust, *Puccinia graminis* var. *secalis*. Can. J. Agr. Sci. 34: 473–482.

Lejeune, A.J., 1946. Correlated inheritance of stem rust reaction, nitrogen content of grain and kernel weight in a barley cross. Sci. Agr. 26: 198–211.

Lejeune, A.J., 1947. A note on the reaction of certain barley varieties to race 15B of stem rust (*Puccinia graminis tritici* Erikss. and Henn.). Sci. Agr. 27: 183–185.

Lejeune, A.J., 1951. The story of Kindred (L) barley. Barley Improv. Conf. Rept., January 23, 1951, Minneapolis.

Luig, N.H., 1985. Epidemiology in Australia and New Zealand. In: A.P. Roelfs & W.R. Bushnell (Eds.). The Cereal Rusts. Vol. II. Diseases, distribution, epidemiology, and control, pp. 301–328. Academic Press, Inc., New York.

McDonald, W.C., 1970. Diseases and other factors affecting average yields of barley in Manitoba, 1954–1968. Can. Plant Dis. Surv. 50: 113–117.

Martens, J.W., K.M. Dunsmore & D.E. Harder, 1989. Incidence and virulence of *Puccinia graminis* in Canada on wheat and barley in 1988. Can. J. Plant Pathol. 11: 424–430.

Melchinger, A.E., 1990. Use of molecular markers in breeding for oligogenic disease resistance. Plant Breed. 104: 1–19.

Michelmore, R.W., I. Paran & R.V. Kesseli, 1991. Identification of markers linked to disease-resistance genes by bulked segregant analysis: A rapid method to detect markers in specific genomic regions by using segregating populations. Proc. Natl. Acad. Sci. USA 88: 9828–9832.

Miller, J.D. & J.W. Lambert, 1955. Variability and inheritance of reaction of barley to race 15B of stem rust. Agron. J. 47: 373–377.

Miller, J.D. & J.W. Lambert, 1956. Reactions of certain spring barley lines to race 59A of stem rust. Plant Dis. Reptr. 40: 340–346.

Mundt, C.C. & J.A. Browning, 1985. Genetic diversity and cereal rust management. In: A.P. Roelfs & W.R. Bushnell (Eds.). The Cereal Rusts. Vol. II. Diseases, distribution, epidemiology, and control, pp. 527–560. Academic Press, Inc., New York.

Parlevliet, J.E., 1979. Components of resistance that reduce the rate of epidemic development. Ann. Rev. Phytopathol. 17: 203–222.

Patterson, F.L., 1950. Adult plant and seedling reactions of barley varieties and hybrids to three races of *Puccinia graminis tritici*. Ph.D. Thesis. University of Wisconsin, Madison.

Patterson, F.L., R.G. Shands & J.G. Dickson, 1957. Temperature and seasonal effects on seedling reactions of barley varieties to three races of *Puccinia graminis* f. sp. *tritici*. Phytopathology 47: 395–402.

Powers, L. & L. Hines, 1933. Inheritance of reaction to stem rust and barbing of awns in barley crosses. J. Agr. Res. 46: 1121–1129.

Roelfs, A.P., 1978. Estimated losses caused by rust in small grain cereals in the United States – 1918–76. U.S. Dept. Agri. Misc. Pub. # 1363.

Roelfs, A.P., 1982. Effects of barberry eradication on stem rust in the United States. Plant Dis. 66: 177–181.

Roelfs, A.P., 1985. Wheat and rye stem rust. In: A.P. Roelfs & W.R. Bushnell (Eds.). The Cereal Rusts. Vol. II. Diseases, distribution, epidemiology, and control, pp. 3–37. Academic Press, Inc., New York.

Roelfs, A.P., D.H. Casper, D.L. Long & J.J. Roberts, 1990a. Races of *Puccinia graminis* in the United States in 1988. Plant Dis. 74: 555–557.

Roelfs, A.P., D.H. Casper, D.L. Long & J.J. Roberts, 1991a. Races of *Puccinia graminis* in the United States in 1989. Plant Dis. 75: 1127–1130.

Roelfs, A.P., D.L. Long, B.J. Steffenson, Y. Jin, M.E. Hughes & D.H. Casper, 1990b. Barley rusts in the United States in 1990. Barley Newsl. 34: 73–76.

