

REVIEW

Progress in breeding for resistance to Ug99 and other races of the stem rust fungus in CIMMYT wheat germplasm

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Abstract Races belonging to the Ug99 (TTKSK) lineage of the wheat stem rust fungus, carrying complex virulence combinations, and their migration to countries in Africa, Middle East and Asia continue to pose a significant threat to global wheat production. The rapid spread of additional races, e.g., TKTF or the Digalu lineage, in several countries causing localized epidemics reminds us of the vulnerability of wheat germplasm to stem rust disease, a formidable foe referenced as early as biblical times. A global rust monitoring system reflecting increased surveillance efforts has identified 13 races within the Ug99 lineage in 13 countries and unrelated lineages are emerging, spreading and posing serious threats to wheat production. Race TKTF has caused localized epidemics in Ethiopia and its variants have been recently implicated in stem rust outbreaks in Europe. Concerted research efforts have resulted in the identification of several new resistance genes and gene combinations for use in breeding. Combining multiple adult plant resistance (APR) genes in high-yielding backgrounds and discovery of new quantitative trait loci conferring stem rust resistance has progressed in the recent years, enhancing the durability of resistance. Effective gene stewardship and new generation breeding materials and cultivars that combine multiple race-specific or minor to intermediate effect APR genes, complemented by active surveillance and monitoring, have helped to limit major epidemics and increase grain yield potential in key target environments.

Keywords adult plant resistance, black rust, race-specific resistance, *Triticum aestivum*

1 Stem rust: “a formidable foe”

Wheat is one of the world’s most important staple cereal crops and a major constituent of daily calorie and protein intake in humans^[1]. On a global scale, wheat is grown on over 240 Mha worldwide, which is a greater area than any other crop, and annual production is close to 750 Mt. Nearly 200 wheat diseases and pests have been documented, 50 of which are considered sufficiently important to cause economic losses^[2]. Potential grain yield losses due to diseases have been estimated at 18% and actual losses with current disease control practices stand at 13%^[3].

Stem rust or black rust caused by *Puccinia graminis* f. sp. *tritici* (Pgt) is a devastating disease of bread wheat (*Triticum aestivum*) and durum wheat (*T. durum*) in the major wheat-growing regions of the world. Wheat, barley (*Hordeum vulgare*) and barberry (*Berberis vulgaris*) have their origins in the Fertile Crescent, suggesting that the complex relationship of these species in the life cycle of stem rust has a very ancient history. Spores of stem rust discovered in archeological sites in Israel have been dated to 1300 BC^[4]. The disease dates back to Biblical times, which describes epidemics of cereal rusts and smuts that were inflicted on the Israelites as divine punishment^[5]. The Roman festival, Robigalia, as described by Numa Pompilius was held as early as 715–672 BCE to propitiate rust gods by prayer and sacrifice. Aristotle (384–322 BC) and Theophrastus attributed cereal rust epidemics to warm and wet weather conditions^[5] and stem rust usually occurs in regions where warm and moist conditions prevail. Infection appears as large brick-red pustules carrying urediniospores on most aerial parts of the plant including stems, leaves, leaf sheath, glumes and awns of susceptible plants^[6]. The disease can cause great damage to susceptible wheat cultivars over wide geographical regions and early infections can quickly escalate into devastating, widespread epidemics in a short interval of time owing to

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favorable weather conditions, which can cause a heavy inoculum build up to be carried on wind currents, causing large-scale deployment to susceptible varieties. The severe infection of stems interrupts the translocation of nutrients to developing heads, resulting in poor grain fill, shriveled grain or no grain production. Heavy stem rust infection can turn stems brittle and cause lodging with a consequent total loss of grain^[7]. Well-documented examples of stem rust epidemics occurred in Europe in 1932 and 1951, with yield losses of 5%–20% in Eastern and Central Europe and 9%–33% in Scandinavia^[8]. Sporadic stem rust epidemics were reported mainly for warmer areas through the mid-20th century, with occasionally severe yield losses^[9,10]. Losses from stem rust have occurred in wheat in southern and north-western India, especially in years of unusually warm weather^[11]. Severe epidemics were reported for wheat crops in northern China and Inner Mongolia in the early 1950s, under high temperatures and frequent rains that favored infection^[12]. Widespread epidemics have also been observed in Australia^[13] and Africa^[14]. In North America, stem rust was limited to the Northern Great Plains, where more than half the yield of the 1935 spring wheat crop in North Dakota and Minnesota was lost to epidemics^[15]. Although the rust epidemics in North America have been curtailed since 1974, the pathogen still poses a great threat under the current climate change scenario.

