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ORIGINAL PAPER

Genetics and mapping of seedling resistance to Ug99 stem rust in Canadian wheat cultivars 'Peace' and 'AC Cadillac'

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Abstract Stem rust (caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn.) has re-emerged as a threat to wheat production with the evolution of new pathogen races, namely TTKSK (Ug99) and its variants, in Africa. Deployment of resistant wheat cultivars has provided long-term control of stem rust. Identification of new resistance genes will contribute to future cultivars with broad resistance to stem rust. The related Canadian cultivars Peace and AC Cadillac show resistance to Ug99 at the seedling stage and in the field. The purpose of this study was to elucidate the inheritance and genetically map resistance to Ug99 in these two cultivars. Two populations were produced, an $F_{2:3}$ population from LMPG/AC Cadillac and a doubled haploid (DH) population from RL6071/Peace. Both populations showed segregation at the seedling stage for a single stem rust resistance (Sr) gene, temporarily named *SrCad*. *SrCad* was mapped to chromosome 6DS in both populations with microsatellite markers and a marker (FSD_RSA) that is tightly linked to the common bunt resistance gene *Bt10*. FSD_RSA was the closest marker to *SrCad* ($\approx$1.6 cM). Evaluation of the RL6071/Peace DH population and a second DH population, AC Karma/87E03-S2B1, in Kenya showed that the combination of *SrCad* and leaf rust resistance gene *Lr34* provided a high level of resistance to Ug99-type races in the field, whereas in the absence of *Lr34 SrCad* conferred moderate resistance. A survey confirmed that *SrCad* is the basis for all of the seedling resistance to Ug99 in Canadian wheat cultivars. While further study is needed to determine the relationship between *SrCad* and other Sr genes on chromosome 6DS, *SrCad* represents a valuable genetic resource for producing stem rust resistant wheat cultivars.

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Introduction

Stem rust, caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn. (Pgt), is a disease of wheat that can cause devastating grain yield losses. The last wheat stem rust epidemic in North America occurred from 1953 to 1955 (Peturson 1958). Since then, resistant cultivars have controlled wheat stem rust in North America. While races of *P. graminis* found in North America are relatively static (Jin 2005; Fetch 2009), new races have been detected in Africa, specifically race TTKSK (Ug99) and its variants (Pretorius et al. 2000; Jin et al. 2008). These races are of particular interest because they are virulent to *Sr31*, which is a broadly deployed stem rust resistance (Sr) gene in Africa and Asia. While *Sr31* has not been deployed in Canada, Ug99-type and other African Pgt races are virulent

to most Canadian wheat cultivars (TG Fetch unpublished data). Since Sr genes previously established long term control of stem rust, incorporating effective resistance into new cultivars should mitigate the threat posed by the possible introduction of these virulent races into North America. Characterizing previously identified and new sources of resistance will allow the development of elite cultivars with effective gene combinations that are broadly resistant to stem rust. There are eight named Sr genes (*Sr13*, *Sr14*, *Sr22*, *Sr28*, *Sr33*, *Sr35*, *Sr42* and *Sr45*) from the primary gene pool of wheat that confer resistance to Ug99 (Jin et al. 2007; TG Fetch unpublished data). The primary gene pool is a particularly important source of genetic diversity for Canadian breeders as no wheat cultivars registered in Canada carry genes derived from a species beyond the primary gene pool.

The Canadian hard red spring wheat cultivars Peace and AC Cadillac were resistant to Ug99 and its variants during field trials in Kenya and in preliminary seedling tests (TG Fetch unpublished data). Neither of these varieties accounts for a large portion of the wheat area in Canada (McCallum and DePauw 2008). The development of Ug99-resistant elite cultivars in North America would represent a proactive approach to protecting the wheat crop from future stem rust epidemics. Furthermore, useful Sr genes could be deployed in areas already affected by Ug99-type stem rust races.

The leaf rust resistance gene *Lr34* confers broad spectrum, partial resistance to multiple biotrophic pathogens (Dyck and Samborski 1982; Singh 1992; Spielmeyer et al. 2005). *Lr34* interacts with other leaf rust resistance genes to enhance the levels of resistance (German and Kolmer 1992). Similarly, *Lr34* interacts with Sr genes and may actually confer resistance to stem rust (Kerber and Aung 1999; Dyck 1987). Both Peace and AC Cadillac carry *Lr34* (S Cloutier unpublished data), and this may contribute to their excellent field resistance to stem rust, including Ug99 and derivatives.

