Virulence Dynamics and Breeding for Resistance to Stripe, Stem, and Leaf Rust in Canada Since 2000

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Wheat (*Triticum* spp.) is a major field crop in Canada in terms of acreage, annual production, and export market value. There are nine classes of Canadian wheat based on growth habit (winter or spring), kernel hardness (hard or soft), seed coat color (red or white), and quality factors (grain protein content and gluten strength) (McCallum and DePauw 2008). Wheat was described by Newman (1928) as “the economic fairy to the industrial and commercial life of Canada, having built practically the whole economic structure of the Prairie Provinces”. Wheat production in Canada is affected by several biotic and abiotic stresses. The major abiotic stresses are frost damage, drought, and heat stress. Among biotic stresses, diseases caused by fungal pathogens are the most important although wheat streak mosaic virus (WSMV) has caused some localized outbreaks in some years (Burrows et al. 2016; Harding et al. 2017). In context of cultivar registration in Canada, there are certain diseases that breeders have to take into account while developing resistant cultivars. The Prairie Recommending Committee for Wheat, Rye, and Triticale (PRCWRT) classify wheat diseases into priority one, priority two, and priority three depending on prevalence and potential damage they can cause (Anonymous 2015). However, priority one diseases are more of a concern and a minimum level of resistance in commercial cultivars is recommended for those.

Priority-One Diseases of Wheat in Canada

There are five priority-one diseases in Canada for which a minimum level of resistance is recommended for cultivar registration (Anonymous 2015). These diseases are defined as those that are considered to cause harm significant enough to warrant regulation through the registration process. The five priority-one diseases in Canada are: Fusarium head blight (FHB, *Fusarium graminearum* Schw. [Petch]), leaf rust (caused by *Puccinia triticina* Eriks.), stem rust (caused by *Puccinia graminis* Pers.: Pers f. sp. *tritici* Eriks. E. Henn, *Pgt*), stripe rust (caused by *Puccinia striiformis* Westend f. sp. *tritici* Eriks., *Pst*), and common bunt (caused by *Tilletia caries*

Bjerk. and *Tilletia laevis* Bjerk.). The common bunt is effectively controlled in Canada mostly by utilizing genetic resistance (*Bt10* being the most widely deployed gene in commercial cultivars) and where genetic resistance is absent, by seed-treatment fungicides (Randhawa et al. 2013).

The three rust diseases of wheat have caused huge losses to global wheat production. In Canada, stem and leaf rust have historically been the most important, but stripe rust has emerged as a significant problem in the last two decades (Brar 2015). Similar to the three rusts, FHB is a devastating and challenging disease to manage because resistance is inherited in a quantitative fashion and greatly influenced by weather conditions. Gilbert and Haber (2013) conducted more detailed Canadian research on wheat FHB. This article will provide insight on Canadian research into the virulence dynamics of the three wheat rust pathogens and resistance breeding efforts to combat rust diseases. We focus on wheat stripe rust and stem rust research on the Ug99 race group in particular because of their great importance at present and lack of dedicated reviews from Canada in the recent past.

Wheat Rusts – A Refresher

The wheat rusts are highly specialized plant pathogens with narrow host ranges that belong to the genus *Puccinia*, order Uredinales, class Basidiomycetes. Like other Uredinales, wheat rust pathogens have a complex life cycle comprising two host species (main host wheat, alternate hosts barberry, mahonia, thalictrum) and produces all five types of spores (pycniospores, aeciospores, urediniospores, teliospores, and basidiospores) (Box 1). Previously, the alternate host for *Pst* was not known, but in 2010 Barberry was identified as the alternate host (Jin et al. 2010). Wheat stripe, leaf, and stem rust are also known as yellow, brown, or black rusts because of the color of asexual urediniospores produced on wheat hosts. The three fungal diseases have several attributes that contribute to their ability to rapidly reduce a seemingly healthy field of wheat to a mass of broken stems or rusted leaves within a few weeks following initial infection. Firstly, the rusts spread quickly by airborne spores that are capable of traveling at a continental and even intercontinental distance (Chen 2005; Visser et al. 2019; Walter et al. 2016). Second, upon deposition of spores onto the wheat plants, infection ensues when germination is stimulated by dew formation, and the fungi enters the plant through the stomata. The fungi quickly proliferate in the mesophyll tissue and forms fruiting structures (uredinia) that produces a new crop of infective spores (urediniospores) in about a week, depending on environmental temperatures (stripe rust prefers cooler conditions whereas

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leaf and stem rusts can tolerate slightly warmer temperatures). The stripe rust pathogen produces stripes of uredinia along the leaf veins in adult wheat, barley (some races with overlapping host boundary), and foxtail barley grass (*Hordeum jubatum* L.) (Fig. 1, Box 1). These urediniospores spores can then re-infect the same field and generate multiple infections in a short period of time or can migrate to infect new fields. Finally, the explosion of the uredia ripping through the stem (for stem rust) or leaf (for stripe and leaf rust) epidermis (Figs. 1 and 2) creates massive holes in the stem tissue that lead to significant water deficit and stem breakage, resulting in up to 100% yield loss or shriveled kernels where loss is not total. The combination of rapid spore production from infection to uredinia formation, quick and long-distance wind dispersal of urediniospores, and large yield and quality losses enables wheat rusts to be the most destructive of all wheat diseases. The host resistance to rusts in wheat is largely classified into all-stage/seedling resistance (ASR, expressed throughout all plant growth stages) and adult plant resistance (APR, expressed only at adult plant stages) (Box 1). The ASR is qualitative in nature and race-specific, and thus is not durable because pathogen races mutate to overcome such resistance whereas the APR is race nonspecific, quantitative, and is often durable. Several reviews on

the pathogens and disease epidemiology have previously been published (Chen 2005; Line 2002; Roelfs 1985; Stubbs 1985).

Stripe/Yellow Rust

Stripe rust in Canada: Pre-2000 and post-2000 eras. Stripe rust was first reported in Canada in Alberta in 1918 on foxtail barley (Fraser and Connors 1925). Subsequently, it was observed in British Columbia, southern Alberta, and western Saskatchewan on wheat and other gramineous hosts (Fraser and Connors 1925; Sanford and Broadfoot 1929, 1932, 1933). The disease was not reported to have an economic impact on wheat production in any of the provinces in the early 1900s. The Canadian Plant Disease Survey journal (<https://phytopath.ca/publication/cpds/>) of the Canadian Phytopathological Society is an excellent resource for disease reports from commercial crops grown in Canada since 1927. Stripe rust infection was common in British Columbia and southern Alberta from 1926 to 1975 and ranged from trace to severe (very rare). From 1976 to 2000, stripe rust was infrequently reported and did not cause significant yield loss, except in 1986 when an epidemic on the soft white spring wheat susceptible cultivar Fielder (carrying *Yr6* and *Yr20*) occurred in southern Alberta (Conner and Kuzyk 1988).

BOX 1 GLOSSARY - CEREAL RUST PATHOLOGY

Accessory host – Also known as auxiliary host. The host other than main and alternate host for rust pathogens, e.g., grasses.

Aeciospore – A binucleate spore produced in an aecium on barberry (alternate host).

Alternate host – Host other than main and accessory hosts which is required for completion of life cycle in uredinales (rusts).

Basidiospore – A sexually produced spore borne on a basidium on main host (wheat) that infects an alternate host (barberry).

Race – A subgroup or biotype of rust pathogen within a species or forma specialis distinguished by virulence but not by morphology, i.e., different in virulence to different genotypes of same host species.

Differentials – The specific varieties or genotypes of host plant species used to determine races (based on infection response) of a rust pathogen species.

