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OPEN ACCESS | Mini-review

Combating a dynamic wheat rust population in Canada

B.D. McCallum[a], C.W. Hiebert[a], T. Fetch[a], M.A. Henriquez[a], J. Thomas[a], A. Bilichak[a], X. Wang[a], M. Liu[b], S. Cloutier[b], G. Humphreys[b], F. Bokore[c], R.E. Knox[c], R. Cuthbert[c], C. McCartney[d], M. Loewen[e], T. Copley[f], S. Barcellos Rosa[f], C. Amarasinghe[g], G.S. Brar[h], A. Foster[i], and G. Bakkeren[j]

[a]Agriculture and Agri-Food Canada, Morden Research and Development Centre, 101 Route 100 #100, Morden, MB R6M 1Y5, Canada; [b]Agriculture and Agri-Food Canada, Ottawa Research and Development Centre, 960 Carling Avenue, Ottawa, ON K1A 0C6, Canada; [c]Agriculture and Agri-Food Canada, Swift Current Research and Development Centre, P.O. Box 1030, Swift Current, SK S9H 3X2, Canada; [d]Department of Plant Science, University of Manitoba, 66 Dafoe Road, Winnipeg, MB R3T 2N2, Canada; [e]National Research Council of Canada, 100 Sussex Drive, Ottawa, ON K1N 5A2, Canada; [f]Centre de recherche sur les grains (CEROM) Inc., 740 chemin Trudeau, Saint-Mathieu-de-Beloeil, QC J3G 0E2, Canada; [g]Manitoba Agriculture, 65-3rd AVE NE, Carman, MB R0G 0J0, Canada; [h]Faculty of Agricultural, Life and Environmental Science, University of Alberta, 9011 116 St. NW, Edmonton, AB T6G 2P5, Canada; [i]Charlottetown Research and Development Centre, AAFC, 440 University Avenue, Charlottetown, PE C1A 4N6, Canada; [j]Agriculture and Agri-Food Canada, Summerland Research and Development Centre, Summerland, BC V0H 1Z0, Canada

Corresponding author: **B.D. McCallum** (email: brent.mccallum@agr.gc.ca)

Abstract

Wheat leaf rust, caused by *Puccinia triticina* Erikss., is one of the most common and damaging diseases of wheat in Canada and throughout the world. To understand the *P. triticina* population virulence analysis of the population in Canada has been conducted annually for over 80 years. The virulence profile of the *P. triticina* population and virulence to key resistance genes changes significantly over time, and differs between regions. Recently, genetic analysis via DNA sequencing of representative isolate from the *P. triticina* populations from 2018 to 2022 initially revealed three diverse groups in Canada. All isolates within group one had the same two mating type alleles, group two isolates all had a second combination of alleles, whereas group three isolates were partitioned into eight subgroups encompassing different genetic clades. A fourth distinct group was later found from British Columbia. To combat leaf rust, the resistance genes *Lr2a*, *Lr13*, *Lr14a*, *Lr16*, *Lr21*, and *Lr34* have been used extensively in Canadian spring wheat cultivars. *Lr34*, *Lr46*, and *Lr67* are unique among resistance genes in that they are non-race-specific, conditioning partial resistance to all isolates, while also providing resistance to other wheat diseases. Critically, *Lr34* and *Lr67* were demonstrated to confer resistance to Fusarium head blight. The complete picture underlying *Lr34* functions is not fully understood, but only *Lr34res* lines accumulate the fungistatic compound 1-*O*-*p*-coumaroyl-3-*O*-feruloylglycerol. *Lr34* also produces leaf tip necrosis; this is enhanced at low temperatures. Combinations of race-specific leaf rust resistance genes, with *Lr34*, *Lr46*, and/or *Lr67*, have the best potential to protect wheat from a dynamic Canadian leaf rust population.

