

# Competitive Ability of Races of *Puccinia graminis* f. sp. *tritici* on Three Barley Cultivars and a Susceptible Wheat Cultivar

J. Q. Liu, D. E. Harder, and J. A. Kolmer

Cereal Research Centre, Agriculture and Agri-Food Canada, 195 Dafoe Road, Winnipeg, Manitoba, Canada R3T 2M9. Contribution 1649 Cereal Research Centre, Winnipeg, Manitoba, Canada.

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## ABSTRACT

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Races QCC (virulent to the resistance gene *Rpg1* in barley) and QFC and TPM (moderately avirulent to *Rpg1*) of *Puccinia graminis* f. sp. *tritici* were mixed and cultured in two experiments for four and six uredinial generations, respectively, on adult plants of the barley cultivars Tupper and Robust (each with resistance gene *Rpg1*), Harrington (*rpg1*), and the stem rust susceptible wheat cultivar Little Club. When mixed in equal proportions, race QCC comprised over 88% of the populations selected on 'Tupper' and 'Robust' after one uredinial generation. By the fourth generation, QCC comprised 90% of the population from 'Harrington' and 80% from 'Little Club'. The competitive advantage of race QCC over races QFC and TPM also was observed when the proportion of race QCC was reduced in the original inoculum mixture. In fit-

ness tests, all populations selected from the sixth uredinial generation showed significant increases in infection frequency (number of uredinia per square centimeter of stem tissue) and urediniospore production (milligrams of urediniospores per square centimeter of stem tissue) as compared with the original inoculum mixture. The changes in infection frequency and urediniospore production of the selection populations, however, was related to the frequency of race QCC in a given population. Selection pressure exerted by widely grown barley cultivars with gene *Rpg1* and a higher competitive ability of QCC relative to other common races on susceptible barley and wheat would explain the widespread distribution and rapid increase of QCC in the northern Great Plains of the United States and Canada.

*Additional keywords:* barley stem rust, *Hordeum vulgare*, specific resistance, specific virulence.

Stem rust of common wheat (*Triticum aestivum* L.), durum wheat (*T. turgidum* L. var. *durum* (Desf.) MK), and barley (*Hordeum vulgare* L.), caused by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn., is an important disease in many parts of the world. In the northern Great Plains of the United States and Canada, stem rust on barley has been controlled for many years by the widespread use of resistant cultivars. The resistance in these cultivars has mainly been due to a single gene, *Rpg1* (34). In the late 1980's, a pathotype designated as QCC (31) of *P. graminis* f. sp. *tritici* with virulence to *Rpg1* appeared throughout the northern Great Plains (24,28). This race has shown a rapid increase in prevalence and has been common in North America since 1988 (10,11,12,13,30).

Changes in the race composition of rust fungal populations often occur as a direct consequence of changes in the frequency of resistant genotypes in the host population (3,5,9,16,36). However, race composition also may change independently of the cultivation of resistant cultivars (8,14,15). The relative prevalence of races 56 and 15B-1 of *P. graminis* f. sp. *tritici* in western Canada over a period of years could not be explained by changes in wheat cultivars grown. Katsuya and Green (15) then showed that an isolate of race 56 had higher competitive ability in terms of a shorter incubation period and higher infection efficiency compared with an isolate of race 15B-1. However, there was a strong environmental effect on their competitive abilities; race 15B-1 predomi-

nated in mixtures with race 56 at 15°C, and race 56 predominated at temperatures over 20°C. The prevalence of these races could then be related to prevailing weather patterns (15). Thus, factors other than host selective effects can influence the frequency and fitness of races in *P. graminis* f. sp. *tritici* populations.

In greenhouse experiments, races of *P. graminis* f. sp. *tritici* in mixtures tend to predominate within a few uredinial generations when cultured on susceptible cultivars (2,15,21,23,25,35). The relative ability of races of *P. graminis* f. sp. *tritici* to compete on a given host has been attributed to a number of factors: infection efficiency and reproductive ability (2,14,25,26,35), interactions among races within a population (e.g., induced resistance and induced susceptibility due to infection) (1,37), environmental influence and the interaction of environment with rust races (4,15,21), and indirect effects of environment on the expression of resistance in the host (22).

With respect to race QCC, Liu and Harder (19,20) showed that this race had significantly higher reproductive potential than other races of *P. graminis* f. sp. *tritici* that previously were common on wheat and barley. It is possible that both the higher reproductive potential of race QCC and the selection pressure exerted by the widespread planting of barley cultivars that carry gene *Rpg1* have contributed to the very rapid increase and widespread distribution of this race. The present study was undertaken to assess the competitive ability of QCC and two other common races of *P. graminis* f. sp. *tritici* in mixtures on adult plants of two barley cultivars with gene *Rpg1*, a barley cultivar that lacks *Rpg1*, and a susceptible wheat cultivar. The changes in race frequencies over four asexual (uredinial) generations were examined, and selection of populations to their respective host cultivars was determined.