All stage resistance (ASR) – Resistance that expresses throughout all growth stages of wheat. The resistance is often complete, race-specific, and not durable.

Adult plant resistance (APR) – Resistance that expresses only at adult plant stage and not at the seedling stage. The resistance is often incomplete, race nonspecific, and durable.

High-temperature adult plant resistance (HTAP) – APR that is expressed only at higher temperatures.

Lineage (genetic) – Races associated with major rust epidemics have been assigned a common name according to their genetic group/lineage defined by molecular genotype (Ali et al. 2017).

Pycniospore – Haploid spore (spermatia) produced in a pycnium on alternate host (barberry).

Teliospore – Thick-walled resting or overwintering spore produced by the rust (Uredinales) and smut (Ustilaginales) fungi in which karyogamy occurs; teliospores germinate to form a promycelium (basidium) in which meiosis occurs.

Urediospore (syn. Urediniospore) – Binucleate, dikaryotic, asexual, one-celled, repeating spore of rust fungi and borne on a uredinium (syn. uredium).

Virulence – The degree of measure of pathogenicity of a rust pathogen often measured by quantifying relative capacity to produce disease.

Fig. 1. Stripe rust lesions/stripes of pustules/uredia along the veins on flag leaf (left), microscopic view of asexual urediniospores in a uredinium/sorus on wheat leaf (center), and natural stripe rust infection on foxtail barley grass (*Hordeum jubatum* L.) (right).

Prior to 2000, stripe rust in Canada was a production problem only in southern Alberta on susceptible soft white spring wheat under irrigation that was late maturing (particularly the susceptible cv. Fielder). This was further compounded by the proximity to the Pacific Northwest (PNW) region of the U.S.A., which is the hotspot of stripe rust in North America. The combination of susceptible, late maturing varieties and irrigation provided conditions conducive to pathogen infection (Conner and Kuzyk 1988). Despite the presence of stripe rust in western Canada before 2000, it never became widespread because *Pst* infection and disease development requires cool, humid conditions, and low (<10°C) nighttime temperatures that do not usually occur in wheat growing regions in central Canada and the Great Plains of the U.S.A. (Environment Canada, https://weather.gc.ca/canada_e.html). Such conducive environmental conditions do prevail in the PNW, which has served as a reservoir of pathogen inoculum since it first entered North America in 1915 (Line 2002).

The epidemiology of stripe rust changed in 2000, with the foreign incursion of a new lineage named *PstSI*, which entered North America and caused a dramatic shift in the population structure of *Pst* (Chen et al. 2002). The races belonging to the *PstSI* lineage, which originated in East Africa, were adapted (increased germination and

aggressiveness) to warmer temperatures typical of the upper Great Plains and the Canadian prairies (Milus et al. 2006, 2009; Walter et al. 2016). The better parasitic fitness of these new *PstSI* races resulted in the replacement of the majority of the older races in the U.S.A. east of the Rocky Mountains. Stripe rust inoculum in Canada mainly arrives from the U.S.A. either via the “Puccinia pathway” from the Great Plains, and/or via wind migration from the PNW. Races of the *PstSI* lineage are believed to have entered Canada in 2000 (Brar et al. 2018b; Su et al. 2003). Not only do the new races have better parasitic fitness, but their virulence on *Yr8* and *Yr9* (located on rye translocation segment on 1BL.1RS) contributed to the rapid multiplication of the pathogen on the majority of winter wheat cultivars in the Midwest of the U.S.A. carrying these genes (mainly *Yr9*) (Chen et al. 2002; Milus et al. 2006).

The year 2000 brought a change in stripe rust prevalence in western Canada, and four stripe rust survey reports appeared in the Canadian Plant Disease Survey in 2000 and 2001 (Fetch and McCallum 2001, 2002; Morrall and Fernandez 2002; Orr and Turkington 2002). The late Dr. Robin Morrall described stripe rust as “an unusual disease of wheat” because stripe rust was uncommon on Canadian wheat crops at the time (Morrall and Fernandez 2002). He further reported 10 to 50% stripe rust severity in all surveyed crops, which is generally significant enough to cause yield loss. Stripe rust was more common than leaf or stem rust in Saskatchewan and Manitoba in 2000 and 2001, which was surprising because leaf and stem rusts favor warmer climates and were well-established in Canada for many decades (Fetch and McCallum 2001, 2002). Higher than normal rust inoculum in 2000 was attributed to environmental conditions favorable to rust infection. While environment did have a partial role in increased rust prevalence, the root cause of the epidemic was a change in the pathogen.

The 2010 and 2011 stripe rust epidemics in western Canada.

Since 2000, stripe rust surveys in commercial crops in western Canada have reported annual occurrence of the disease (<https://phytopath.ca/publication/cpds/>) (Fig. 3). The most recent and widespread epidemics of stripe rust in western Canada were in 2010 and 2011 (Kutcher et al. 2012). As mentioned previously, stripe rust severity in Canada is generally dependent on inoculum migrating from the U.S.A. In 2010, stripe rust was widespread in 31 states of the U.S.A. (Wan and Chen 2014). The Cereal Pathology lab of Agriculture and Agri-Food Canada (AAFC) Lethbridge documented stripe

Fig. 2. Wheat infected with stem rust showing the explosion of uredia through the epidermal tissue.

Fig. 3. Snapshot of stripe rust infected CDC Falcon (susceptible) winter wheat crop and flag leaf photos from the 2013 disease survey conducted in central Saskatchewan.

rust incidence and severity in 103 commercial fields, as well as stripe rust nurseries in 2010. Data were also collected from western Canadian co-op trials, commercial crops, and disease nurseries on several important cultivars in 2011 (Puchalski and Gaudet 2011; Randy Kutcher, unpublished data). In 2010, stripe rust was first detected in Lethbridge (southern Alberta) in late June, indicating that the pathogen probably did not overwinter from 2009. By the first week of July, stripe rust severity on flag leaves of the susceptible winter wheat cultivar AC Bellatrix reached 80% and by late July, severity on many commercial winter wheat crops of cultivar AC Radiant (carrying *Yr10*) reached 30%, suggesting the defeat of the *Yr10* gene. Although stripe rust severity in commercial winter wheat crops was high, it remained low in some hard red spring wheat crops with 'Lillian' (carrying *Yr18*, *Yr36*, possibly *Yr30*, and *QYr.spa-5A*) the most resistant cultivar to date. However, stripe rust severity of other hard red spring wheat cultivars, such as 'Harvest' and 'CDC Go' (carrying *Yr29*) was up to 10% and 'CDC Abound' and 'Superb' up to 30% by late July. Cool and wet conditions led to severity levels of 70 to 80% by mid-August in most susceptible cultivars. Half of the 10 durum crops surveyed in southern Alberta had flag leaf severity up to 5%. Stripe rust severity of >20% was observed in juvenile winter wheat crops in late September in the Cardston, Magrath, and Lethbridge areas of southern Alberta. Urediniospore production was high in most commercial crops in 2010, and the occurrence of an early winter snow provided cover to enable overwintering of stripe rust in southern Alberta in 2010.

Stripe rust appeared in the spring of 2011 as early as 1 May to 18 May in southern Alberta, which was 40+ days earlier than 2010, suggesting overwintering of the pathogen (Fig. 4) (Kutcher et al. 2012).