Key words: wheat, leaf rust, virulence, resistance

Introduction

Wheat is the largest crop in Canada, and has always been since production increased in western Canada over 100 years ago (McCallum and DePauw 2008). Leaf rust, caused by *Puccinia triticina* Erikss., is the most common and widely distributed of all the cereal rusts (Chester 1946). It has been one of the most destructive diseases of wheat in Canada (McCallum et al. 2016), and throughout the world (Huerta-Espino et al. 2011). Inoculum of *P. triticina* arrives each year in the form of urediniospores, which can be carried over long distance by wind currents from wheat growing regions of northern Mexico and the USA into Canada (Samborski 1985; Aboukhaddour et al. 2020). Wheat breeding efforts in Canada initially focused on controlling stem rust (caused by *Puccinia graminis* Pers.), but once good genetic resistance was incorporated for stem rust, developing resistance to leaf rust became the primary goal (McCallum and DePauw 2008; Brar et al. 2019). Since the 1990s, Fusarium head blight (FHB, caused in Canada primarily by *Fusarium graminearum* Schwabe) has become the primary disease of concern in Canadian wheat primarily due to the health concerns related to mycotoxin contamination that is associated with the disease and the downgrading in end-use quality (McCallum and DePauw 2008). New wheat cultivars therefore need to have good resistance to FHB, stem rust, leaf rust, along with common bunt and stripe rust in western Canada (Brar et al. 2019). This review is divided into two main parts. First, to develop effective genetic resistance to combat wheat leaf rust, the evolution of the *P. triticina* population in Canada over time, for both virulence and genetic diversity was analyzed and presented. Second is the use of resistance genes, and gene combinations, in Canadian wheat cultivars to combat the effects of wheat leaf rust and other wheat diseases.

The *Puccinia triticina* population in Canada

To develop effective genetic resistance to combat wheat leaf rust, the pathogen population has been monitored closely and analyzed for its virulence spectrum since the 1930s (Kolmer 1991). This process has improved and expanded over these years: Initially a set of cultivars was used as differential lines. This was followed by the development of a set of near-isogenic wheat lines utilizing the leaf rust susceptible cultivar Thatcher as the recurrent parent. Subsequently, this set of Thatcher near-isogenic differential lines expanded further (Kolmer 1991). Since 1989, a standard set of 12 Thatcher near-isogenic differential lines has been used in both Canada and the USA (Long and Kolmer 1989). A letter coding system was initiated at that time with one letter representing the avirulence/virulence of each isolate on each set of four differential lines, resulting in a three-letter code for the reactions on the set of 12 differential lines (Long and Kolmer 1989). This was subsequently expanded, by one additional set of four Thatcher near-isogenic differential lines, that currently constitutes a set of 16 lines and a four-letter code (Kolmer and Liu 1997).

To conduct annual national virulence analyses, wheat leaves infected with *P. triticina* are collected each growing season from wheat growing areas throughout Canada. Single pustule isolates are made from these rust urediniospore collections, which are each analyzed for virulence by inoculation onto the wheat differential lines outlined above (McCallum et al. 2021*b*). The spectrum of virulence phenotypes found in each region varies by year, though the populations in western Canada have been somewhat different from those found in eastern Canada, with some virulence phenotypes in common (Kolmer 1991; McCallum et al. 2021*b*). The frequencies of virulence to some key resistance genes have also changed over time and diverged between western and eastern Canada. Some examples include an increased frequencies of virulence to *Lr9*, *Lr17*, and *Lr21* in recent years, while the frequencies of virulence to *Lr2a*, *Lr2c*, and *Lr16* have declined (McCallum et al. 2021*b*).

The genetic relatedness of individuals within the Canadian population was analyzed by DNA sequencing representative isolates from these annual virulence surveys then comparing them for single nucleotide polymorphisms (SNPs) which were correlated for their virulence profiles from 2018 to 2020 (Wang et al. 2023). For virulence, collections from Manitoba and Saskatchewan were similar and those from Ontario and Quebec were also similar to each other; however, those from western Canada were different from those in eastern Canada. Using the genetic similarity revealed by SNPs, phylogenetic analysis grouped these isolates into three clades (1, 2, and 3). Clades 1 and 2 were each large and diversified groups of isolates found in most regions of Canada, isolates from these groups make up the majority found each year. Clade 3 was also diverse, though was found less commonly than clades 1 and 2 and was only found in eastern Canada (Wang et al. 2023). These clades differed from each other in their relative frequencies of virulence to many of the tested differential lines.

Genetic analysis of the mating type loci in *P. triticina* has revealed that each haploid nucleus within the dikaryotic fungal cells has a different mating type allele, similar to the related rust species *Puccinia striiformis* f.sp. *tritici* (Holden et al. 2023). Therefore, each *P. triticina* isolate has two different mating type alleles. Each *P. triticina* clonally reproducing group has a different combination of two of the six mating type alleles found to date in Canada, while all isolates within a clonal group have the same two mating type alleles. The two largest *P. triticina* groups in Canada are clades 1 + 2 (Wang et al. 2023), discussed above. Clade 3, reported by Wang et al. (2023), is actually a collection of several smaller groups, in which members of the same group have the same combination of mating type alleles, and are similar in their genomes and virulence profiles. A distinct group was revealed subsequently from isolates sampled in British Columbia, all with the same mating type allele combination that was different from any other group in Canada. These clonally reproducing groups differ significantly from each other for the frequencies of virulence to certain resistance genes, therefore shifts between the predominance of each group led to changes in the frequencies of virulence to many resistance genes.