When the role of barberry as an alternate host for stem rust became clear, eradication programs for common barberry (*Berberis vulgaris*) in Europe and North America were successfully conducted in the early 1900s. To combat stem rust and reduce the frequency of epidemics, breeding programs in Australia, the USA, at CIMMYT (International Maize and Wheat Improvement Center) and in other major wheat production regions developed and deployed resistant cultivars that for decades provided effective genetic control. With stem rust largely under control in several wheat-growing regions of the world due to cultivation of resistant cultivars, prediction models estimate that the annual global wheat grain losses would most likely be over 6.2 Mt in the absence of these resistant cultivars and if favorable conditions caused epidemics^[16].

Stem rust has reemerged as a major threat in recent years with the detection of a unique race called “Ug99”, identified in Uganda in 1998^[17]. Designated TTKSK according to the North American stem rust nomenclature system^[18], Ug99 is virulent to the important resistance genes *Sr31* and *Sr38*, as well as several others present in cultivars of diverse origin. In large-scale field testing conducted in Kenya under natural stem rust infection, more than 80% of wheat germplasm from worldwide sources was either susceptible or lacked adequate resistance to Ug99^[18,19]. Subsequent to the identification of the Ug99 strain TTKSK, new variants of that lineage have appeared and overcome other resistance genes, including TTKST

with virulence to resistance gene *Sr24* identified in 2006^[20], TTKSK with virulence to *Sr36* identified in 2007^[21], and most recently races TTKTK and TTKTT with virulence to *SrTmp* in 2014^[22,23].

2 Status of Ug99 race group

In response to the resurgence of stem rust in eastern Africa and the threat of Ug99, in 2005 the international wheat research and development community, with support from key funding agencies, established the Global Rust Initiative—later renamed the Borlaug Global Rust Initiative—to significantly reduce the vulnerability of wheat crops worldwide to three rusts diseases^[23]. Increased pathogen-monitoring activities as part of this initiative greatly improved tracking of the occurrence and spread of new and virulent variants in the Ug99 race group, as well as identification of other new stem rust races that are able to break down the resistance of widely grown wheat cultivars and cause severe local epidemics.

Global surveillance and monitoring of wheat rusts has been undertaken in a coordinated manner for over a decade, and it has been observed that the pathogen populations are evolving rapidly and wheat rusts are moving between regions/countries with increasing frequency. With such dynamic pathosystems and emerging threats to wheat production, sustained global surveillance and monitoring has become increasingly important. Through the dedicated efforts of global partners, the evolution and spread of important *Pgt* races have been successfully tracked^[24]. A brief summary of the current status of key *Pgt* races is given here.

Singh et al.^[25] provided a recent and comprehensive overview of the status of the Ug99 race group, describing the rapid evolution of new races and its geographical expansion, with eight races reported in 13 countries. New races have continued to emerge and, by 2019, 13 had been identified (Table 1), all within the same 13 countries. Similarly, in 2014, five new variants of Ug99 were detected in Kenya^[23,26,27]. Two of these, TTKTK and TTKTT, were highly significant because they had acquired virulence to stem rust gene *SrTmp*, a key resistance gene in popular eastern African bread wheat cultivars such as cv. Robin in Kenya and cv. Digalu in Ethiopia. Race TTKTK was also detected in Egypt, Rwanda and Uganda in 2014^[26], indicating its rapid and possibly widespread dispersal. No new Ug99 variants have been identified since 2015. However, Terefe et al.^[28] reported the first occurrence of Ug99 race PTKSK in South Africa in 2017, that was previously identified in Ethiopia, Kenya and Yemen. It is not known if this represents a new incursion into southern Africa or if it is a locally occurring mutation. The current known distribution of the Ug99 race group is shown in Fig. 1.

Table 1 *Puccinia graminis tritici* races belonging to Ug99 lineage identified until 2019 in various countries with avirulence/virulence status on discriminating resistance genes (updated from Singh et al.^[25])