A cool and wet spring in 2011 provided conducive conditions for rapid multiplication of urediniospores on susceptible wheat cultivars, and by mid-July the disease had progressed further and covered most of southern Alberta. By the beginning of August, the disease had spread to northern and central Alberta, and by mid-August, severe stripe rust was recorded in most of Saskatchewan (Fig. 4). The maximum severity (90%) occurred on susceptible cv. AC Barrie. In 2011, *Yr10*, carried by 'AC Radiant,' was no longer effective and stripe rust symptoms were even observed on the flag leaves of 'Lillian' (<10% severity), which carries at least four stripe rust resistance genes/quantitative trait loci (QTLs) (Fig. 5). It is noteworthy that the slow rusting genes *Yr18* and/or *Yr29* carried by multiple cultivars were less effective in the 2011 epidemic, and cvs. Sadash and Lillian were the only ones with <10% severity (Fig. 6). Yield loss in the 2011 epidemic was much higher than previous years and ranged from 15 to 35% on susceptible cultivars, 5 to 20% on cultivars with intermediate resistance, and 2 to 10% for resistant cultivars.

***Pst* population structure.** Race characterization of stripe rust isolates (genetically uniform isolates derived from a single spore or pustule or distinct single lesion) is an important part of population structure studies, because only by race typing can one determine the virulence spectrum of prevalent races/isolates. Race characterization of *Pst* isolates in Canada has not been performed to the same scale as in the U.S.A., as the disease was initially limited to the small acreage of irrigated soft white wheat in southern Alberta. Few studies have investigated the *Pst* race composition in Canada. Newton and Johnson (1936) were able to differentiate between European and North American isolates, and they reported races from Olds, AB, were able to defeat 'Chinese 166,' which

Fig. 4. Incidence of stripe rust in western Canada in 2011.

Fig. 5. Levels of stripe rust severity on a set of cultivars (from different market classes) from May to mid-August in 2011.

Fig. 6. Reaction of selected wheat cultivars to stripe rust from 2009–2011. Genes carried: 5701PR (*Yr18*), AC Barrie (none/unknown), CDC Kernen (*Yr18*), Stettler (*QYr.sp.a-2A*, *QYr.sp.a-5B*, *QYr.sp.a-4A*), Unity VB (none/unknown), Waskada (none/unknown), McKenzie (none/unknown), Lillian (*Yr18*, *Yr36*, *QYr.sp.a-5A*, possibly *Yr30*), CDC Teal (*Yr18*), Laura (*Yr18*), Avonlea (unknown), Radiant (*Yr10*), Fielder (*Yr6*, *Yr20*), AC Andrew (*Yr18*, *Yr29*), Sadash (*Yr29*).

carries the *Yr1* gene. A dedicated effort for race characterization of *Pst* isolates in Canada began after the incursion of the *PstS1* races in 2000 (Su et al. 2003). Subsequent race characterization studies in Canada were published after the 2011 epidemic (Brar and Kutcher 2016; Holtz et al. 2013; Kumar et al. 2012). At present, research groups from AAFC in Lethbridge, the Field Crop Development Centre (FCDC) of Alberta Agriculture and Food in Lacombe, and the Crop Development Centre at the University of Saskatchewan in Saskatoon are characterizing stripe rust isolates on a regular basis. In eastern Canada, wheat researchers at the University of Guelph began working on stripe rust pathogen characterization since they observed widespread occurrence in 2016 (Ali Navabi, personal communication). Unlike the long-term, well recognized research on race characterization for stem and leaf rust, virulence characterization of the stripe rust pathogen in Canada is still in its infancy.

The majority of the differential wheat genotypes used in first race characterization study by Su et al. (2003) overlapped with the European differential set and the standard set of 20 U.S. differentials (Wan et al. 2017). Until the last decade or so, stripe rust researchers used differentials (including some cultivars) that carried more than one *Yr* gene and that too in different genetic backgrounds, which is not ideal. Wellings and colleagues made a great effort to develop a set of 20 single-gene differentials in a susceptible Australian cultivar Avocet background (Wellings et al. 2004), which are used by many research groups including some recent race characterization studies in Canada. However, a common set of differentials to characterize and name races is still lacking, in Canada and globally, making it impossible to directly compare races among countries.

Although direct comparison of *Pst* races in Canada has not been done, virulence frequency on individual *Yr* genes can be easily compared (Table 1). With the incursion of the *PstS1* lineage in 2000, a rapid increase in virulence on *Yr8* and *Yr9* occurred and is fixed in recent races (Table 1). Virulence on *Yr6*, *Yr7*, *Yr27*, and *Yr32* is almost fixed and these genes are not effective against the majority of *Pst* races. Virulence on *Yr10* was low until the release of the winter wheat cultivar AC Radiant in 2009 that carried this gene, and races virulent on *Yr10* increased in frequency after 2009 likely due to selection pressure (Table 1). Although *Yr24* is not present in any commercial wheat cultivars in Canada, virulence on *Yr24* followed a similar trend as *Yr10* because avirulence loci (*Avr* effector genes) in *Pst* for both *Yr* genes in wheat are believed to be tightly linked (Wan et al. 2017).

Field trap nurseries. Another quick method of conducting virulence surveys is to establish trap nurseries at several locations across a geographical region as done by researchers in Canada (Brar et al. 2015, 2017, 2018a; Xi et al. 2015). It is important to test differentials and key commercial cultivars for natural stripe rust infection in Canada as some all-stage or seedling resistance genes differ in phenotypic expression at the adult stage, e.g., *Yr17* and *Yr28*. This has been documented in stem rust for gene *Sr21* and for leaf rust resistance gene *Lr21* (McIntosh 2010). Virulence on *Yr17* and *Yr28* in seedling tests is not observed in the field because lines carrying these genes are highly effective at the adult stage (Brar et al. 2017, 2018a). It is believed that *Yr17* is tightly linked to an unknown high-

temperature, adult plant resistance (HTAP) gene (Xianming Chen, personal communication) and thus gives a resistant reaction in warm prairie growing seasons, although *Yr17* itself is not effective against the dominant races in Canada (Brar and Kutcher 2016; Holtz et al. 2013; Kumar et al. 2012). The tight linkage of *Yr17* with the unknown HTAP could be the reason for difficulties in accurate infection type (IT) recording on differentials carrying the gene as described in the preceding section. Similarly, the *Yr28* resistance effect is enhanced in warm climates (Singh et al. 2000; Ravi Singh, personal communication). The trap nurseries comprising differentials and local commercial wheat cultivars are also valuable to collect stripe rust samples for population characterization.

Genetic characterization. In addition to traditional characterization of virulence using physiologic methods, *Pst* populations also have been genetically characterized using DNA-based molecular markers or whole-genome shotgun sequencing. The *Pst* population in Canada has a clonal population structure and a small number of molecular genotypes or lineages (Brar et al. 2018b; Holtz et al. 2014). Genotyping of the *Pst* population from Alberta using microsatellite markers by Holtz et al. (2014) was unable to define lineages in the global context. Brar et al. (2018b) was the first in North America to use *Pst*-specific microsatellite markers to identify four lineages in the western Canadian population. These lineages are: *PstS0* (consisting of old northwestern European races), *PstS1* (MLG-99 and MLG-99v; high-temperature adapted), *PstS1-related* (possibly a hybrid of *PstS1* with other lineages), and *PstPr* (Fig. 7). The lineages *PstS0* and *PstS1* have been described previously (Ali et al. 2017), whereas *PstS1-related* and *PstPr* are specific to the Canadian *Pst* population. The *Pst* races belonging to lineages *PstS1-related* and *PstPr* are characterized by high telia production (a characteristic feature of sexual populations), as compared with *PstS1* and *PstS0* (Brar et al. 2018b; Fig. 8). Races belonging to *PstS1* and *PstS1-related* are dominant in western Canada. Additionally, races in the *PstPr* lineage have a wider virulence spectrum and are closely related to the devastating ‘Warrior’ and ‘Kranich’ races identified in Europe that caused large yield losses in commercial crops (Ali et al. 2017). The *PstPr* lineage is not native to Canada and was a foreign incursion. Thus, it is important to genotype the dominant races with *Pst*-specific markers to compare and identify foreign incursions.