Combating wheat leaf rust and other diseases using resistance genes

To combat losses due to leaf rust infection, wheat breeders have incorporated resistance genes into wheat cultivars over time. There are 81 named leaf rust resistance genes that have been mapped to specific locations on wheat chromosomes. Most of these are race-specific resistance genes that condition resistance only to some leaf rust races. There are, however, a small number of non-race-specific resistance genes that condition resistance to all leaf rust races, and to multiple wheat diseases. These include *Lr34*, *Lr46*, and *Lr67* (Spielmeyer et al. 2013; Kolmer et al. 2015). They are all adult plant resistance genes. The most common resistance genes in Canadian wheat include *Lr2a*, *Lr13*, *Lr14a*, *Lr16*, *Lr21*, and *Lr34* (McCallum et al. 2016). Of these *Lr2a*, *Lr21*, and *Lr34* were deployed in cultivars currently seeded to over 50% of the wheat acreage in Canada (B. McCallum and C. Hiebert, unpublished results). Virulence in the Canadian pathogen population has evolved to all these genes, except *Lr34* (McCallum et al. 2021*b*). To date *Lr46* has been deployed in a few Canadian spring wheat cultivars, such as Carberry (Bokore et al. 2022). *Lr67* has not yet been deployed (unpublished B. McCallum). Both of these genes are effective against all the Canadian *P. triticina* isolates that have been tested. Analysis of the resistance genes in Carberry revealed that both *Lr34* and *Lr46* demonstrated additive resistance in combination with the other resistance gene present (Bokore et al. 2022).

In addition to conditioning non-race-specific, multi-pathogen resistance, *Lr34*, *Lr46*, and *Lr67* combined with other resistance genes in an additive manner (McCallum and Hiebert 2022). The Thatcher near-isogenic lines (NILs) with either *Lr34* or *Lr67* were crossed with Thatcher NILs containing *Lr13*, *Lr16*, or *Lr32* (McCallum and Hiebert 2022) to create populations in the Thatcher background that segregated for two resistance genes, one of which was either *Lr34* or *Lr67*. The doubled haploid populations developed from these crosses were genotyped to determine the allele present for both genes in each cross andtested for leaf rust resistance over four years. *Lr34* positively interacted with each of *Lr13*, *Lr16*, and *Lr32*, while *Lr67* had a significant positive interaction with *Lr16* and *Lr32*, but not with *Lr13* (McCallum and Hiebert 2022). Another example of the interaction between these non-race-specific genes and other resistance genes was documented in the genetic analysis of the leaf rust resistance in the cultivar Carberry (Bokore et al. 2022); where both *Lr34* and *Lr46* interacted in an additive manner with *Lr2a*, *Lr16*, *Lr13*, and *Lr23* to produce the high level of leaf rust resistance present in this cultivar.

To determine the effect of *Lr34* on stem rust, twenty pairs of near-isogenic sister lines were created in the Sumai 3 background (McCallum et al. 2011). Sumai 3 was selected because it was highly susceptible to stem rust when the resistant allele of *Lr34* was replaced with the susceptible allele in this genetic background. One sister in each pair had the resistant allele at the *Lr34* locus while the other had the susceptible allele. In nearly all pairs of lines, the sister line with the resistant allele at the *Lr34* locus had significantly less stem rust severity than the sister with the susceptible *Lr34* allele when tested in field trials over multiple years (McCallum et al. 2011). These results (McCallum et al. 2011) were part of the evidence leading to the designation of *Lr34* as the stem rust resistance gene *Sr57*.

FHB is currently the most important wheat disease in Canada. To determine if *Lr34* and/or *Lr67* had an effect on FHB resistance, double haploid populations that segregated for either *Lr34* or *Lr67* were tested for visual FHB symptoms and deoxynivalenol (DON) accumulation over five site years of field trials (McCallum et al. 2024). Both *Lr* genes were significantly associated with lower DON accumulation and the presence *Lr67* was also associated with significantly reduced visual symptoms of FHB on the plants (McCallum et al. 2024).