Race ¹	Common alias	Resistance genes and avirulence (A) or virulence (V) status						Confirmed countries (year detected)
		<i>Sr31</i>	<i>Sr21</i>	<i>Sr24</i>	<i>Sr36</i>	<i>Sr9h</i>	<i>SrTmp</i>	
TTKSK	Ug99	V	V	A	A	A	A	Uganda (1998), Kenya (2001), Ethiopia (2003), Sudan (2006), Yemen (2006), Iran (2007), Tanzania (2009), Eritrea (2012), Rwanda (2014), Egypt (2014)
TTKSF		A	V	A	A	A	A	South Africa (2000), Zimbabwe (2009), Uganda (2012)
TTKST	Ug99 + <i>Sr24</i>	V	V	V	A	A	A	Kenya (2006), Tanzania (2009), Eritrea (2010), Uganda (2012)
TTTSK	Ug99 + <i>Sr36</i>	V	V	A	V	A	A	Kenya (2006), Tanzania (2009), Ethiopia (2010), Uganda (2012), Rwanda (2014), Egypt (2014)
TTKSP		A	V	V	A	A	A	South Africa (2007)
PTKSK		V	A	A	A	A	A	Kenya (2009), Ethiopia (2007), Yemen (2009), South Africa (2017)
PTKST		V	A	V	A	A	A	Ethiopia (2007), Kenya (2008), South Africa (2009), Eritrea (2010), Mozambique (2010), Zimbabwe (2010)
TTKSF+		A	V	A	A	V	A	South Africa (2010), Zimbabwe (2010)
TTKTT	Ug99 + <i>Sr24</i> + <i>SrTmp</i>	V	V	V	A	A	V	Kenya (2014)
TTKTK	Ug99 + <i>SrTmp</i>	V	V	A	A	A	V	Kenya (2014), Egypt (2014), Eritrea (2014), Rwanda (2014), Uganda (2014)
TTHSK		V	V	A	A	A	A	Kenya (2014)
PTKTK		V	A	A	A	A	A	Kenya (2014)
TTHST		V	V	V	A	A	A	Kenya (2013)

Note: ¹ Race designation follows the North American nomenclature system described by Jin et al.^[20]. Race TTKSF+ is given a temporary name as it exceeds the current North American 20 differential gene set.

3 Stem rust epidemics caused by races unrelated to Ug99 lineage

While the Ug99 race group continues to evolve in Africa, global monitoring has shown that new races genetically unrelated to Ug99 are also emerging, spreading and posing serious threats to wheat production. Genotyping of these isolates has detected two new lineages, or clades, that have shown rapid geographical expansion and causing damaging outbreaks of stem rust at scale. Clade IV, typified by race TKTTF and variants, is now detected across a wide geographical range^[25]. Race TKTTF caused damaging, localized epidemics in Ethiopia in 2013 and 2014, owing to its virulence on *SrTmp* and the susceptibility of the widely grown cv. Digalu^[29]. Evidence indicates that TKTTF was likely an incursion into eastern Africa from the Middle East^[30]. In 2014, Clade IV races were also responsible for unusual outbreaks of stem rust in Germany^[30] and the re-appearance of stem rust in the

UK^[31]. Stem rust outbreaks in Sicily, Italy, in 2016^[32] were caused by another lineage, Clade III, typified by race TTRTF. First detected in Georgia in 2014, TTRTF and its variants are spreading rapidly, being reported in Egypt and Eritrea and spreading in Ethiopia and Kenya. The Clade III race RRTTF was also recently detected in Ecuador^[33]. Races in Clades IV and III now predominate over the Ug99 race group (Clade I) in eastern Africa.

Another significant development is the recent detection of several populations of stem rust fungus with very strong signals of recombination through the completion of the sexual part of the life cycle. In northern Kazakhstan and western Siberia, large-scale stem rust epidemics recorded since 2015, have affected millions of hectares of wheat^[34]. Sampling in these regions has revealed high race diversity, with hundreds of races identified. Similar high race diversity was reported from a localized stem rust outbreak in Sweden in 2017^[35] and Georgia (USDA Cereals Disease Laboratory, unpublished data). In these cases,