Fig. 7. A neighbor-joining phylogenetic tree showing four *Puccinia striiformis* f. sp. *tritici* lineages detected from Canada (*PstS0*, *PstS1*, *PstS1-related*, and *PstPr*). Each colored dot represents an isolate and each color belongs to a defined lineage. Races belong to *PstS1* and *PstS1-related* are predominant.

Table 1. Virulence frequency of *Puccinia striiformis* f. sp. *tritici* isolates collected and characterized between 1984 and 2018 on some key *Yr* genes

Years (number of isolates)	<i>Yr7</i>	<i>Yr8</i>	<i>Yr9</i>	<i>Yr10</i>	<i>Yr24</i>	<i>Yr27</i>	<i>Yr32</i>
1984–1999 (<i>n</i> = 33)	42	6	3	6	- ^a	-	30
2000–2002 (<i>n</i> = 24)	100	92	92	4	-	-	8
2005–2008 (<i>n</i> = 37)	100	100	100	3	19	92	73
2009–2010 (<i>n</i> = 33)	100	100	100	16	9	100	96
2011–2012 (<i>n</i> = 58)	100	100	100	19	10	100	81
2013–2018 (<i>n</i> = 38)	100	97	95	18	13	100	100

^a Could not be determined as none of the differentials used at the time carried the gene.

Overwintering studies. The Canadian wheat growing region on the prairies usually receives more snow than in most parts of the U.S.A. It is believed that continuous snow cover might protect latent *Pst* hyphae or spores on winter wheat in central Alberta and enable overwintering of the pathogen (Conner et al. 1988; Kumar et al. 2013). Although *Pst* can overwinter both as spores and hyphae/mycelia in plants, most research suggests that mycelia are hardier than the spores. Stripe rust was reported to overwinter in Canada as early as 1927 (Sanford and Broadfoot 1929, 1932). Canada has a short growing season, and spring wheat planting overlaps with winter wheat seeding, thus providing a green bridge to the pathogen (Xi et al. 2015). Kumar et al. (2013) reported that continuous snow cover is imperative for survival of overwintered inoculum, and from an epidemiological viewpoint, spring wheat crops in proximity to an overwintering site might experience greater disease pressure depending on cultivar resistance. In 2015–16, Aboukhaddour et al. (2018) reported overwintering of *Pst* in Alberta.

Breeding for stripe rust resistance. Breeding for stripe rust resistance in Canada was not a priority until after the incursion of the *PstS1* lineage in 2000, which had a wider virulence spectrum and was adapted to high temperature conditions that exist across the Prairie region. This resulted in increased production risk on several millions of acres of wheat, instead of the limited area in Alberta under irrigation. The first evaluation for the response of commercial wheat cultivars to stripe rust from Canada was performed in 2006 (McCallum et al. 2007), followed by others reporting resistance of commercial wheat cultivars in several regions of Canada (Brar et al. 2017, 2018a; Randhawa et al. 2012). Despite minor epidemics in 2000, 2001, and 2011, yield losses in commercial crops were not

as high as Canadian growers have observed from stem and leaf rust epidemics (McCallum et al. 2016). The reason for the reduced impact on grain yield was the presence of pleiotropic APR gene *Yr18/Lr34* (on chromosome 7DS) in the majority (>50%) of Canadian commercial wheat cultivars (McCallum et al. 2007; Randhawa et al. 2012, 2013; Toth et al. 2019; Table 2). Since the 1970s, an increasing portion of the wheat cultivars in Canada have incorporated the multi-pest resistance gene *Lr34/Yr18* (McCallum et al. 2011). This gene conditions resistance to many diseases including leaf, stem, and stripe rust. It is also a race nonspecific resistance gene that has not been overcome by changes in the pathogen population while deployed widely over the world for many years. The deployment of *Yr18* in commercial wheat cultivars was not intentional, as breeders were targeting gene *Lr34* for leaf rust resistance. Cloning of *Lr34/Yr18* in 2009 delivered perfect molecular markers that have made it easier to deploy this resistance in commercial wheat cultivars (Krattinger et al. 2009). Despite the presence of *Yr18* in the majority of cultivars, the phenotypic expression level varies (Brar et al. 2018a). This may be attributed to the fact that the gene enhances the effect of other rust resistance genes, and genetic backgrounds of the carrier cultivars/wheat lines affect phenotypic expression of the gene (Kolmer et al. 2011). As *Yr18* is slow rusting and does not provide complete protection, it is less effective under high disease pressure as was observed in the 2011 epidemic (Brar et al. 2018a; Kutcher et al. 2012). Increased plant height (Johnston et al. 2017) and a slight reduction in yield (Chen et al. 2016) associated with leaf tip necrosis can be detrimental, but is offset by the durability of the gene, its frequency in elite germplasm, and the yield protection it confers by mitigating disease caused by multiple rust pathogens. Therefore, *Lr34* is the most important gene in Canadian wheat breeding programs for rust resistance.

The ASR genes carried by commercial Canadian wheat cultivars were targeted in Canadian wheat breeding programs and these genes came along with other favorable genes that were the focus of breeders (Table 2; Brar et al. 2017; Randhawa et al. 2013). Gene *Yr7* is tightly linked with stem rust resistance gene *Sr9g* (McIntosh et al. 1981). ‘Thatcher’ carrying *Sr9g/Yr7* was the backbone of wheat breeding for stem rust resistance in the past, and thus *Yr7* could be present in many Canadian wheat cultivars although the virulence is fixed for the gene in *Pst* races from Canada and elsewhere. *Yr17* is part of a VPM (*A. ventricosum*/*T. persicum*/*T. aestivum* cv. Marne) translocation on 2AS that also carries multiple rust resistance genes *Lr37/Sr38*. Except for *Yr17*, no deployed ASR gene is effective against most *Pst* races and virulence is almost fixed (Brar and Kutcher 2016; Wan et al. 2017; Xi et al. 2015).

Since the 2011 epidemic, researchers have focused on identifying resistance in local germplasm and cultivars, although studies are scarce as compared with other countries. Singh et al. (2014) and Bokore et al. (2017) identified several QTLs for resistance to stripe rust in ‘Carberry,’ ‘AC Cadillac,’ ‘Stettler,’ ‘Vesper,’

Fig. 8. Two *Puccinia striiformis* f. sp. *tritici* isolates showing difference in telia production ability five weeks after inoculation. Isolate W054 (belonging to *PstS0* lineage) and Isolate W055 (belonging to *PstS1*-related lineage).