The objectives of this research were to study the inheritance of the seedling resistance to Ug99 found in Peace and AC Cadillac, genetically map the resistance, determine if this source of Ug99 resistance is enhanced by *Lr34* and assess the distribution of the resistance in Canadian wheat cultivars.

Materials and methods

Populations and stem rust testing

A population was produced by crossing LMPG (Little Club//Prelude*8/Marquis/3/Gabo), a stem rust susceptible line, with AC Cadillac (BW90*3/BW553; DePauw et al. 1998). F_2 ($n = 191$) and F_3 ($n = 188$) seedling populations were inoculated with urediniospores of Ug99 Pgt when the first leaf was fully emerged. Inoculations were performed by suspending urediniospores in light mineral oil (Bayol 55, Imperial Oil Canada, Toronto, ON, Canada) and spraying the suspension onto the seedlings. Inoculated seedlings were incubated in a dew chamber for 16 h and then were dried slowly under light. Plants were transferred to growth chambers and grown at approximately 20°C with 16 h of light daily. Two weeks after inoculation seedlings were rated for their infection types (IT) following the scale described by Stakman et al. (1962).

A second population was generated from the cross of RL6071 (Prelude/8*Marquis*2/3/Prelude//Prelude/8*Marquis) with Peace (BW90*3/BW553//BW90'S'/Katepwa). The F_1 plants were used to make a doubled haploid (DH) population using the maize pollination method to generate haploids followed by colchicine-induced chromosome doubling (Thomas et al. 1997). DH lines ($n = 295$) were tested with Pgt races RTQSC and TTKSK as described above except that seedlings inoculated with race RTQSC were grown in a greenhouse instead of a growth cabinet. In 2008, 167 DH lines were tested in field plots (two 1 m rows per plot per DH line) at the Kenyan Agricultural Research Institute, Njoro, Kenya. Pgt inoculum for the field was increased on lines carrying *Sr31* to select Ug99-type races. Experimental lines were hand-planted in two 1 m rows. Clumps of plants containing a mixture of cultivars susceptible to Ug99 were grown adjacent to the experimental plots and were inoculated at jointing to produce inocula for natural dispersal to the test materials. Plots were rated for stem rust severity and response using a modified Cobb scale (Peterson et al. 1948). Ratings were performed at anthesis and repeated about 10 days later.

An additional DH population ($n = 83$) from AC Karma/87E03-S2B1 (Radovanovic and Cloutier 2003) was tested in Kenya in 2009 following the above procedures. AC Karma, like AC Cadillac and Peace, carries seedling resistance to Ug99 inherited from BW553 and 87E03-S2B1 carries *Lr34*.

Mapping stem rust resistance to Ug99

Microsatellite (SSR) markers (Röder et al. 1998; Somers et al. 2004) were used for mapping stem rust resistance in both populations. Young leaves were collected and lyophilized for DNA extraction. DNA was extracted using a modified ammonium acetate extraction (Chao and Somers, http://maswheat.ucdavis.edu/PDF/DNA0003.pdf, accessed July 2009) based on the procedures of Pallotta et al. (2003). PCR amplification and fragment analysis with an ABI 3100 genetic analyzer (Applied Biosystems, Streetsville, ON, Canada) were performed as described by Somers et al.

(2004). A map of all 21 chromosomes was constructed for the LMPG/AC Cadillac population using 221 SSR markers with 94 F_2 individuals. After a genomic location of the Sr gene was established, all individuals were used for mapping the identified region in both the LMPG/AC Cadillac ($n = 188$ F_2 plants) and RL6071/Peace ($n = 295$ DH lines) populations using SSR markers and a PCR marker, FSD_RSA, linked to the bunt (*Tilletia tritici* (Bjerk.) Wint.) resistance gene *Bt10* (Laroche et al. 2000). The PCR conditions used for FSD_RSA were: 1× PCR buffer, 1.5 mM $MgCl_2$, 0.2 mM each dNTP, 12 pmol FSD forward primer, 3.5 pmol RSA reverse primer, 1U *Taq* DNA polymerase and 50 ng of genomic DNA. The PCR program was 3 min (94°C), then 35 cycles of 30 s (94°C), 1 min 45 s (44°C) and 2 min (72°C) followed by 10 min (72°C). PCR products were separated on 1.5 % agarose gels that were run at 80 V for 2 h. Genetic maps were constructed using MapMaker version 3.0 (Lander et al. 1987) and genetic distances were calculated using the Kosambi mapping function (Kosambi 1944). The SSR marker csLVMS1 (Spielmeyer et al. 2008) was used to postulate the presence or absence of *Lr34* in the DH populations.