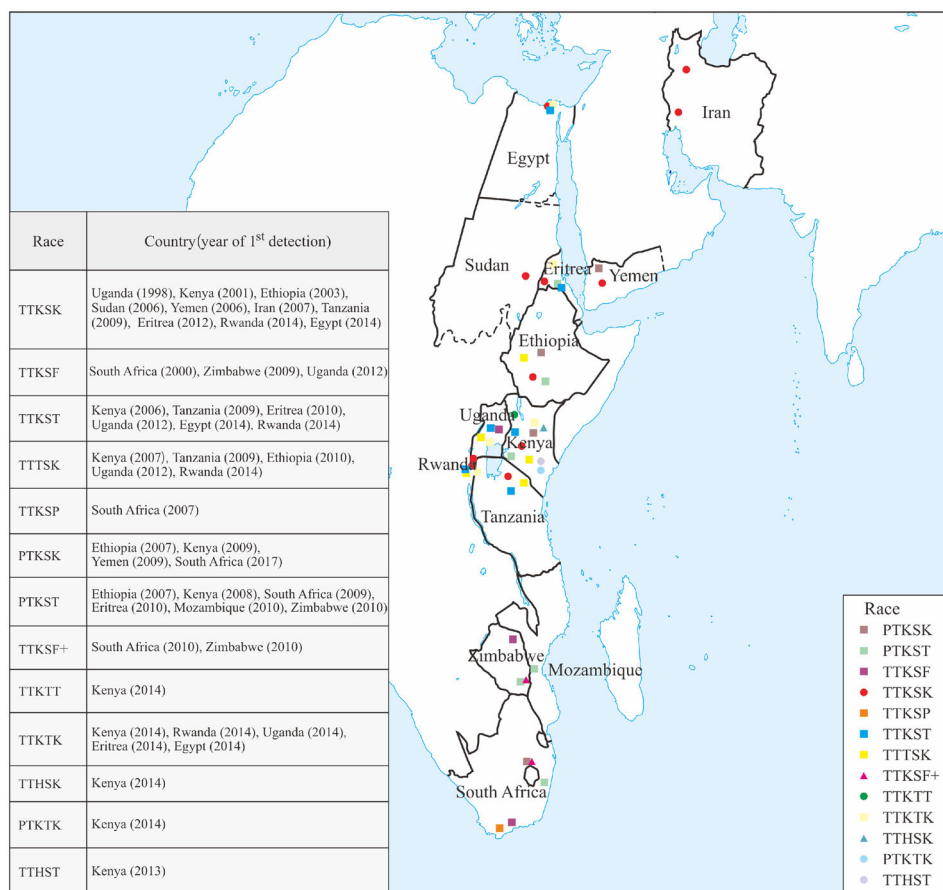


Fig. 1 Detection and distribution of *Puccinia graminis tritici* races belonging to Ug99 race group in 2019. Updated from Singh et al.^[25]. (审图号: GS (2020) 7206号)

Berberis spp. have been associated with the stem rust outbreaks and likely contributed to the observed race diversity.

4 Phenotyping platforms facilitating screening and breeding for stem rust resistance

A flagship objective of the Durable Rust Resistance in Wheat and Delivering Genetic Gains in Wheat (DGGW) projects during the last decade was to establish operational phenotyping platforms in Kenya and Ethiopia to screen and evaluate wheat accessions from all over the world at key hot-spot sites wherein maximum diversity of the pathogen exists. Testing was to be conducted at a quarantine facility and to facilitate breeding to identify and develop new resistant lines. Effective partnership between CIMMYT, Kenya Agriculture Livestock Research Organization and Ethiopian Institute of Agriculture Research under the DGGW project have had a crucial role in evaluating international wheat materials and identified new sources of resistance in breeding and pre-

breeding populations. This arrangement also supported Mexico-Kenya shuttle breeding by CIMMYT, pathogen surveys and surveillance, varietal releases in Kenya and other countries, and mapping of new sources of resistance and genomic selection studies.

Over 650000 wheat and barley accessions that include commercial cultivars, breeding materials, genetic resources and mapping populations from as many as 25 countries have been evaluated at Njoro, Kenya (Fig. 2) and over 100000 durum wheat accessions at Debre Zeit, Ethiopia. Over the decade of screening operations in Kenya and Ethiopia there has been a clear trend of increased resistance in both CIMMYT and national program breeding materials from wheat-growing countries with about 10%–20% entries showing promising levels of resistance and another 20% intermediate levels of resistance on average for all countries, compared to large proportion (as high as 90%) of susceptible materials when screening began in 2008 (unpublished data). Over 100 resistant or moderately resistant wheat cultivars have been released in different wheat-growing regions, clearly demonstrating the progress made in breeding for stem rust resistance globally.