Both *Lr34* and *Lr67* have been cloned. *Lr34* codes for an ABC transporter (Krattinger et al. 2009), while *Lr67* is a sugar transporter (Moore et al. 2015). Most cloned rust resistance genes are race-specific genes and code for nucleotide binding site-leucine-rich repeat genes, which are the largest group of plant resistance genes (Shao et al. 2019), and act by recognizing fungal avirulence effectors. Therefore, both *Lr34* and *Lr67* function differently from these other resistance genes. There are five haplotypes (H1-H5) of *Lr34* described to date in spring wheat (Dakouri et al. 2014). The resistant allele H1 is null/C for the mutation sites in exons 11/12 and the susceptible haplotypes H2-H4 are all TTC/T at these exons. A rare null/T haplotype was found in only two accessions of the 700 analyzed, both of which had an intermediate leaf rust resistance phenotype (Dakouri et al. 2014). Each of these accessions was crossed to both Thatcher and Thatcher-*Lr34* and the progeny were analyzed for leaf rust resistance in field trials (Cloutier et al. 2023). This analysis revealed that both mutations at exons 11 and 12 had significant effects on reducing leaf rust severity and these were additive with each other (Cloutier et al. 2023).

One of the substrates that *Lr34* transports is abscisic acid (ABA) (Krattinger et al. 2019), and ABA accumulation at the leaf tip leads to leaf tip necrosis (Bräunlich et al. 2021), a pleiotropic effect of *Lr34*. Exactly how ABA accumulation is involved with *Lr34* disease resistance is not clear (Krattinger et al. 2019), as it can act as either an enhancer or suppressor of disease resistance in plants (Ton et al. 2009). Biochemical analysis revealed that near isogenic lines with the resistant allele of *Lr34* accumulated a phenylpropanoid diglyceride, identified as 1-*O*-*p*-coumaroyl-3-*O*-feruloylglycerol (CFG), but lines with the susceptible allele did not (Rajagopalan et al. 2020). CFG has antifungal properties to both *P. triticina* and *F. graminearum*. In addition products from its breakdown in plants are much more fungicidal than CFG. CFG was also broken down upon pathogen infection, releasing these more fungicidal components. This suggests CFG may serve as a storage form of its more potent metabolites, that are accessed by the plant, as a result of CFG breakdown, during defense responses (Rajagopalan et al. 2020).

The pleiotropic effect of leaf tip necrosis is evident on flag leaves of adult plants with the resistant allele of *Lr34* (Singh 1992). Leaf tip necrosis can also be observed on seedling plants, along with leaf rust resistance, if the plants are grown at low temperatures (8–10 °C) (McCallum et al. 2021*a*). When this cold period was extended to the heading stage, leaf tip necrosis could be quite extensive and some spikes were sterile in plants with the resistant *Lr34* allele (McCallum et al. 2021*a*). A similar effect of extensive leaf tip necrosis was observed in transgenic *Lr34res* barley plants at normal temperatures (Risk et al. 2013). These studies demonstrate that while *Lr34* confers excellent durable multipest resistance it can also have some trade-offs in certain circumstances.

Summary

The incorporation of *Lr* resistance genes into wheat cultivars has had a significant effect on reducing susceptibility and combating this dynamic rust population in Canada. When 45 historic Canadian wheat cultivars, released from 1870 up to 2001 were grown together in field plots, the more modern cultivars generally displayed lower leaf rust severity due to incorporation of leaf rust resistance genes over time (Martens et al. 2014). Current cultivars often have combinations of many resistance genes, such as Carberry, in which *Lr34* and *Lr46* interact in a synergistic manner with both race-specific and race-non-specific *Lr* resistance genes. To maintain and improve on this high level of disease resistance the multipest resistance genes *Lr34*, *Lr46*, and *Lr67* should be incorporated along with other effective race-specific resistance genes. Continual monitoring of the pathogen population will enable the selection of the most effective resistance genes, and track the evolution of this ever-changing pathogen on a continental scale.

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Data availability

Data are primarily published previously. Unpublished data are available upon request.

Author information

Author ORCIDs

B.D. McCallum https://orcid.org/0000-0003-2331-1461
F. Bokore https://orcid.org/0000-0002-1073-9816
R. Cuthbert https://orcid.org/0000-0002-1640-4929

Author notes

T. Fetch, J. Thomas, and R.E. Knox are currently retired.

Author contributions

Conceptualization: BDM, CWH, TF, MAH, JT, AB, XW, ML, SC, GH, FB, REK, RC, CM, ML, TC, SBR, CA, GSB, AF, GB
Data curation: BDM, CWH, MAH, SC, ML, GB
Formal analysis: BDM, FB
Investigation: BDM, CWH, TF, JT, AB, XW, SC, GH, FB, RC, CM, ML, TC, SBR, CA, GSB, GB
Methodology: JT
Visualization: BDM
Writing – original draft: BDM, CWH, TF, MAH, AB, XW, ML, SC, GH, FB, REK, RC, CM, ML, TC, SBR, CA, GSB, AF, GB
Writing – review & editing: BDM, CWH, TF, MAH, JT, AB, XW, ML, SC, GH, FB, REK, RC, CM, ML, TC, SBR, CA, GSB, AF, GB

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