Corresponding author: D. E. Harder; E-mail address: dharder@mbrswi.agr.ca

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## MATERIALS AND METHODS

**Composition of race mixtures.** Different virulence phenotypes within collections of race QCC of *P. graminis* f. sp. *tritici* have been identified in the prairie region of Canada (7). Therefore, eight different single-uredinial isolates of this race, originally collected from cultivated and wild barley in Manitoba, were included to obtain a more diverse population. The isolates of QCC chosen were all virulent to gene *Rpg1*. Races QFC and TPM were relatively homogeneous for virulence (D. E. Harder, unpublished data). Therefore, only four isolates of each race, collected from wheat in Manitoba, were chosen to represent these races. In the first experiment (experiment 1), 5 mg of urediniospores of each QCC isolate and 10 mg of each QFC and TPM isolate were bulked to form an initial mixture (population). In a second experiment (experiment 2), 5 mg of urediniospores from each isolate of QCC and 15 mg from each isolate of QFC and TPM were bulked. The purity of the races was verified on 12 standard wheat differentials (31) plus an additional 24 wheat lines with single genes (*Sr*) for stem rust resistance.

**Host genotypes and growth conditions.** The barley cultivars Tupper and Robust (PI 476976), with gene *Rpg1* for stem rust resistance, and Harrington (Canadian PGR accession 12181), without *Rpg1*, were chosen as the selective barley hosts. The wheat cultivar Little Club (CI 4066), susceptible to all three races, was used as a selective wheat host. 'Tupper' and 'Robust' had moderately susceptible to susceptible (MS-S: moderately large to large pustules with little or no chlorosis) infection responses to all isolates of race QCC and moderately resistant to moderately susceptible (MR-MS: moderately small to moderately large pustules with some or little chlorosis) infection responses to all isolates of QFC and TPM. 'Harrington' was moderately susceptible to susceptible (MS-S: moderately large to large pustules with some or little chlorosis) and 'Little Club' wheat was highly susceptible (HS: large pustules with no chlorosis) to all isolates in the initial population. Seeds of each cultivar were planted every 3 weeks in 13-cm-diameter peat pots filled with clay loam, sand, and peat moss in a 1:1:1 ratio (vol/vol/vol) and grown in a growth cabinet at day/night temperatures of 22:16°C with 16 h/day of fluorescent and incandescent light. Plants were fertilized weekly with 15-30-15 or 20-20-20 (N-P-K) water-soluble fertilizer. For each generation, 'Little Club' wheat was seeded about 4 weeks earlier than the barley cultivars to synchronize heading stages.

**General procedures.** Urediniospores of the initial populations were cultured on adult plants of the four host cultivars for six and four successive generations, respectively, in experiments 1 and 2.

TABLE 1. Infection types of races QCC, QFC, and TPM of *Puccinia graminis* f. sp. *tritici* on primary leaves of seven wheat differential lines, each with a different single gene (*Sr*) for stem rust resistance, and the wheat cultivar McNair 701

<i>Sr</i> gene or cultivar	Race and infection type <sup>a</sup>		
	QCC	QFC	TPM
8a	;1 to 2-	4	4
8b	;1/4 <sup>b</sup>	4	4
9a	;1 to 1+/4 <sup>b</sup>	4	;1
9e	;1	;1	4
13	3 to 4/2 to 2+ <sup>b</sup>	;1 to 1+	;1 to 1+
35	4	4	0;
'McNair 701'	;1	4	4

<sup>a</sup> Infection types are based on a 0 to 4 scale (32): 0 = no uredinia or other macroscopic sign of infection, ; = hypersensitive necrotic or chlorotic flecks, 1 = small uredinia often surrounded by necrosis, 2 = small to medium-sized uredinia often surrounded by chlorosis or necrosis, 3 = medium-sized uredinia that may be associated with chlorosis, and 4 = large uredinia without chlorosis or necrosis. Infection types 0, 1, and 2 are indicative of avirulence, whereas infection types 3 and 4 are indicative of virulence. The '+' and '-' symbols denote more or less sporulation, respectively.

<sup>b</sup> / = either avirulent or virulent, depending on the isolates of QCC involved.