Table 2. Stripe rust resistance genes (*Yr* genes) carried by commercial wheat cultivars and advanced breeding lines in Canada

<i>Yr</i> gene	Type of resistance	Cultivars/advanced breeding lines carrying the gene
<i>Yr6</i>	All-stage resistance	Fielder
<i>Yr7</i>	All-stage resistance	Thatcher, Marquis, Neepwa, Manitou, Sinton
<i>Yr9</i>	All-stage resistance	Pasqua
<i>Yr10</i>	All-stage resistance	AC Radiant, W576, W577, W578
<i>Yr17</i>	All-stage resistance	CDC Stanley, Moats, Sunrise, McClintock, Emerson, AAC Iceberg, PT479
<i>Yr18</i>	Adult plant resistance	Pacific, Roblin, Pasqua, 5602HR, CDC Alsask, Shaw, Leader, Lancer, Laura, CDC Teal, AC Eaton, AC Elsa, AC Cadillac, Glencross, Burnside, CDC Bounty, CDC Imagine, Lillian, Carberry, Muchmore, CDC Kernen, CDC Utmost, Peace, Muchmore, CDC Osler, AAC Brandon, AAC Magnet, CDC Plentiful, CDC Titanium, CDC Kernen, BW1013, BW5011, HW049, PT459, 5701PR, 5702PR, Amazon, AC Corinne, Bluesky, Glenlea, Rama, Snowbird, Howard, and many more
<i>Yr27</i>	All-stage resistance	Selkirk
<i>Yr29</i>	Adult plant resistance	CDC Go
<i>Yr36</i>	High-temperature adult plant resistance	Lillian, AC Conquer, Somerset, Burnside, Glencross, PT468, W568

'Lillian,' and 'Red Fife' and while some overlapped with previously mapped genes such as *Yr18* and *Yr36*, they also mapped major and potentially novel QTLs as well. One QTL named *QYr.spa-2A* (present in Stettler and AC Cadillac) could be *Yr32*, and the presence of *Yr32* in Canadian wheat may have led to an increase of virulence on the gene in the *Pst* population (Table 1). Lin et al. (2018) identified two major QTLs (*QYr.usw-5B* and *QYr.usw-7B*) in a durum wheat diversity panel, and the 7B QTL was detected in a number of Canadian durum wheat cultivars, thus explaining the resistance in these cultivars.

Despite the fact that stripe rust has become an economic problem and the PRCWRT of the Prairie Grain Development Commission (PGDC) recommended at least an intermediate level of resistance for cultivar registration as of 2017, the majority of wheat breeders focus mainly on *Yr18*, and somewhat on *Yr36* and *Yr29*, largely to avoid linkage drag from deployment of new genes. Also, most wheat growers in Canada apply fungicides to protect their crops from Fusarium head blight, another priority one disease, which also manages rusts. As *Pst* overwinters regularly at a few locations and there may be widespread overwintering under conducive winter conditions, breeders should focus on stacking quantitative APR genes with effective ASR genes to mitigate crop infection at the seedling to flag leaf stages of wheat. Stacking multiple APR/ASR genes can provide

durable resistance in commercial wheat crops and minimize the need for fungicide application in stripe rust epidemic years.

Stem Rust

Wheat stem rust has historically been the most devastating of all cereal rust diseases in Canada. More research has been done on the host resistance, pathogen virulence, epidemiology, physiology, biochemistry, and histology of wheat stem rust than any other plant disease (Roelfs 1985).

Stem rust in Canada: history and virulence dynamics. Johnson (1961) wrote an excellent treatise on the history of rust research in Canada in the first half of the 20th century. The earliest record of rust damage in western Canada dates back to 1891, with frequent minor epidemics, up to a major stem rust epidemic in 1916, which caused an estimated 43% yield loss. The 1916 epidemic, along with moderate losses in 1919 and 1921 and severe losses in 1923, prompted the Minister of Agriculture (W. R. Motherwell) to designate funding to build the Dominion Rust Research Laboratory in Winnipeg, Manitoba, during the winter of 1925–26. The focus of the "Rust Lab" scientists was to study the epidemiology, physiology, and biology of the cereal rust pathogens and to breed for rust resistant varieties. One of the first major discoveries at the Rust Lab occurred in 1927, when the function of the pycnia fruiting structure on the upper leaf surface of

Fig. 9. Life cycle of wheat stem rust (reproduced from Menzies and Gilbert 2003).

the alternate Barberry (*Berberis vulgaris* L.) host in the sexual cycle of the wheat stem rust pathogen (Fig. 9) was elucidated (Craigie 1927). While an association between stem rust on wheat and the rust on Barberry was previously made by Anton De Bary in 1865, which resulted in eradication laws in several countries (including Canada in 1916) to remove and destroy Barberry bushes (Fig. 10), the function of the pycnia in the Barberry alternate host to complete the sexual cycle had not been determined. This discovery was critical in the control of wheat stem rust, as it was the primary mechanism in the creation of new strains with increased virulence.

Knowledge of the variation in virulence in the pathogen is critical in order to identify effective resistance genes in the host that can be incorporated into the development of disease resistant cultivars. Studies characterizing the virulence of *Pgt* began at the University of Minnesota in 1917 by E. C. Stakman and colleagues, who found differences in pathogenicity of stem rust isolates across various grass species, which were called biologic forms. Subsequently, stem rust isolates were evaluated for seedling infection reaction on 25 wheat hosts and were found to react differentially, i.e., some wheat lines exhibited a resistant response and some were susceptible to the various stem rust isolates. A dichotomous key to identify the isolates was developed based on the seedling reactions

of 12 selected “differential lines” to stem rust infection (Stakman and Levine 1922), which later became known as the “physiologic race” of the isolates. The term “physiologic race” is unique to the rust fungi in the characterization of virulence, as while isolates of stem rust are not distinguishable from each other based on spore morphology, the isolates are easily differentiated based on differences in the physiologic (phenotypic) reaction observed on wheat lines with different resistance genes.

Several changes in the methodology and nomenclature systems to identify stem rust races have occurred since the original key created by Stakman and Levine in 1922. Races in the “Stakman system” were numbered and added sequentially as discovered, and the wheat differentials used were cultivars that often contained several stem rust resistance (*Sr*) genes. The discovery of the ‘Gene-for-Gene’ association between host resistance and pathogen virulence (Flor 1956), where resistance genes in the host have corresponding virulence genes in the pathogen, indicated the need to change the differential lines to ones containing single *Sr* genes. Ausamus et al. (1946) were the first to identify individual *Sr* genes, which were numbered sequentially upon their identification. While Green et al. (1960) appear to be the first to develop wheat lines with single *Sr* genes, it was in the ‘Marquis’ wheat background, which contains at least four known *Sr* genes (*Sr7b*, *Sr18*, *Sr19*, *Sr20*). Loegering and Harmon (1969) were the first to develop single-gene near-isogenic lines (NILs) in a susceptible wheat (Chinese Spring) background. Since then, almost all differential lines used to characterize virulence in *Pgt* are available in a single-gene background.

Concurrently, new nomenclature systems also evolved to more precisely characterize the virulence in an isolate. Watson and Luig (1963) modified the Stakman system and included six additional lines (13 today), which are still used today in Australia. Green (1965) developed the “formula method = C method” using eight NILs with single *Sr* genes in the ‘Marquis’ background, which was expanded to 23 NILs in 1981 (Green 1981). In 1972, Roelfs and McVey developed a letter-code system of nomenclature, which was later modified by Roelfs and Martens (1988) and used 12 NILs with single *Sr* genes. Fetch et al. (2009) reviewed the various systems of stem rust nomenclature and the differential lines used by rust researchers in different countries in an attempt to develop a shared set of differential lines and a common naming system. While there was not total agreement among rust workers with regard to the system to use, the letter-code nomenclature was endorsed as it is based on a mathematical system that allows easy comparison of virulence across

Fig. 10. Bush of common Barberry (*Berberis vulgaris*).

Fig. 11. Virulence dynamics in the *Puccinia graminis* f. sp. *tritici* population in Canada from 1956–2015.

racess/isolates. Currently, most stem rust workers worldwide use 20 wheat differential lines (Jin et al. 2008) and the letter-code system of nomenclature to characterize the virulence dynamics of populations in their country.