Survey of resistance in Canadian wheat cultivars

There are 10 Canadian wheat varieties that have BW553, the donor of seedling stem rust resistance to Peace and AC Cadillac, as a parent in their pedigree. These varieties were surveyed for the presence of the seedling Sr gene by assessing a tightly linked DNA marker and by reaction to Ug99 at the seedling stage. Marker testing and stem rust response screening were performed as described above.

Results

Phenotyping populations

The LMPG/AC Cadillac population segregated for a single dominant gene conferring resistance to Ug99 (TTKSK) in both the F_2 and F_3 generations. In the F_2 there were 150 resistant and 41 susceptible progeny which fit a 3:1 ratio ($\chi^2_{3:1} = 1.71$, $p = 0.19$). In the F_3 36 families were homozygous resistant, 105 segregating and 47 homozygous susceptible ($\chi^2_{1:2:1} = 1.27, p = 0.26$). The IT of resistant F_2 progeny was not predictive of the zygotic state of the seedling resistance gene. There were three F_2 plants that did not produce sufficient seed for F_3 progeny testing and were discarded. Six F_2 seedlings scored as resistant were homozygous susceptible in the F_3 progeny testing. Misclassification likely occurred due to light infection on some of the F_2 seedlings. This underscores the importance of the progeny testing of mapping populations.

The DH population from RL6071/Peace also segregated for a single gene; there were 132 resistant (IT 1 ± to 12) and 163 susceptible (IT 33 + to 4) lines ($\chi^2_{1:1} = 3.26$, $p = 0.07$). All of the lines that showed resistance to Ug99 were also resistant to race RTQSC, a race native to North America, and the all of the lines susceptible to Ug99 were susceptible to race RTQSC. Thus both races detected segregation of the same resistance gene.

Mapping resistance to Ug99

In total, 201 SSR loci were mapped genome-wide in the LMPG/AC Cadillac population. Twenty of 21 chromosomes had at least some marker coverage; the lone exception being chromosome 3D. The minimum number of markers found on a chromosome was two (chromosome 1D) and the maximum number was 21 (chromosome 3B). The number of markers mapped varied by genome, with the A, B and D genomes having 72, 83 and 46 mapped loci respectively. The A genome showed the most uniform coverage. Only markers located on chromosome 6DS showed linkage to the Ug99 resistance gene. Thus, this chromosome region was targeted for further mapping in the LMPG/AC Cadillac and the RL6071/Peace populations. In both populations flanking SSR markers on the short arm of chromosome 6D showed linkage with the resistance gene (Fig. 1). Only one SSR marker, CFD49, was polymorphic in both populations. The other DNA marker shared between the two maps was FSD_RSA. CFD49 and FSD_RSA flanked the Sr gene in both maps and showed very similar genetic distances placing the Sr gene in a ≈9 cM interval. The closest marker to the Sr gene was FSD_RSA with a mean genetic distance of 1.6 cM. We temporarily named this gene *SrCad*.

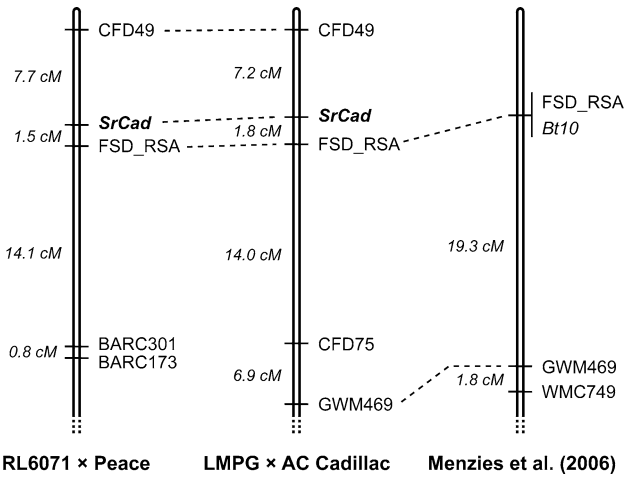

Fig. 1 Genetic maps of the RL6071/Peace DH and LMPG/AC Cadillac F_2 populations showing the position of *SrCad* compared to a previously constructed map including *Bt10* on chromosome 6DS