For each generation, stems of 20 plants per cultivar were inoculated at postanthesis with urediniospores from the previous generation. Four milligrams of urediniospores/milliliter of Dustrol light mineral oil (Ciba-Geigy Canada, Winnipeg) were inoculated using a quantitative inoculator (6). The inoculated plants were air-dried for 1 to 2 h to ensure full evaporation of oil from plant surfaces and then incubated in a dew chamber (Percival ID-60, Percival Manufacturing Co., Boone, IA) for 16 to 18 h in darkness at 20°C. After incubation, the plants were placed on greenhouse benches and covered with transparent plastic sheets for about 4 h to prevent excessively rapid drying. To prevent cross-contamination among the *P. graminis* f. sp. *tritici* populations, the cultivars were maintained in four separate greenhouses at 22 ± 3°C with 8 h of supplemental fluorescent light (276 μmol m<sup>-2</sup> s<sup>-1</sup>) per day. When sporulation began (about 12 to 14 days after inoculation), a cyclone spore collector was used to collect urediniospores from each host cultivar into size 00 gelatin capsules. Collections were made every 2 to 3 days for a 2-week period and stored in an ultra-freezer at -80°C. Urediniospores obtained on different days from plants of the same genotype were bulked, and a portion of the mixture was used to inoculate the same host cultivar for the next uredinial generation.

**Evaluation of race frequencies.** The susceptible wheat cultivar Little Club was seeded in 11-cm-diameter peat pots and grown under continuous fluorescent light at approximately 20°C. Seedlings were treated with maleic hydrazide at emergence to retard the emergence of second leaves and to increase the size of uredinia. Seven days after seeding, 'Little Club' seedlings were inoculated with urediniospores of the *P. graminis* f. sp. *tritici* populations (15 pots/population) in an inoculation booth equipped with a rotating table. After incubation in a dew chamber for 16 to 20 h, the pots with the 'Little Club' seedlings were capped with plastic cones and moved to a greenhouse. Five to six uredinia were isolated from each pot of 'Little Club' using the method of Kolmer (17), and 60 to 80 single-uredinial isolates from each selection population were evaluated for virulence phenotypes using seven wheat differentials. Six single-gene differential lines of wheat and the wheat cultivar McNair 701 (PI 518817) were used (Table 1) to identify virulence phenotypes in the initial populations and in selection populations from the first, second, and fourth generations. The barley-virulent isolates of race QCC were avirulent to 'McNair 701'. The differential sets were scored for infection types, using the 0 to 4 scale of Stakman et al. (32), 2 weeks after inoculation. Infection types 0; to 2 were considered as avirulent, and infection types 3 to 4 were considered as virulent. The data were used to measure changes in race frequencies in the populations cultured on each of the four host cultivars.

The initial populations of *P. graminis* f. sp. *tritici* were evaluated for race frequencies by measuring three samples over a period of 8 months to determine if race frequencies obtained by testing on differential sets were biased by differences in urediniospore viability and sampling variance. No changes occurred in urediniospore viability or race frequencies during storage in an ultrafreezer at -80°C ( $\chi^2 = 4.294$ ,  $P > 0.830$  in experiment 1 and  $\chi^2 = 3.769$ ,  $P = 0.904$  in experiment 2). Therefore, data were pooled, and the means were used as a baseline for measuring changes in virulence phenotype frequency in the selection populations. Frequencies of races in each selection population were plotted over generations. Four by two contingency table analyses (33) were computed, and logits of race frequencies in the selection populations were regressed on the number of generations to determine if race frequencies changed significantly over generations (18). A one-tailed *t* test was used to determine if the slopes of the regression lines were significantly different from zero (33).

**Evaluation of infection frequency and urediniospore production.** To determine if *P. graminis* f. sp. *tritici* populations had increased in their levels of compatibility to the selective host cultivars, the initial and selection populations from generation 6 in

experiment 1 were evaluated for infection frequency and urediniospore production on adult plants of the four selective host cultivars. Urediniospores of the initial and selection populations from generation 6 were individually inoculated onto 16 to 20 main stems of adult plants of each selective host at a concentration of 4 mg of urediniospores/ml of mineral oil. Infection efficiency was determined by counting the number of uredinia that developed on the top two stem internodes 14 days after inoculation. Urediniospores produced on the stem tissue of each plant were collected into individual, preweighed gelatin capsules using a cyclone spore collector. Urediniospores were collected every 2 to 3 days for a 2-week period and stored at 4 to 5°C. Urediniospore production was calculated from the total weight of urediniospores divided by the surface area (perimeter × length in centimeters) of the stem internodes. The experiment was arranged in a completely randomized design with four replicates (pots) per host cultivar-uredinial population combination and four subsamples (plants) per replicate. The data were tested for homogeneity of variance and log-transformed to equalize the variances within each selection population. Analysis of variance (33) was performed using the general linear model (GLM) procedure in SAS (SAS User's Guide: Statistics, V5, SAS Institute Inc., Cary, NC) to detect the effects of host cultivar, uredinial population, and their interactions on infection frequency and urediniospore production. Fisher's protected least significant difference was used to determine statistical significance of differences among treatment means (host cultivars within each uredinial population under study and uredinial populations within each selective host cultivar). Preplanned contrasts (27) were used to determine statistical significance of differences in infection frequency and urediniospore production between the initial population and selection populations of generation 6, between pathogen populations cultured on barley cultivars with and without gene *Rpg1*, and between selective host cultivars within each selected *P. graminis* f. sp. *tritici* population.