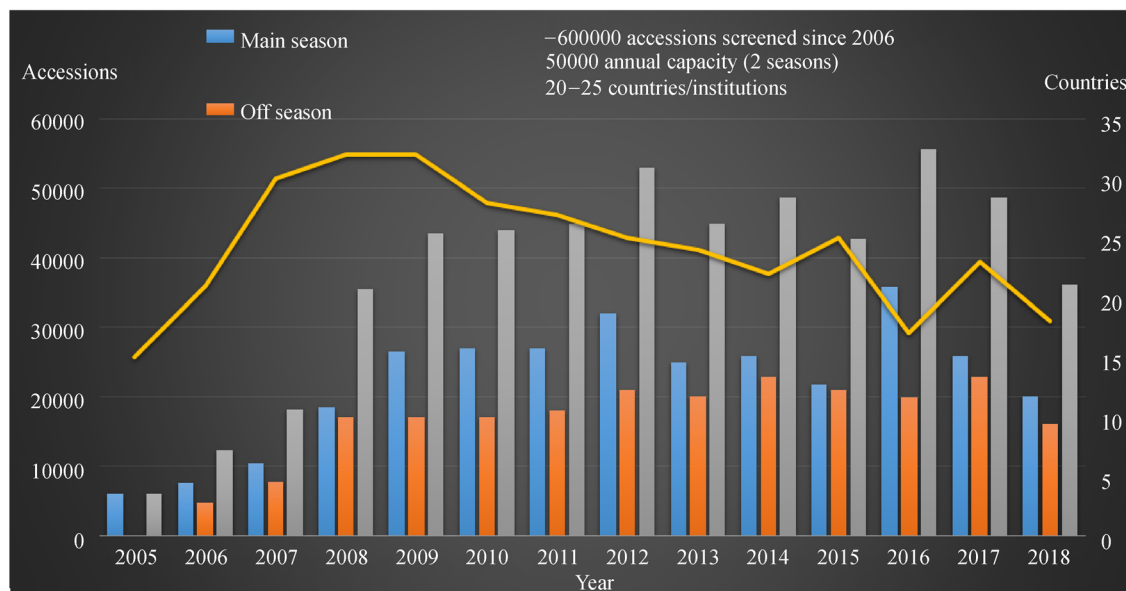


Fig. 2 Wheat accessions phenotyped during 2005–2018 for Ug99 resistance at Njoro (Kenya) and participating countries, in partnership with Kenya Agriculture Livestock Research Organization, Kenya

5 Resistance in wheat germplasm to current races

5.1 Race-specific resistance genes

Resistance to diseases can be broadly classified as race specific and race-nonspecific^[36]. Race-specific genes (R-genes) have been traditionally preferred by plant breeders for their dominant, major-effect resistant phenotypes, which facilitated easy selection and deployment in breeding programs^[37]. However, it has long been noted that the resistance of R-genes, particularly when deployed singly, breaks down quickly, in what has been often referred to as boom-bust cycles^[38] and the use of one or more widely deployed R-genes favors the selection of new pathogen races with virulence to one or more widely deployed R-genes. The unique and broad virulence spectrum of the Ug99 race group has rendered not only several important R-genes ineffective but also several important wheat cultivars and breeding materials all over the world^[39–41].

Even though some of the race-specific genes confer resistance to the current races, they have limited use in breeding owing to negative linkage drag, unadapted backgrounds, and their secondary and tertiary gene pool origin necessitating considerable research efforts for utilization through breeding. About 20% of the CIMMYT current advanced breeding materials carry effective R-genes. *Sr13*, *Sr22*, *Sr25*, *Sr26* and markers are routinely used to test for stem rust genes. *Sr13*, *Sr22*, *Sr23*, *Sr25*, *Sr26*, *Sr32*, *Sr33*, *Sr35*, *Sr38*, *Sr42*, *Sr47*, *Sr50*^[42–54] and temporarily designated genes *SrHuw234*, *SrND643*,

SrNing and *SrYanac*^[55,56] (Table 2), along with multiple adult plant resistance (APR) genes including *Sr2* in the background can be used in the breeders tool box for pyramiding using marker assisted selection. However, efficient gene stewardship measures need to be adopted to limit the occurrence of boom-bust cycles. Even though the wheat genome is large and complex, significant progress has been made in cloning six Ug99 resistance genes, including *Sr13*, *Sr22*, *Sr33*, *Sr45*, *Sr35* and *Sr50*^[57–61]. More resistance genes are necessary to diversify the combinations of resistance genes deployed as gene pyramids, or in transgenic cassettes, to provide durable resistance^[25].

5.2 Race-nonspecific APR

Race-nonspecific APR is effective against multiple races of a pathogen species and/or effective against broad range of pathogens. Van der Plank^[62] provided the theoretical basis of the concepts of resistance, which was widely used for breeding for stem rust resistance by Borlaug^[63], for leaf rust resistance by Caldwell^[64] and for yellow rust resistance by Johnson^[65]. APR is generally quantitative, exhibiting partial or incomplete resistance typically triggered at later stages of development, so is therefore considered to be APR. These genes usually exhibit slower disease progress through an increased latency period, reduced infection points and lower spore production. The phenotypic effect of such genes is relatively minor to moderate, however, additive effects of multiple APR genes (4–5) in combinations can result in very high levels of resistance^[66,67]. In contrast to most R-genes, some APR

Table 2 Molecular markers linked to stem rust resistance genes conferring seedling resistance and widely used in CIMMYT breeding program