Effect of *Lr34* and *SrCad* on field resistance

The 167 DH lines from RL6071/Peace evaluated in Kenya were classified into four genotypic categories: (1) those that carried *SrCad* and *Lr34*, (2) those that carried only *SrCad*, (3) those that carried only *Lr34* and (4) those that carried neither gene. These classifications were assigned by seedling phenotype for *SrCad* and by DNA marker profile (csLVMS1) for *Lr34*. The numbers of lines in each category were 47, 30, 39 and 51 respectively and fitted the expected distribution for segregation at two independent loci ($\chi^2_{1:1:1:1} = 6.20$, $p = 0.10$). The average stem rust severity was calculated for each genotypic class (Fig. 2a). Peace had a stem rust severity of 5% and RL6071 had a severity of 80%. Among the DH lines the combination of *SrCad* and *Lr34* produced the lowest stem rust severity and only individuals that carried both genes had severities as low as Peace. Furthermore, the presence of both *SrCad* and *Lr34* resulted in significantly lower stem severities than of *SrCad* alone ($p < 0.001$). There was no significant interaction between *SrCad* and *Lr34* ($p = 0.13$), thus it appears the effects of the genes were additive. These two loci accounted for 71% of the variation in stem rust severity leaving 29% to account for other genes that may be segregating, errors in rating and other sources of error.

The AC Karma/89E03-S2B1 population was divided into the same four genotypic groups as above except that genotypes were assigned by markers for *SrCad* (RSD_FSA) and by phenotype and markers (csLVMS1) for *Lr34*. The numbers of lines in each category (22, 19, 17 and 23 respectively) fit a two gene ratio ($\chi^2_{1:1:1:1} = 1.12$, $p = 0.77$). The pattern of field resistance observed in the AC Karma/89E03-S2B1 population was similar to the RL6071/Peace population (Fig. 2b). Again, both *SrCad* and *Lr34* had a significant effect on stem rust severity ($p < 0.001$). In this instance, the interaction of *SrCad* and *Lr34* bordered on significance ($p = 0.010$). The combination of *SrCad* and *Lr34* showed a less marked reduction in stem rust severity in the AC Karma/89E03-S2B1 population in 2009 compared to the RL6071/Peace population in 2008 (Fig. 2). *SrCad* and *Lr34* accounted for 52% of the variation in stem rust severity.

Survey of Sr gene distribution in Canadian wheat cultivars

Ten registered Canadian wheat varieties are derivatives of BW553 (Neepawa*8//Red Bobs*2/PI178383). Of these, eight were positive for the FSD_RSA marker (Table 1). Seedling tests of 80 spring wheat cultivars, previously or currently grown in Canada, with Ug99 showed that only the genotypes positive for FSD_RSA were resistant (data not shown). One of the susceptible cultivars was Neepawa, the recurrent parent of BW553.

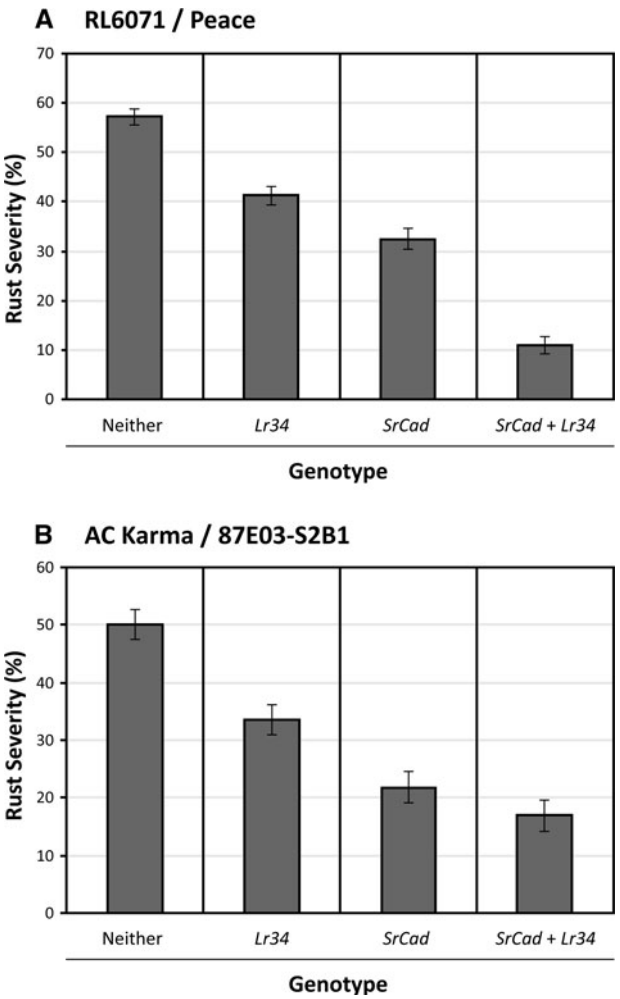

Fig. 2 **a** Mean stem rust severities of four genotypic classes from the RL6071/Peace DH population tested in the field in Kenya, 2008. **b** Mean stem rust severities of four genotypic classes from the AC Karma/87E03-S2B1 DH population tested in the field in Kenya, 2009. *Bars* indicate the standard errors