## RESULTS

**Race frequencies.** In experiment 1, the frequencies of races QCC, QFC, and TPM in the populations selected on 'Tupper' and 'Robust' changed significantly according to the chi-square values, but the slopes of the logistic regressions were not significantly different from zero (Table 2). Deviation from straight lines was obviously caused by a rapid increase of QCC in these two selection populations after one uredinial generation (Fig. 1A and B). Although races QFC and TPM decreased rapidly on 'Tupper' and 'Robust' from their initial frequencies of about 30% to 2 to 5% after one uredinial generation, they could still be found in the

populations after four uredinial generations. In the 'Harrington' population, QCC increased while races QFC and TPM decreased significantly over generations (Fig. 1C), as indicated by the significant chi-square values and significant slopes of the race frequency logits regressed on generation number (Table 2). In the population cultured on 'Little Club' wheat, frequencies of QCC, QFC, and TPM changed significantly over generations (Fig. 1D) according to the chi-square values, but the slopes of the logistic regression lines were not significantly different from zero (Table 2).

The selective effect of host cultivars on race QCC also was observed in experiment 2. Race QCC increased from an initial frequency of 22.7% to 77.0 to 83.1% in the second uredinial generation and predominated in the populations selected on 'Tupper' (92.7%) and 'Robust' (95.5%) by the fourth generation (Fig. 2A and B). The increase in frequency of QCC with uredinial generation in these two populations was significant based on the chi-square values and positive slopes of the frequency logits regressed on generation number (Table 2). In the populations cultured on 'Harrington' and 'Little Club' wheat, QCC also increased significantly with uredinial generation (Table 2), but at apparently lower rates than when cultured on 'Tupper' and 'Robust' (Fig. 2). Races QFC and TPM decreased over generations on all four host cultivars, although changes in frequencies of QFC and TPM were not significantly different ( $P = 0.05$ ) when uredinial populations were cultured on 'Harrington' barley and 'Little Club' wheat, respectively (Table 2).

**Infection frequency.** Infection frequencies were significantly influenced by the effects of selective host cultivars ( $F = 220.74$ ,  $P = 0.001$ ), uredinial populations ( $F = 31.11$ ,  $P = 0.001$ ), and their interactions ( $F = 2.47$ ,  $P = 0.011$ ) (Table 3). Within each host cultivar, significant differences in infection frequency were observed between the initial population and selection populations and/or among the selection populations. On 'Tupper' and 'Robust', the initial population had significantly lower infection frequencies than any of the selection populations. On 'Harrington' and 'Little Club', however, no significant differences were observed in infection frequency between the initial population and the population selected on 'Little Club' wheat. Contrast tests showed that the populations selected on the barley genotypes carrying gene *Rpg1* had significantly higher infection frequencies on 'Tupper' ( $F = 7.36$ ,  $P = 0.009$ ) and 'Robust' ( $F = 5.29$ ,  $P = 0.025$ ) than the populations from 'Harrington' lacking *Rpg1* and 'Little Club' wheat. In comparison, the populations from susceptible hosts, 'Harrington' and 'Little Club', did not show specific adaptation to their respective hosts.

Significant differences in degree of resistance or susceptibility were observed among selective host cultivars within each *P.*

TABLE 2. Chi-square values for homogeneity of race frequencies and slopes from regression of race frequency logits on generation number in populations of *Puccinia graminis* f. sp. *tritici* cultured for four generations on the barley cultivars Tupper, Robust, and Harrington, and the susceptible wheat cultivar Little Club