Knowledge of the virulence dynamics of rust populations in or near the geographical location of *Sr* genes deployment in wheat cultivars is critical. Annual surveys to collect wheat samples infected with stem rust to ascertain the virulence in the population of *Pgt* began in Australia, Canada, and the United States in 1919, and in South Africa in the early 1980s (Terefe et al. 2016). Virulence in the *Pgt* population in North America was quite variable in the first half of the 20th century, with 71 races identified from 1919 to 1955 (Johnson and Green 1957). This can be attributed to the presence of the alternate Barberry host, which has been estimated to generate one race per every four collections of aecia (Stakman et al. 1934). Eradication of Barberry in Canada and the United States began in earnest in 1919 subsequent to the passing of the “Barberry Act,” and by 1957 very few Barberry bushes could be found in Manitoba (Johnson 1961) or in the rest of western Canada and the Great Plains of the United States. Because of this, the population of *Pgt* became primarily asexually generated, with few races (Roelfs 1982). Removal of common Barberry from the wheat production areas of the Great Plains of the United States and the Prairie region of Canada was the primary factor in the rapid reduction of races detected, and limited appearance of novel races, in the population of *Pgt* since the last major epidemics from 1953 to 1955.

Surveys to characterize the population of *Pgt* in Canada and the United States continued following the last major epidemics. Virulence in the *Pgt* population has become stable, with few races detected since 1955 (Fig. 11). This is interesting because the number of differential lines has increased from 12 in 1955 to 20 that are currently used and should result in an increase in the races detected as there will be more discrimination among races (if found) with more differential lines. In Canada, only four races (TPMK, QFCS, QCCJ, RCRS) have been dominant over the past 60 years. While “old” races (MCCF, RKQS) continue to be found occasionally, there have been very few that dominate, and the primary rationale for this is the deployment of *Sr* genes in wheat cultivars grown in the United States and Canada.

Resistance breeding efforts in Canada. The control of wheat stem rust through the use of genetic resistance has been one of the greatest success stories of plant breeding. In North America, the first major success story was the release of ‘Thatcher’ wheat in 1935 by the Minnesota Agricultural Experiment Station. While the exact composition of *Sr* genes in ‘Thatcher’ is unknown, it contains *Sr5* (Kanred parent), *Sr12*, and *Sr16* (Iumillo parent), plus other *Sr* genes, and is the backbone of stem rust resistance in Canadian wheat varieties. While the ‘Thatcher’ resistance is not effective against the race 15 group (= “T” races), in combination with genes derived from ‘McMurachy’ (*Sr6*), ‘Kenya Farmer’ (*Sr7a*, *Sr9b*, *Sr11*), and ‘Hope’ (*Sr9d*, *Sr17*), most current wheat varieties grown in Canada and the United States contain a stack of *Sr* genes that has provided complete protection against the races in the North American *Pgt* population since 1955. However, this does not hold true for races of *Pgt* that exist elsewhere in the world.

Stakman (1947) once said that *P. graminis* is a “shifty enemy” and this is certainly true for wheat stem rust as several new races with increased virulence have appeared over the past 20 years. The most notable new stem rust threat was identified in Uganda in 1999, known as Ug99 (race TTKSK) and has virulence to most deployed *Sr* genes including *Sr31* (Pretorius et al. 2000). Ug99 rapidly spread across East Africa to Kenya, Ethiopia, Eritrea, Egypt, Tanzania, down to South Africa, and mutated to new races. As of 2016, there were 13 variants of the Ug99 lineage spread across eastern Africa (Fetch et al. 2016) and the lineage has spread to Yemen and Iran. The detection of Ug99 spurred the development of the “Global Rust Initiative” in 2005, led by Dr. Norman Borlaug (which later became the Borlaug Global Rust Initiative [BGRI]). This initiative, along with federal government funding in both Canada and the United States, supported a massive research effort to find and characterize new sources of stem rust resistance that could be incorporated into wheat cultivars to control the Ug99 threat. In Canada, over \$14

million Canadian has been invested since 2008 in the effort to find new genes and incorporate them into the development of new wheat varieties by Agriculture & Agri-Food Canada (AAFC). Several new genes have been discovered by Fetch, Hiebert, and colleagues (Ghazvini et al. 2012; Hiebert et al. 2010, 2011) that were incorporated into Canadian wheat breeding programs beginning in 2008. This has resulted in the recent release of new Canadian wheat varieties (such as ‘AC Tenacious’) with resistance to Ug99 and to common North American races.

In addition to the Ug99 threat, other new races of *Pgt* have emerged that could harm wheat production in North America. Olivera et al. (2012) described race TRTTF (the ‘Digalu’ race) in Ethiopia with high virulence to durum wheat, which had previously been found in Yemen and Pakistan. While avirulent to gene *Sr31* (thus not a Ug99 variant), this race is virulent on many accessions of spring wheat and is virulent on genes *Sr9e* and *Sr13*, which confer stem rust resistance in most durum wheat cultivars. Fetch et al. (2012) found a similar race (RRTTF) to be virulent on 55% of Canadian spring wheat. Barnes et al. (2018) identified race RRTTF from heavily infected plots of wheat in Ecuador in 2016 that was genotypically identical to an isolate of TRTTF from Ethiopia. While RRTTF could not be windborne from Ethiopia to Ecuador, it was unknown if this was a de novo variant from existing races in South America or a long-distance exotic introduction. Subsequent to the discovery of TRTTF in Ethiopia, a different race (TKTTF) caused a severe stem rust epidemic in the Arsi/Bale region of Ethiopia in 2013 to 2014, with losses approaching 100% (Olivera et al. 2015). Race TKTTF was not genotypically related to TRTTF, but was an exotic introduction, possibly from Turkey. In 2016, another new race (TTTTF) caused moderate to severe losses in durum wheat in Sicily (<https://rusttracker.cimmyt.org/?p=7083>), which last saw epidemics of stem rust almost 60 years ago. Finally, stem rust was found in the Almunge region in Sweden in 2017, which has not seen severe stem rust since 1951 (<https://rusttracker.cimmyt.org/?p=7148>). While the Swedish rust isolate has not yet been pathotyped to race, it was suggested to have arisen from Barberry as a sexual population.

Thus, while currently in North America the threat of stem rust epidemics has been brought under control by the development and deployment of resistant wheat varieties for over 60 years, this ancient foe is not yet defeated. New races of *Pgt* are being detected worldwide, arising from both asexual mutation of existing races and from sexually reproducing populations from Barberry. Diligent surveillance to detect new races as they develop, research to identify effective sources of resistance to these new races, and breeding to incorporate a stack of *Sr* genes into new wheat cultivars must be funded and continued in this ongoing battle with the stem rust pathogen. As Johnson and Newton (1946) summarized, “the price of security from rust damage is a continuous vigilance in the form of surveys to detect any pathogenic changes in the economically important rusts and unrelenting efforts to develop cereal varieties resistant to any virulent races that may arise.”

Leaf Rust

Wheat leaf rust is a perennial production problem in Canada. Wheat cultivars grown in the early part of the 20th century were primarily susceptible to leaf rust and suffered significant yield losses in epidemic years (McCallum et al. 2016). ‘Thatcher’ was the most frequently grown wheat cultivar in Canada from the 1930s to the 1970s (McCallum and DePauw 2008). It was resistant to stem rust, but highly susceptible to leaf rust, which led to damaging epidemics of leaf rust most years when ‘Thatcher’ was the dominant cultivar (McCallum et al. 2016). Thatcher was replaced in the eastern prairies by ‘Selkirk’ from 1955 to 1967 due to its improved stem and leaf rust resistance (McCallum and DePauw 2008). During this time, however, the *P. tritricina* population rapidly evolved virulence to the resistance genes in ‘Selkirk’ (*Lr10*, *Lr14a*, and *Lr16*) (Samborski 1985). By 1968, both ‘Thatcher’ and ‘Selkirk’ were replaced by other stem rust resistant cultivars such as ‘Manitou,’ ‘Neepawa,’ and ‘Katepwa.’ These were derived from ‘Thatcher’ but also included *Lr13* for leaf rust resistance, to which the pathogen rapidly became

virulent a few years after the introduction of ‘Manitou’ (Samborski 1985). ‘AC Barrie,’ the most popular wheat cultivar from 1998 to 2005 (McCallum and DePauw 2008), was initially resistant to leaf rust, but became more susceptible over time due to the evolution of virulence on its resistance genes *Lr13* and *Lr16* (McCallum et al. 2016).