Gene	Reported linked marker	Marker type	Reference stock	Reference
<i>Sr13</i>	<i>barc104, dupw167, CD926040, BE471213</i>	SSR	Kofa, Kronos	[42]
<i>Sr22</i>	<i>wmc633, cfa2123</i>	SSR	Sr22Tb, Steinwedel	[43]
<i>Sr23</i>	<i>Xgwm210</i>	SSR	AC Domain	[44]
<i>Sr25</i>	<i>wMAS000032, wmc221</i>	SSR	Agatha, Misr#1	[45]
<i>Sr26</i>	<i>Sr26#43, BE518379</i>	STS	WA1	[46]
<i>Sr32</i>	<i>csSr32#1, csSr32#2</i>	STS	Angas, Aroona, Westonia	[47]
<i>Sr33</i>	<i>barc152, cfd15, BE405778, BE499711</i>	SSR	RL5288	[48,49]
<i>Sr35</i>	<i>cfa2170, cfa2076, wmc169, wmc559</i>	SSR	G2919	[50]
<i>Sr38</i>	<i>CIMwMAS0004, Ventriup/LN2</i>	SNP, STS	VPM1	[51]
<i>Sr42</i>	<i>barc183, FSD_RSA</i>	SSR	Norin 40	[52]
<i>Sr47</i>	<i>Xrwgs38</i>	SSR	DAS15	[53]
<i>Sr50</i>	<i>Sr50-5p-F3/R2</i>	SSR	Gabo1BL.1RS and Gabo1DL.1RS-DR.A	[54]
<i>Sr-6DS</i>	<i>gpw5182, cfd49</i>	SSR	Niini, Coni, Blouk	[55]
<i>SrND643</i>	<i>Xgwm350, Xwmc219</i>	SSR	ND643	[56]
<i>SrHuw234</i>	<i>wmc332</i>	SSR	Huwa	[53]
<i>SrYanac</i>	<i>barc200</i>	SSR	Yaye	[53]

genes have proven to be highly durable, such as stem rust resistance gene *Sr2*, transferred to cvs Hope and H44-24a from Yaroslav emmer wheat by McFadden in the early 1920s, which has provided resistance to stem rust for over 100 years.

This approach of breeding for slow development of the three rusts has been integral to CIMMYT's bread wheat improvement program for over 40 years, with a significant impact, averting major epidemics over the last few decades^[68]. Significant progress has also been made in understanding the genetic basis and the mechanisms of such resistance and is being routinely applied in breeding at CIMMYT. Combinations of *Sr2* with other unknown genes, commonly known as the *Sr2*-complex, have provided a basis of durable resistance to stem rust in germplasm from Australia, Canada, Mexico and the USA^[69,70]. *Sr2* is linked to a morphological marker called pseudo-black chaff phenotype and is known to confer modest levels of APR under high disease pressure^[67-71], including infection by strains of the Ug99 race group^[25,41,72]. Three pleiotropic APR genes in addition

to *Sr2* (= *Yr30*) locus, viz. *Sr55* (= *Lr67/Yr46/Pm46*), *Sr57* (= *Lr34/Yr18/Pm38/Sb1/Bdv1*) and *Sr58* (= *Lr46/Yr29/Pm39*), conferring multi-pathogen resistance^[73-76] were identified in CIMMYT wheat germplasm and used in marker assisted selection (Table 3)^[77-80]. These genes in combination with other APR genes confer enhanced APR to the three rusts^[81]. Several mapping studies using CIMMYT semidwarf wheat cultivars showing high levels of resistance to the Ug99 race group indicated the presence of three to five quantitative trait loci conferring APR^[82-84]. Notably, all studies indicated that *Sr2* was the most important APR gene conditioning resistance to stem rust.

Recent cloning of pleiotropic APR genes, *Lr34* and *Lr67*, provided valuable insights into the mechanisms of race-nonspecific resistance. The two genes were found to respectively encode an ATP binding cassette transporter and a hexose transporter^[85,86]. In addition to broad-spectrum multi-pathogen resistance, both genes express a leaf-tip necrosis phenotype, which is also observed in genotypes that carry the currently uncloned gene, *Lr46*. These phenotypic similarities suggest a common

Table 3 Molecular markers for pleiotropic adult plant resistance (APR) genes used in CIMMYT wheat breeding program

Gene	Reported linked marker	Marker type	Reference stock	Reference
<i>Lr34/Yr18/Pm38/Sr57</i>	<i>wMAS000003, wMAS000004</i>	STS, SNP	Parula, Thatcher, Glenlea, Jupateco R, Opata, Bezostaya, Chinese Spring.	[75]
<i>Lr46/Yr29/Pm39/Sr58</i>	<i>csLV46, csLV46G22</i>	CAPS	Pavon 76, Parula,	[76]
<i>Lr67/Yr46/Pm46/Sr55</i>	<i>csSNP856</i>	SNP	RL6077	[77]
<i>Sr2/Yr30</i>	<i>csSr2, wMAS000005</i>	CAPS	Pavon76	[78]

mechanism and their additive nature in interaction with other APR genes supports the value of their use in combinations to enhance the durability of resistance.

Despite significant progress in characterizing new sources of APR to stem rust over the last decade, mapping of APR genes can be tedious and challenging owing to their minor effects and their significant interaction with the environment. However, the additive nature of the gene interactions has enabled breeders at CIMMYT to select transgressive progenies that combine multiple minor genes, resulting in enhanced levels of resistance. High levels of APR to the Ug99 race group identified in some semi-dwarf lines was largely due to the selection environments at the phenotyping platforms in Kenya and Ethiopia, and this has allowed targeted breeding effort to build such genetically complex resistance within CIMMYT germplasm^[27,40,72].