Race	<i>P. graminis</i> f. sp. <i>tritici</i> population cultured on											
	'Tupper' ( <i>Rpg1</i> )			'Robust' ( <i>Rpg1</i> )			'Harrington' ( <i>rpg1</i> )			'Little Club'		
	$\chi^2$	Slope <sup>a</sup>	<i>t</i>	$\chi^2$	Slope	<i>t</i>	$\chi^2$	Slope	<i>t</i>	$\chi^2$	Slope	<i>t</i>
Experiment 1												
QCC	99.18 <sup>b</sup>	0.245	1.57	125.29 <sup>b</sup>	0.315	1.71	52.68 <sup>b</sup>	0.247	6.46 <sup>c</sup>	30.17 <sup>b</sup>	0.155	3.20
QFC	51.42 <sup>b</sup>	-0.232	1.87	51.15 <sup>b</sup>	-0.211	1.36	19.28 <sup>b</sup>	-0.189	12.75 <sup>d</sup>	30.10 <sup>b</sup>	-0.338	2.88
TPM	37.56 <sup>b</sup>	-0.186	1.15	65.44 <sup>b</sup>	-0.317	1.77	26.76 <sup>b</sup>	-0.236	5.72 <sup>c</sup>	18.33 <sup>b</sup>	-0.042	0.26
Experiment 2												
QCC	116.84 <sup>b</sup>	0.388	5.66 <sup>c</sup>	136.05 <sup>b</sup>	0.445	5.95 <sup>c</sup>	40.39 <sup>b</sup>	0.191	4.32 <sup>c</sup>	26.53 <sup>b</sup>	0.156	4.29 <sup>c</sup>
QFC	30.04 <sup>b</sup>	-0.256	4.96 <sup>c</sup>	44.40 <sup>b</sup>	-0.301	7.32 <sup>c</sup>	4.86	-0.060	2.38	10.13 <sup>c</sup>	-0.110	17.33 <sup>d</sup>
TPM	82.24 <sup>b</sup>	-0.357	1.58	67.61 <sup>b</sup>	-0.424	7.15 <sup>c</sup>	24.85 <sup>b</sup>	-0.182	14.43 <sup>d</sup>	6.23	-0.071	3.20

<sup>a</sup> Slope of  $\log(q_n/1 - q_n)$  regressed on generation,  $q_n$  = the frequency at which the race detected in  $n$  generation.

<sup>b</sup> Significant at  $P = 0.001$ .

<sup>c</sup> Significant at  $P = 0.05$ .

<sup>d</sup> Significant at  $P = 0.01$ .



*graminis* f. sp. *tritici* population (Table 3). All barley cultivars had significantly fewer uredinia produced on stems than 'Little Club' wheat after inoculation with the initial and selection populations of generation 6. 'Little Club' wheat had the greatest number of uredinia produced on the stem tissue, followed by 'Harrington', and then by 'Robust' and 'Tupper' with significantly fewer uredinia. No significant differences were observed in the number of uredinia per square centimeter of stem tissue between 'Tupper' and 'Robust' regardless of which pathogen population was used for inoculation. Contrasts indicated that the significant host cultivar  $\times$  uredinial population interaction was primarily due to the greater production of uredinia on 'Tupper' and 'Robust' with the

populations cultured on these two cultivars with gene *Rpg1* than was expected based on the mean performance of the initial and other selection populations.

**Urediniospore production.** Urediniospore production was significantly influenced by the effects of host cultivars ( $F = 17.46$ ,  $P = 0.001$ ) and uredinial populations ( $F = 113.46$ ,  $P = 0.001$ ) (Table 4). Mean comparisons among uredinial populations within each selective host or among host cultivars within each uredinial population were not performed, since the host cultivar  $\times$  uredinial population interaction was nonsignificant ( $F = 0.52$ ,  $P = 0.890$ ). Significant differences ( $P < 0.05$ ) in urediniospore production were detected by contrasts between the initial population and all