Roelfs, A.P. & D.V. McVey, 1973. Races of *Puccinia graminis* f. sp. *tritici* in the USA during 1972. Plant Dis. Reptr. 57: 880–884.

Roelfs, A.P. & J.W. Martens, 1988. An international system of nomenclature for *Puccinia gramminis* f. sp. *tritici*. Phytopathology 78: 526–533.

Roelfs, A.P., B.J. Steffenson, M.E. Hughes, D.L. Long, D.H. Casper, Y. Jin & J. Huerta, 1991b. Barley rust in the United States in 1991. Barley Newsl. 35: 71–77.

Schafer, J.F. & A.P. Roelfs, 1985. Estimated relation between numbers of urediniospores of *Puccinia graminis* f. sp. *tritici* and rates of occurrence of virulence. Phytopathology 75: 749–750.

Sellam, M.A. & R.D. Wilcoxson, 1976. Development of *Puccinia graminis* f. sp. *tritici* on resistant and susceptible barley cultivars. Phytopathology 66: 667–668.

Shands, R.G., 1939. Chevron, a barley variety resistant to stem rust and other diseases. Phytopathology 29: 209–211.

Søgaard, B. & P. von Wettstein-Knowles, 1987. Barley: Genes and chromosomes. Carlsberg Res. Commun. 52: 123–196.

Stakman, E.C. & J.G. Harrar, 1957. Principles of Plant Pathology. Ronald Press Co., New York.

Stakman, E.C., D.M. Stewart & W.Q. Loegering, 1962. Identification of physiologic races of *Puccinia graminis* var. *tritici*. U.S. Dept. Agric., Agric. Res. Serv. E-617.

Steffenson, B.J., 1989. Durable resistance to wheat stem rust in barley. Barley Newsl. 33: 119.

Steffenson, B.J. & L.S. Dahleen, 1991. The potential use of molecular markers for mapping disease resistance genes in barley. In: L. Munck (Ed.). Barley Genetics VI, pp. 644–646. Munksgaard Int. Pub. Ltd., Copenhagen.

Steffenson, B.J., Y. Jin, T.G. Fetch, Jr. & J.D. Miller, 1990. Reaction of five barley cultivars to infection by race QCC of *Puccinia graminis* f. sp. *tritici*. Barley Newsl. 34: 99–100.

Steffenson, B.J., A. Kilian & A. Kleinhofs, 1992. Identification of molecular markers linked with the *Rpg*1 gene for stem rust resistance in barley. (Abstr.) Phytopathology 82: 1083.

Steffenson, B.J., J.D. Miller & Y. Jin, 1991. Detection of the T gene for resistance to *Puccinia graminis* f. sp. *tritici* in barley seedlings. (Abstr.) Phytopathology 81: 1229.

Steffenson, B.J. & R.D. Wilcoxson, 1987. Receptivity of barley to *Puccinia graminis* f. sp. *tritici*. Can. J. Plant Pathol. 9: 36–40.

Steffenson, B.J., R.D. Wilcoxson & A.P. Roelfs, 1985. Resistance of barley to *Puccinia graminis* f. sp. *tritici* and *Puccinia graminis* f. sp. *secalis*. Phytopathology 75: 1108–1111.

Steffenson, B.J., R.D. Wilcoxson & A.P. Roelfs, 1984. Inheritance of resistance to *Puccinia graminis* f. sp. *secalis* in barley. Plant Dis. 68: 762–763.

Stubbs, R.W., J.M. Prescott, E.E. Saari & H.J. Dubin, 1986. Cereal Disease Methodology Manual. Centro Internacional de Mejoramiento de Maiz Y Trigo (CIMMYT), Mexico.

Vanderplank, J.E., 1968. Disease Resistance in Plants. Academic Press, New York.

Waterhouse, W.L., 1948. Studies in the inheritance of resistance to rust of barley. Part II. J. Roy. Soc. N. S. W. 81: 198–205.

Wiebe, G.A. & D.A. Reid, 1961. Classification of barley varieties grown in the United States and Canada in 1958. U.S. Dept. Agr. Tech. Bull. # 1224.

Wolfe, M.S. & J.A. Barrett, 1980. Can we lead the pathogen astray? Plant Dis. 64: 148–155.

Wych, R.D. & D.C. Rasmusson, 1983. Genetic improvement in malting barley cultivars since 1920. Crop Sci. 23: 1037–1040.