Discussion

Seedling resistance to Ug99 in segregating populations derived from AC Cadillac and Peace was conferred by a single partially dominant gene temporarily designated *SrCad*. This gene mapped to the short arm of chromosome 6D approximately 7 cM proximal of CFD49, the terminal SSR marker on the genetic map of 6DS (Somers et al. 2004). FSD_RSA showed closer linkage to *SrCad* ($\approx$1.6 cM) and is well suited for marker-assisted selection. While the LMPG/AC Cadillac and RL6071/Peace maps only have two markers in common, CFD49 and FSD_RSA, these shared markers were the nearest flanking markers to

Table 1 Postulation of *SrCad* in Canadian wheat cultivars with BW553 it their lineages based on seedling responses to TTKSK and the marker FSD_RSA

Cultivar	IT[a]	FSD_RSA[b]	*SrCad*
Alvena	−	−	−
Helios	3+	−	−
AC Foremost	2−	+	+
AC Taber	2−	+	+
AC Crystal	2−	+	+
AC Karma	2−	+	+
AC 2000	−	+	+
5700 PR	2+	+	+
AC Cadillac	12−	+	+
Peace	12−	+	+

[a] Infection type: were based on the scale described by Stakman et al. (1962); IT 3 or higher considered susceptible. '−' indicates that the cultivar was not tested with TTKSK

[b] Dominant PCR marker closely linked to *SrCad*; the positive allele (+) is linked in coupling to *SrCad*

SrCad and showed very similar distances in both maps (Fig. 1).

The linkage between *SrCad* and *Bt10* appears to be tight. *Bt10* was mapped using FSD_RSA and SSR markers (Laroche et al. 2000; Menzies et al. 2006). Menzies et al. (2006) reported complete linkage between *Bt10* and FSD_RSA. However, the DH population used in that study consisted of only 42 lines. By comparing the maps reported here to the map produced by Menzies et al. (2006) it appears that *SrCad* and *Bt10* are approximately 2 cM apart (Fig. 1). Considering the size of the population used by Menzies et al. (2006), tighter linkage between *Bt10* and *SrCad* may exist; even the possibility of a single pleiotropic gene conferring resistance to two diseases cannot be excluded.

The uniqueness of *SrCad* is unknown. Three Sr genes were previously mapped to chromosome 6D. These are *Sr5* (Sears et al. 1957), *Sr29* (Dyck and Kerber 1977) and *Sr42* (*SrNorin 40*, see McIntosh et al. 1995). *Sr29* is reported to be carried on the long arm of chromosome 6D (Dyck and Kerber 1977), whereas *SrCad* is located on the short arm. Both *Sr5* and *Sr42* were mapped to the short arm of chromosome 6D (McIntosh et al. 1995). Although *Sr5* does not confer resistance to Ug99 (Jin et al. 2007), *SrCad* cannot currently be excluded as an allele of *Sr5*. *Sr42* confers resistance to Ug99 and produces a similar low seedling infection type to *SrCad*. It is also possible that *SrCad* is an allele of *Sr42* or is the same gene. Allelism tests will be required to determine if *SrCad* represents a new gene/allele.

In all cases, seedling resistance to Ug99 in Canadian hexaploid wheat cultivars could be attributed to *SrCad*, thus the basis of current resistance is genetically narrow. This gene was introduced into Canadian germplasm via the breeding line BW553. The purpose of using BW553 as a parent in Canadian breeding programs was to incorporate the bunt (caused by *T. tritici* (Bjerk.) Wint.) resistance gene *Bt10* into new cultivars. The first Canadian wheat cultivar to carry *Bt10* was AC Taber (Knox et al. 1992). Since then, *Bt10* was bred into seven additional cultivars (Table 1). *SrCad* was co-inherited with *Bt10* into these cultivars. The close coupling linkage of *Bt10* and *SrCad* was unknown prior to this study. Thus, Canadian wheat breeders unintentionally selected for resistance to Ug99 (*SrCad*) by selecting for bunt resistance conditioned by *Bt10*. The appearance of *SrCad* in several registered cultivars indicate that there are no apparent deleterious effects on agronomics or grain quality caused by *SrCad* or other tightly linked genes.