6 Breeding for stem rust resistance in CIMMYT's international spring wheat germplasm

CIMMYT has been the largest provider of improved germplasm for most wheat producing countries. The germplasm is distributed in targeted yield trials, screening nurseries and trait-based nurseries, providing a rich source of diversity for various traits of interest to breeding programs. Selected lines from these trials and nurseries are either released directly as cultivars or used in breeding by several national breeding programs in Africa, Asia, Latin America, the Middle East and South Europe. The shuttle-breeding approach developed by Borlaug in the 1940s, originally with the idea of advancing two generations per year in two contrasting locations, shortened the breeding cycle by half. Furthermore by advancing segregating populations and other breeding materials twice each year at two distinct field sites, Ciudad Obregon and Toluca, in Mexico, the germplasm developed from CIMMYT became broadly adapted to various diverse wheat-growing regions and such an effort has continued to result in successful cultivars that are grown over large areas in many countries^[87,88].

McFadden^[89] developed wheat cv. Hope, derived from a cross between the North American cv. Marquis and stem rust resistant tetraploid wheat cv. Yaroslav. A sister line derived from cv. Hope, H44-24a, became an important source of stem rust resistance for many wheat breeding programs because it has better agronomic characteristics than Hope. Further genetic characterization identified three resistance genes, *Sr7b* from Marquis, and *Sr9b* and *Sr17* from Yaroslav^[90–92]. Breeding for durable stem rust resistance in CIMMYT wheat breeding program started in the late 1940s when cv. Newthatch was introduced from North America that combined stem rust resistance from cvs Hope and Thatcher derived from tetraploid parents, emmer

cv. Yaroslav and durum cv. Iumillo, respectively^[93]. Although several race-specific genes have been found in Hope and Thatcher, the most effective and durable component of the resistance in these two cultivars has been their APR.

Cv. Hope and its derivative cv. Chris formed the foundation of the high-yielding, semi-dwarf, stem rust resistant wheat cultivars in CIMMYT that were extensively used by Borlaug and led to the “Green Revolution” in the 1970s. Importantly the two Green Revolution cvs Sonalika and Siete Cerros, also possess adequate levels of resistance to the Ug99 race group in Kenya. The first stem rust resistant tall cultivar released in Mexico in the 1950s, cv. Yaqui 50, and other *Sr2*-carrying semi-dwarf cultivars largely controlled the stem rust problem in Mexico. Several other resistance genes, e.g., *Sr11*, *Sr24*, *Sr31*, *Sr36* and *Sr38*, were widely used in various breeding programs to control stem rust in the early 1980s. However, gene *Sr31* (1BL-1RS translocation) became widely used in many breeding programs including CIMMYT, which almost made stem rust non-existent for over 30 years until the detection of race Ug99 in Uganda. Another rust management strategy has been to rapidly replace susceptible cultivars with available resistant cultivars and continue breeding to incorporate diverse resistance genes and APR into high-yielding, adapted cultivars and new germplasm. Finally, a sustainable long-term control strategy is to identify, develop and deploy cultivars with high to adequate levels of durable APR to limit or delay the evolution and selection of new virulence.

Testing of wheat lines from Australia, CIMMYT and the USA at the phenotyping facility in Njoro, Kenya in 2005–2006 identified a group of materials that conferred high levels of resistance to Ug99 due to the presence of resistance gene *Sr24* located on a *Thinopyrum elongatum* translocation. The resistant Kenyan cv. KS Mwamba, released in 2001 and known to carry *Sr24*, was widely adopted by farmers, but *Sr24* succumbed to stem rust race TTKST, initially detected in low frequency in 2006 but which caused a large-scale epidemic in 2007^[20]. As an ongoing effort to mitigate the threat of Ug99, seven cultivars resistant to Ug99 races were released in 2009, 2010 and 2012 in Kenya. Among these, cv. Kenya Robin, released in 2009, became widespread due to higher yield potential and resistance (postulated to carry gene *SrTmp*). Severe stem rust infections were observed on cv. Kenya Robin in 2013 and two *SrTmp* variants, TTKTT and TTKTK, within Ug99 lineage detected. In Ethiopia in the same year, the unrelated race TKTTTF overcame *SrTmp* in the widely-grown cv. Digalu, causing a severe but localized stem rust outbreak. Race analysis of samples from Kenya in 2014 and 2015 confirmed the migration of TKTTTF to Kenya. This race had been previously reported in Turkey^[94,95], Lebanon and Iran^[25] and was introduced by wind dispersal^[31].