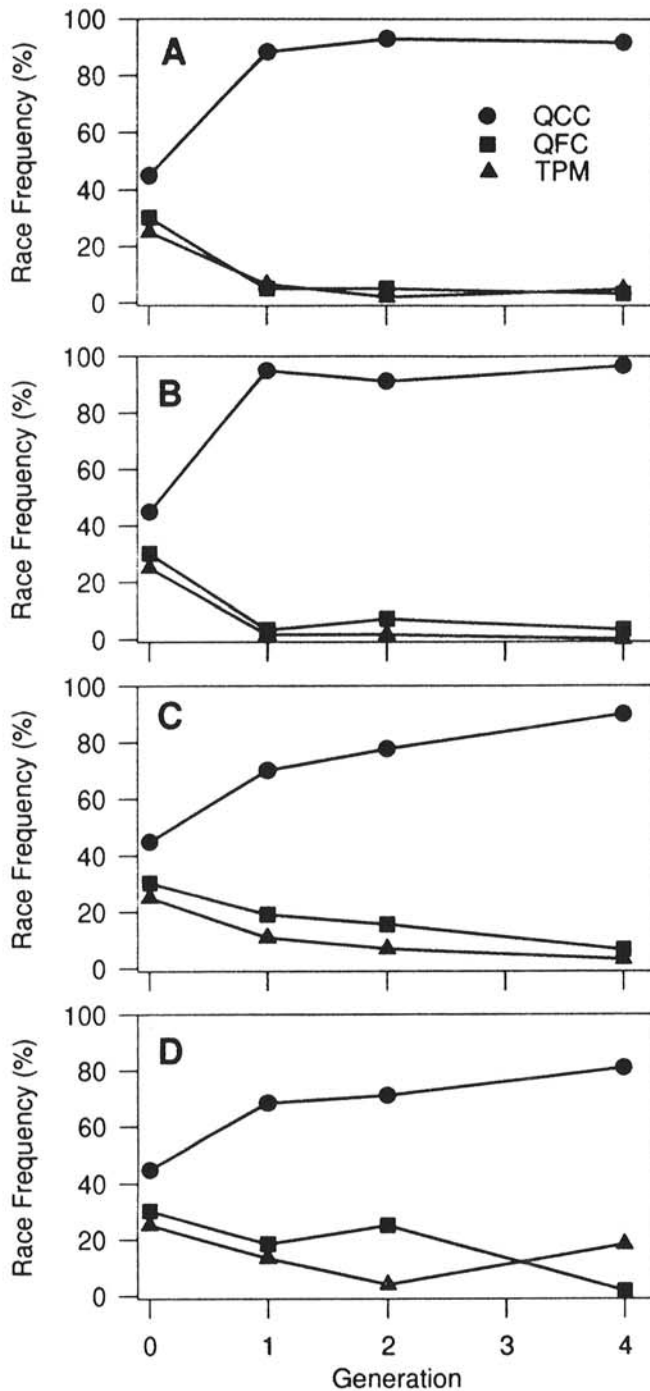


Fig. 1. Experiment 1. Frequencies of races QCC, QFC, and TPM of *Puccinia graminis* f. sp. *tritici* selected over four uredinial generations on adult plants of the barley cultivars A, Tupper and B, Robust with the *Rpg1* gene; C, Harrington without known genes for stem rust resistance; and D, the susceptible wheat cultivar Little Club.

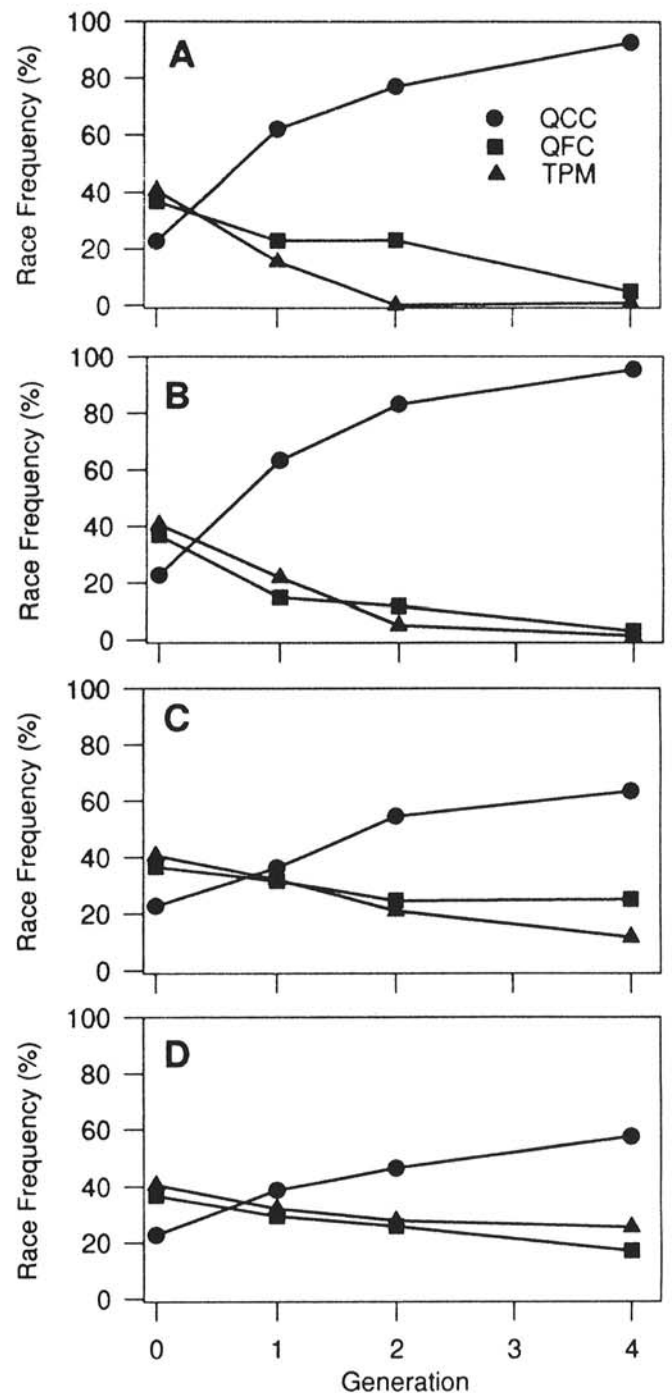


Fig. 2. Experiment 2. Frequencies of races QCC, QFC, and TPM of *Puccinia graminis* f. sp. *tritici* selected over four uredinial generations on adult plants of the barley cultivars A, Tupper and B, Robust with the *Rpg1* gene; C, Harrington without known genes for stem rust resistance; and D, the susceptible wheat cultivar Little Club.