Since *P. tritricina* is highly variable and has demonstrated its ability to overcome host resistance through virulence changes, an annual virulence survey has been conducted on the Canadian *P. tritricina* population since the 1930s. It is done by collecting infected wheat leaves across Canada, isolating single pustule isolates from these pustules, and testing these isolates on a standard set of 16 single resistance gene differentials, in the susceptible ‘Thatcher’ wheat genetic background. Virulence to additional differential lines are then conducted using a subset of isolates, representing all the unique virulence phenotypes (races) found on the standard set of 16 lines (McCallum et al. 2016).

During the annual virulence surveys in Canada, 200 to 400 isolates from across the country are analyzed, and typically over 40 virulence phenotypes are found each year (McCallum et al. 2016). There is a fairly large annual change in the composition of these virulence phenotypes, though the dominant phenotypes tend to be found commonly for a few years before they are replaced by other dominant phenotypes (Table 3). The populations found in western Canada tend to be different from those found in eastern Canada, although some virulence phenotypes are found in both eastern and western Canada, and the eastern Canadian populations tend to be more diverse than those found in the west (McCallum et al. 2016). The *P. tritricina* population in Prince Edward Island was also different from that in Ontario and Quebec (McCallum et al. 2018). Therefore, regional differences are important for *P. tritricina* in Canada reflecting difference in the wheat cultivars grown, but also in the source of inoculum coming into Canada from different regions in the U.S.A.

The frequencies of virulence to each of the resistance genes tested also tends to change annually, although long-term trends can be observed such as the increase in virulence frequencies to *Lr9* and *Lr21*, and the fluctuations in the frequencies of virulence to *Lr2a*, *Lr16*, *Lr17*, and *Lr24* in Manitoba and Saskatchewan (Fig. 12). Through the virulence survey, changes over time in the *P. tritricina* population have been documented such as the increase in virulence to *Lr10*, *Lr14a*, and *Lr16* following the adoption of ‘Selkirk’ wheat in the eastern prairie region (Samborski 1985). Similarly, virulence to *Lr13* and *Lr16* increased with the increased acreage of ‘AC Barrie,’

resulting in ‘AC Barrie’ becoming a moderately susceptible cultivar from one that had been resistant prior to these changes (McCallum et al. 2016). Virulence to some genes such as *Lr16* can be difficult to quantify. Some isolates of *P. tritricina* have a very low avirulent infection type on the Thatcher-*Lr16* near isogenic wheat line, whereas others have a much higher infection type while still being classified as avirulent. Most isolates in recent years have this higher avirulent infection type, with the result that wheat lines such as Thatcher-*Lr16* and ‘AC Barrie’ sustain significant damage in the field, even though the *P. tritricina* population is classified as avirulent to *Lr16*. More recently, these virulence surveys have been useful in documenting the 2011 appearance of virulence to *Lr21* for the first time in Canada, and subsequent increase of this virulence in the pathogen population over time. Resistance gene *Lr21* is incorporated into many of the modern wheat cultivars in Canada, and therefore virulence on this gene has important implications for disease control. The regional differences noted above for virulence phenotypes are reflected in differences in the frequency of virulence between different regions in Canada. For example, virulence to *Lr18* is often found in eastern Canada but not western Canada, and virulence to *Lr21* has been confined to western Canada to date (B. McCallum, unpublished).

Currently, the portion of wheat cultivars in Canada with *Lr34* is estimated to be over 50%. Other common genes in Canadian wheat cultivars include *Lr2*, *Lr10*, *Lr13*, *Lr14a*, *Lr16*, *Lr21*, and *Lr22a* (McCallum et al. 2016). Virulence is common for these resistance genes in the Canadian *P. tritricina* population, except for *Lr22a*. Most isolates are scored as avirulent to *Lr16*, although wheat lines with *Lr16* suffer severe leaf rust infection and losses in the field, as stated previously.

Most western Canadian wheat cultivars have a high level of resistance to leaf rust, often conditioned by a pyramid of a few genes in each cultivar, which commonly includes *Lr34*. This is a major improvement in overall leaf rust resistance since the 1970s (McCallum et al. 2016). Also, since the 1990s, fungicide use on wheat in the eastern prairie region has increased substantially due to disease concerns that include leaf rust, but primarily focused on Fusarium head blight. This increased fungicide use, along with the predominance of genetically resistant cultivars, has resulted in very low losses to leaf rust annually in recent years.

Reliable linked or diagnostic markers have been developed for many of the key leaf rust resistance genes including *Lr14a* (Rasheed et al. 2016), *Lr16* (Kassa et al. 2017), *Lr21* (Neelam et al. 2013),

Table 3. Frequency (%) of predominant *Puccinia tritricina* virulence phenotypes in Canada from 2000 to 2018

Virulence phenotype ^a	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
MBDS	54.1	18.5	30.2	13.4	10.0	4	1.4	1.3	0.5	0.3	0.0	1.4	6.4	12.5	5.0	18.1	14.1	6.9	1.3
MBTN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	2.8	4.2	4.3	9.1	5.0	2.2	0.8	3.4	0.4
MFDS	0.0	0.0	0.0	0.0	0.0	0.2	5.1	0.8	5.7	1.0	0.5	0.7	0.0	0.8	0.0	0.9	0.0	0.0	0.0
MFPS	0.0	0.0	0.0	0.0	0.0	5.7	4.8	3.9	4.9	4.5	3.5	6.0	3.0	6.3	4.0	4.8	3.5	2.3	0.0
MLDS	0.0	0.0	0.7	0.0	0.0	0.0	1.4	8.4	18.9	20.6	26.1	7.7	2.6	7.5	3.0	4.8	1.2	0.0	0.0
MLPS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	8.0	8.4	2.4	1.9	1.3
MMPS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.9	4.0	4.8	5.1	1.5	1.3
MNPS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	15.7	37.2	29.4
MPPS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	7.1	5.0	2.6
TBBG	0.0	0.0	0.0	0.0	14.8	10.2	1.7	0.0	0.2	0.0	4.5	7.7	19.2	11.3	13.0	5.7	0.4	15.3	28.5
TBBJ	0.6	1.7	9.5	47.4	41.2	7.1	3.4	0.0	0.2	0.3	1.3	0.7	0.9	0.8	0.0	0.4	0.0	0.4	3.5
TDBG	0.0	0.0	0.0	0.0	0.3	44.5	50.1	54.3	22.9	15.8	11.8	10.5	2.6	2.0	17.0	0.0	0.4	0.0	0.0
TDBJ	0.3	0.0	0.0	0.0	0.6	8.6	16.7	16.5	23.1	28.1	22.8	12.5	6.4	7.0	3.0	0.4	0.8	0.4	0.0
TGBJ	21.6	39.5	22.0	3.1	3.3	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
THBJ	5.7	14.6	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TNBJ	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	1.0	2.1	14.5	10.2	7.0	15.0	3.9	2.7	4.8
TNBJ	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.8	0.4	0.9	0.4	2.0	4.4	2.0	1.9	0
Others	17.7	25.6	36.2	36.1	29.7	19.0	15.0	14.7	22.6	29.4	25.7	47.9	46.0	41.3	36.0	44.8	58.7	29.9	28.2
Isolates	366	362	295	97	330	420	353	381	407	310	399	284	234	265	100	227	255	261	228

^a Data sources summarized in McCallum et al. (2018) and B. McCallum (unpublished). Samples from Manitoba and Saskatchewan make up the majority of the samples in each of the years.