Gene combinations and interactions are key components of improved disease resistance. The results of this study showed that *Lr34* played a significant role in enhancing field resistance to Ug99-type races of stem rust. In the RL6071/Peace population, the presence of *Lr34* significantly improved the resistance of lines carrying *SrCad* (Fig. 2a). Furthermore, *Lr34* markedly improved resistance to stem rust in the absence of *SrCad* in both DH populations ($p < 0.001$; Fig. 2). The four genotypic classes (neither gene, *Lr34*, *SrCad* and *SrCad* + *Lr34*) in the RL6071/Peace population had average stem rust severities that were significantly different (Fig. 2a). In the AC Karma/87E03-S2B1 population all classes were distinct except the "*SrCad*" and "*SrCad* + *Lr34*" classes (Fig. 2b); however the mean stem rust severity was less when both genes were present. This lack of statistical separation can be attributed to two data points in the "*SrCad* + *Lr34*" class. Unexpected ratings of 40 S and 60 S were recorded for two lines. As the genotype of *SrCad* in this population was assigned by markers, it is possible that recombination between *SrCad* and FSD_RSA resulted in erroneous classification of some DH lines. *SrCad* had the largest effect on stem rust response in the population, thus misclassification based on the marker would have a marked effect on phenotype.

The importance of *Lr34* as a leaf rust (*P. triticina* Eriks.) and stripe rust (*P. striiformis* Westend.) resistance gene is well established (Singh 1992). However, the data presented here also confirms that *Lr34* can have a significant effect on stem rust resistance response (Dyck 1987). Unlike *SrCad*, *Lr34* is relatively widespread in Canadian cultivars (McCallum et al. 2008). The presence of *Lr34* could, at minimum, provide a basal level of resistance to new races of stem rust in some genetic backgrounds. The effect of *Lr34* on stem rust resistance in Thatcher-type cultivars has

been well documented (Kerber and Aung 1999; Spielmeyer et al. 2008; Vanegas et al. 2008). Thatcher comprises a large component of the parentage of Peace and AC Cadillac (McCallum and DePauw 2008), thus the effect of *Lr34* on stem rust response in these populations is not unexpected. The parents of the AC Karma/89E03-S2B1 population have a much smaller coefficient of parentage for Thatcher (<3 and 18%, respectively; McCallum and DePauw 2008) yet *Lr34* showed a similar effect as in the Peace and AC Cadillac populations. However, there are examples of lines carrying *Lr34* that are highly susceptible to stem rust (e.g. Chinese Spring, Sumai 3). Given its effect singly, and more importantly as an enhancer of other rust resistance genes, *Lr34* is an important gene in breeding strategies to control all wheat rusts.

The DNA markers identified in this study will facilitate selection and stacking of *SrCad* with other Sr genes. If *Sr42* is a different locus from *SrCad*, recombinants could be selected where *SrCad*, *Sr42* and *Bt10* would provide a desirable linkage of disease resistance genes that would be easy to track and select in wheat breeding populations. When desirable genes are linked in coupling, as is the case for *SrCad* and *Bt10*, breeding populations can be easily enriched with the linked genes. In contrast, *Lr16* and the wheat midge resistance gene *Sm1* were closely linked in repulsion in Canadian wheat germplasm (McCartney et al. 2005) and efforts to increase the frequency of *Sm1* in breeding populations resulted in a corresponding decrease in the frequency of *Lr16*.

Conducting research using Ug99 in global regions where it is not endemic is challenging as this requires the careful handling and control of an exotic stem rust race. The use of containment laboratories is effective, but adds costs and restraints on work routines and space. In this study we were able to track *SrCad* in the RL6071/Peace DH population by using Canadian race RTQSC. With a sound knowledge of host genetics and the virulence attributes of the stem rust pathogen globally it is possible to conduct genetic studies using local isolates rather than exotics. However, screening for resistance to new localized races does require initial phenotypic screening with the exotic race, but this can often be achieved in the original location.

With an increased emphasis on improving stem rust resistance, *SrCad* represents an additional genetic resource for wheat breeders. The fact that *SrCad* is found in commercial cultivars demonstrates its suitability for wheat breeding. The markers identified here will allow the deployment of *SrCad* in gene combinations that are more likely to be durable.

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