selection populations within each host cultivar ( $F = 13.74, 18.35, 10.99, \text{ and } 9.63$  for 'Tupper', 'Robust', 'Harrington', and 'Little Club', respectively). Significant differences in urediniospore production were observed on 'Tupper' between the populations selected on the barley hosts and the population selected on 'Little Club' wheat ( $F = 7.61, P = 0.007$ ). Moreover, the populations from the barley cultivars carrying gene *Rpg1* had a significantly higher level of urediniospore production on 'Tupper' than the population from 'Harrington' ( $F = 6.07, P = 0.017$ ). Within each uredinial population, urediniospore production was significantly higher on 'Little Club' wheat than on any of the barley cultivars ( $P = 0.001$ ), but there were no significant differences in urediniospore production among the barley cultivars.

## DISCUSSION

Race QCC of *P. graminis* f. sp. *tritici* clearly showed a competitive advantage relative to races QFC and TPM on all four cultivars under study. This race dominated the *P. graminis* f. sp. *tritici* populations within a few uredinial generations, but the rate at which race QCC increased was influenced by the selective host cultivars. Differences in the competitive ability between races with and without specific virulences were most evident on the barley cultivars Tupper and Robust with gene *Rpg1*. The rapid increase of race QCC in the populations selected on these two cultivars indicated a strong selection against races QFC and TPM, which induced MR-MS infection responses on barley genotypes with gene *Rpg1*. Races QFC and TPM were previously found to have an apparent reproductive disadvantage relative to QCC on barley lines with gene *Rpg1*, since they produced fewer uredinia per unit area of stem tissue, had lower levels of urediniospore production, and induced longer latent periods (19,20). Most commercial barley cultivars grown in the northern Great Plains of the United States and Canada carry gene *Rpg1* (34). Therefore, directional selection caused by the specific resistance in barley cultivars is an important factor contributing to the increase of race QCC in the *P. graminis* f. sp. *tritici* population in North America.

Virulence to specific host resistance genes, however, may not be sufficient to explain the prevalence of particular *P. graminis* f. sp. *tritici* races. Ogle and Brown (26) observed that differences in the competitive ability between two stem rust races were related to their relative reproductive potentials, measured as the rate of uredinial growth, the size of uredinia, and the number of uredinio-

spores per uredinium. Other studies (14,15,25) also suggested that the relative reproductive abilities of races could affect the frequency of races in mixtures. In the present study, race QCC increased significantly in the populations selected on the susceptible barley cultivar Harrington and 'Little Club' wheat. This indicated that QCC was relatively more fit than QFC and TPM, although both 'Harrington' barley and 'Little Club' wheat appeared to be equally susceptible, respectively, to all three races.

The differences in reproductive abilities of the races of *P. graminis* f. sp. *tritici* tested further supported the conclusion of directional selection and significant changes in race frequencies of the selected *P. graminis* f. sp. *tritici* populations. All selection populations showed considerable improvement in the characters related to pathogen fitness as compared with the initial population. The populations selected on 'Tupper' and 'Robust' for six generations clearly showed adaptation to their respective hosts with respect to infection frequencies and urediniospore production. In comparison, the populations cultured on 'Harrington' and 'Little Club' showed relatively smaller increases in infection frequency and urediniospore production, although significant changes in race frequencies were observed over the course of the experiments. The changes in infection frequencies and urediniospore production of the selected *P. graminis* f. sp. *tritici* populations were related to the frequency of QCC in a given population. The changes in the frequencies of the three races on the four selective hosts were influenced by the presence or absence of race-specific resistance in the host and by the greater fitness of QCC relative to races QFC and TPM on all hosts.

Results from the present greenhouse study showing that race QCC could quickly dominate the pathogen population were consistent with field observations on the prevalence of races of *P. graminis* f. sp. *tritici* (10,11,12,13,30). Race QCC has increased rapidly since its first appearance in 1988 and has become one of the most common races of *P. graminis* f. sp. *tritici* collected from cultivated barley, wild barley, and susceptible wheat in stem rust nurseries in the prairie region of Canada. The inoculum of the northern prairie population of *P. graminis* f. sp. *tritici* originates in the southern and central plains region of the United States where winter wheats are grown.