Lr22a (Thind et al. 2017), and *Lr34* (Lagudah et al. 2009). These have been used to identify these resistance genes in cultivars with complex genetic resistance but have also been used to stack resistance genes together in new cultivars (Toth et al. 2019). Together with phenotypic selection for leaf rust resistance, these selectable markers have helped to improve the leaf rust resistance in Canadian wheat.

Most Canadian wheat cultivars have a combination of leaf rust resistance genes, which makes it more difficult for a single change in virulence in the pathogen to overcome host resistance. Some cultivars such as ‘McKenzie’ that have *Lr21* (McCallum and Seto-Goh 2010) have become more susceptible with virulence appearing on *Lr21*, though it is not completely susceptible because of additional resistance genes, whereas cultivars with only *Lr21* have become susceptible. Gene combinations involving *Lr34* are particularly effective because of the way that *Lr34* interacts in an additive manner with other resistance genes (German and Kolmer 1992).

Future efforts to control wheat leaf rust will focus on developing these pyramids of effective resistance genes, particularly including *Lr34*. Other methods to control leaf rust such as endogenous silencing of *P. tritici* pathogenicity genes have been demonstrated in the lab (Panwar et al. 2018). This could lead to novel control strategies in the future, which target the pathogen in different ways than the current resistance genes.

Looking Forward: Scientific Advances and Research Priorities

Over the last many decades, we have learned much about the three rust pathogens, disease epidemiology, pathogens’ population biology, migration routes of the pathogens, and disease management strategies (reviewed in Wan et al. 2017). Although disease epidemiology of wheat stripe rust is well-studied on the main host (wheat), it is not well-understood on the alternate hosts, nor is their role in introducing variations in the natural populations, partially because the alternate host was discovered fairly recently. In addition to studying pathogens, over 50 genes for each of the rust pathogens have been mapped in wheat or wheat relatives, and quite a few are cloned.

The advances in DNA sequencing technologies have helped wheat researchers to disentangle many genomic features of the pathogens and their wheat host. The genome-guided approaches have a great potential to correlate DNA variation in genomes with the host phenotype (R-genes) or pathogen virulence phenotype (*Avr*-genes) and eventually identify/isolate the causative alleles. With implementation and aid of modern sequencing technologies, now the high-quality annotated reference genomes of wheat and all three rust pathogens are available (Duplessis et al. 2011; IWGSC 2018; Kiran et al. 2016; Schwessinger et al. 2018). Genome-sequencing and annotation of rust pathogens have allowed researchers to compare the gene structures and other genome characteristics. One area of interest among rust researchers is to understand the evolution of virulence in pathogens and effector biology. With availability of high-quality reference genomes and inexpensive sequencing technologies, researchers are now able to clone genes at a much faster pace than in the past (Betgenhaeuser and Krattinger 2019). Using modern advances in such techniques, researchers are now headed toward identification, characterizing, cloning, and introgressing of novel rust resistance genes in cultivars and studying ways to build durable resistance in modern wheat cultivars. On the pathogen side, researchers are using comparative genomics approaches to link effectors with the virulence phenotypes, study pan-genome variation in rust pathogens, and eventually understand why rust pathogens are so successful.

Take-Home Message

Cereal rust diseases have caused numerous epidemics resulting in large yield losses worldwide, due to their ability to rapidly infect wheat and produce wind-blown spores that can migrate to reinfest neighboring fields. In Canada, several rust epidemics occurred in the first half of the 20th century but have greatly diminished due to the development of resistant varieties containing stacks of several rust resistance genes. There have been no epidemic losses due to rust disease in Canada for several decades. However, cereal rust pathogens have shown great ability to mutate and generate new races with increased virulence. It is critical to monitor worldwide virulence dynamics in all three cereal rust pathogens, so that early detection of new races with virulence on key

Fig. 12. Frequency of virulence (%) from 2000–2018 in the Manitoba and Saskatchewan population of *P. tritici* to near-isogenic lines containing *Lr2a*, *Lr9*, *Lr16*, *Lr24*, *Lr17*, or *Lr21*. Data sources summarized in McCallum et al. (2018) and B. McCallum (unpublished).

resistance genes is achieved. In concert with this work, discovery and characterization of new rust resistance genes will empower plant breeders with new, effective rust genes that can be combined to develop wheat cultivars with stacks of genes effective against new virulence races as they arise. While we have managed to achieve a temporary advantage in this battle against the cereal rusts, the war is not over, and the shifty rust enemy has the ability to mutate and attack our wheat if we do not remain vigilant.

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Gurcharn S. Brar

Gurcharn Singh Brar is a research officer in wheat pathology and wheat genetics & breeding research groups in the Crop Development Centre and Department of Plant Science at the University of Saskatchewan, Canada. Gurcharn is starting his new role as an assistant professor (plant pathology and host-pathogen interaction) at the University of British Columbia (UBC), Vancouver, in January 2020. Gurcharn received a Bachelor of Science in agriculture (honors in plant protection) from Punjab Agricultural University, India, in 2012. Then, he moved to the University of Saskatchewan to pursue his M.Sc. (March 2015) and Ph.D. (March 2019) with Drs. Randy Kutcher and Pierre Hucl. Gurcharn's graduate training focused on the study of plant pathogens, genetics/genomics of pathogen populations, genetics of host-pathogen interactions, resistance breeding, and plant imaging obtained through the University of Saskatchewan, Agriculture and Agri-Food Canada (AAFC), National Research Council of Canada, the Canadian Light Source (CLS), and the International Maize and Wheat Improvement Centre (CIM-MYT). Currently, Gurcharn is working in the areas of gene cloning and functional pathogenomics with collaborators from across Canada, the U.K., and Australia. Gurcharn is very passionate about wheat and wheat rust pathogens. He often describes wheat as the "king of cereals" and has described his career as a "long-term relationship" with wheat and stripe rust.

Thomas Fetch

Thomas Fetch earned his Ph.D. in plant pathology from North Dakota State University in 1996. He joined AAFC in May 2000 as a stem rust pathologist at the Cereal Research Centre in Winnipeg. He has authored or co-authored over 100 publications on stem rust resistance genes, pathogen virulence, and development of new barley, oat, and wheat varieties. Dr. Fetch is recognized as a world authority on virulence in populations of *Puccinia graminis* (stem rust of wheat, barley, and oat), and stem rust resistance genetics in wheat, barley, and oat. He has identified several new stem rust resistance genes and their genetics of inheritance, and developed new wheat, oat, and barley cultivars with stem rust resistance. His ongoing projects include identifying Barberry species in South America and their associated rust species, tracking the movement and virulence changes in Ug99 stem rust, characterizing the virulence spectrum in Canadian populations of *Puccinia graminis*, and barley, oat, and wheat cultivar development (stem rust resistance component) with AAFC. He is a collaborator with the Durable Rust Resistant Wheat project funded by Bill & Melinda Gates Foundation and U.K. International Development Agency, secretary of the Canadian Phytopathological Society (CPS), associate editor-in-chief and senior editor (Genetics and Resistance section) of the Canadian Journal of Plant Pathology, and is a member of the American Phytopathological Society (APS) and the Disease Evaluation Teams of Prairie Grain Development Committee.

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