Results from this study and previous analyses of components of resistance (19,20) indicated that QCC was highly fit on both barley and susceptible wheat cultivars. Isolates of QCC would have a competitive advantage relative to other *P. graminis* f. sp. *tritici*

TABLE 3. Infection frequencies (number of uredinia per square centimeter of stem tissue) of *Puccinia graminis* f. sp. *tritici* on adult plant stems of three barley cultivars and the susceptible wheat cultivar Little Club after inoculation with races QCC, QFC, and TPM mixed in equal proportion and with asexual populations selected on their respective host cultivars for six generations

Uredinial population	Host cultivar				Row mean
	Tupper ( <i>Rpg1</i> )	Robust ( <i>Rpg1</i> )	Harrington ( <i>rpg1</i> )	Little Club	
Initial population	1.12 cz <sup>a</sup> (0.209)	0.958 cz (0.106)	2.448 by (0.248)	5.645 cx (0.319)	1.69 c
Population selected from:					
'Tupper' ( <i>Rpg1</i> )	2.91 az (0.193)	2.62 az (0.031)	3.67 ay (0.174)	7.18 ax (0.555)	2.93 a
'Robust' ( <i>Rpg1</i> )	2.65 az (0.197)	2.60 az (0.186)	3.44 ay (0.531)	6.95 abx (0.401)	2.90 a
'Harrington' ( <i>rpg1</i> )	1.84 bz (0.089)	2.20 abz (0.121)	3.72 ay (0.302)	6.56 bx (0.379)	2.56 ab
'Little Club'	1.79 bz (0.166)	1.74 bz (0.193)	2.49 by (0.322)	5.76 cx (0.272)	2.28 b

<sup>a</sup> Values are means of four replicates. Means followed by the same letter within each column (abc) and row (xyz) are not significantly different at  $P = 0.05$  according to Fisher's protected least significant difference (33). Values in brackets are standard errors.

TABLE 4. Urediniospore production (milligrams of urediniospores per square centimeter of stem tissue) of *Puccinia graminis* f. sp. *tritici* on adult plant stems of three barley cultivars and the susceptible wheat cultivar Little Club after inoculation with races QCC, QFC, and TPM mixed in equal proportion and with uredinial populations selected on their respective host cultivars for six generations

Uredinial population	Host cultivar				Row mean
	Tupper ( <i>Rpg1</i> )	Robust ( <i>Rpg1</i> )	Harrington ( <i>rpg1</i> )	Little Club	
Initial population	1.00 <sup>a</sup> (0.111)	1.09 (0.096)	1.15 (0.168)	3.53 (0.276)	1.69 c
Population selected from:					
'Tupper' ( <i>Rpg1</i> )	2.25 (0.262)	2.23 (0.151)	2.10 (0.201)	5.13 (0.269)	2.93 a
'Robust' ( <i>Rpg1</i> )	2.15 (0.359)	2.37 (0.216)	1.81 (0.161)	5.26 (0.372)	2.90 a
'Harrington' ( <i>rpg1</i> )	1.53 (0.241)	1.91 (0.179)	1.89 (0.314)	4.91 (0.347)	2.56 ab
'Little Club'	1.32 (0.288)	1.67 (0.209)	1.68 (0.238)	4.44 (0.378)	2.28 b
Column mean	1.65 y	1.85 y	1.73 y	4.65 x	

<sup>a</sup> Values are means of four replicates. Means followed by the same letter within each column (abc) and row (xyz) are not significantly different at  $P = 0.05$  according to Fisher's protected least significant difference (33). Values in brackets are standard errors.

races on any susceptible winter wheats and wild grasses in the southern plains of the United States. Race QCC, however, has not completely dominated the northern plains stem rust population. Barley is a minor crop in the southern United States, thus has a less selective effect on the initial population that subsequently spreads northward. In 1994 and 1995, race TPM declined sharply in the prairie *P. graminis* f. sp. *tritici* population (D. E. Harder, unpublished data). The next most common race after QCC in recent years has been QFC. A number of winter wheat cultivars grown in the southern plains of the United States have resistance derived from Triumph (29). The Triumph resistance is effective against QCC and QFC, but is ineffective against TPM and, thus, may have contributed to the prevalence of TPM in the northern plains *P. graminis* f. sp. *tritici* population until 1993. Gene *Sr31*, which confers resistance to all current North American stem rust races, is now becoming more prevalent in winter wheat cultivars in the southern and central plains. All spring wheat cultivars grown in the northern plains and eastern prairie region of Canada are resistant to races QCC, QFC, and TPM. The increase in cultivars resistant to TPM in the major wheat-growing areas could partially explain the decline in prevalence of this race, although race QFC, with similar avirulence, has remained relatively more common. Barley cultivars with gene *Rpg1*, however, are widespread in the northern plains of the United States and eastern prairies of Canada and would provide a selective advantage for QCC. The general reproductive advantages of race QCC and its current position as a major component of the *P. graminis* f. sp. *tritici* population in the northern great plains of the United States and Canada indicate that this race and possible future variants may pose problems for barley and, possibly, wheat production in this region.

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