Knowing the consequences of dependence on single,

race-specific genes for controlling stem rust, CIMMYT undertook breeding for durable APR based on minor additive genes early on. The gene *Sr2*, which slows rust development, provides only modest levels of resistance by itself, as evidenced by large-scale testing in Kenya where genotypes with pseudo-black chaff expression showed varying degrees of stem rust severity compared to highly susceptible materials. These observations indicated that although *Sr2* continues to confer at least some resistance, the gene alone was insufficient to provide adequate resistance under high disease pressure in Kenya. *Sr2* was detected in several highly-resistant old, tall Kenyan cultivars, including cv. Kenya Plume^[55] and CIMMYT-derived semi-dwarf wheat cvs Kingbird, Parula, Kiritati, Huirivis#1, Juchi, Muu and Pavon 76, which showed high-to-adequate levels of APR to Ug99 races. Wide testing of improved wheat germplasm has also helped in identifying additional sources of APR since the initial screening about a decade ago. These sources are being used at CIMMYT to incorporate durable APR into high-yielding, widely adapted wheat cultivars. In addition to *Sr2*, pleiotropic genes *Sr55*, *Sr57* and *Sr58* conditioning multi-pathogen resistance identified in CIMMYT germplasm are being used to build high levels of APR.

Using the similar strategy of accumulating multiple minor genes as demonstrated for leaf rust and yellow rust^[93], breeding efforts were initiated to reconstitute high levels of APR to stem rust in wheat germplasm. A targeted breeding approach began in 2006 to develop lines that combine stem rust resistance in high-yielding spring wheat germplasm (Table 4). This was accomplished by extending the shuttle-breeding scheme to Kenya and maintaining two crop seasons per year in both Mexico and Kenya. Breeding populations in F₃ (from simple crosses) and F₄ (from BC₁ and three-way crosses) generations are introduced to Kenya from Mexico, selected in the off-season and then in the main-season, and then returned to Mexico for final selection. A selected-bulk scheme^[96] to advance segregating population is used in successfully combining multiple minor genes and high yield^[25]. This breeding strategy has resulted in the identification of rare transgressive segregants that combine yield and stem rust resistance. Moreover, resistance derived from old, tall Kenyan cvs Kenya Swara and Kenya Fahari has been introgressed into new elite lines such as cv. Kasuko, identified for release in Kenya. Even though breeding for APR to stem rust only started just over a decade ago, there has been significant progress in identifying, characterizing and deploying complex resistance in high-yielding elite germplasm.

7 New technologies to improve stem rust resistance in wheat germplasm

Breeding for rust resistance is the major resource-intensive activity next to yield in most breeding programs including

those undertaken by CIMMYT. Several new tools such as marker-assisted selection (MAS), genome-wide association study (GWAS) and genomic selection (GS) are routinely used at CIMMYT to complement (or) as alternatives for combining high-yielding wheat with adequate levels of polygenic APR^[97,98]. Diagnostic markers can be assayed for the presence of resistance gene without the cost of greenhouse or field evaluations thereby reducing the number of plots for evaluation^[97]. MAS is a promising strategy for improving the efficiency and accuracy of selection for major effect qualitative genes and can be used to pyramid genes and confirm the presence of genes and gene combinations in released cultivars. MAS would greatly facilitate effective “gene stewardship” measures to develop and deploy varieties that carry multiple resistance genes in combination and diversity for resistance within breeding materials. MAS can be successfully used in rapid introgression strategies, or forward selection approaches to ensure developed lines remain competitive. However, lack of diagnostic markers and the cost associated with developing reliable markers, limit most breeding programs to rely on phenotypic selection. The other limitation in using the pyramiding approach is the need to reconstruct the stack every time a new cross is made, as the genes tend to segregate unless reliable markers are used in tandem to select lines with multiple gene combinations. One of the intrinsic problem of MAS is in improving complex traits controlled by multiple minor effect genes^[99]. Besides, the number of molecular markers linked to resistance genes remain insufficient to conduct marker-assisted selection. Therefore, GWAS and GS are promising alternatives for identifying and accumulating favorable alleles for rust resistance traits^[99].

Rapid advancement in high-throughput genotyping technologies in recent years have greatly reduced the cost of genotyping and have made a large number of markers routinely available that enables the use GWAS and GS to overcome the limitations of MAS^[100]. GWAS enables the detection of QTL or causal genes for a target trait without using bi-parental segregating populations^[99] and on the other hand uses training populations to calibrate prediction models and enabling the selection of superior individuals based on genomic estimated breeding values (GEBV), which take into account the effects of multiple genes controlling a target trait^[98].

At CIMMYT, cross-validation studies have been performed to evaluate the potential of GS for APR to stem rust^[100,101] and results suggested that GS could lead to increased genetic gain compared to MAS and phenotypic selection^[98,102]. However, recent studies concluded that by implementing both genomic and phenotypic selection strategies in parallel for quantitative stem rust resistance^[102] under similar selection intensities, genetic gains from genomic and phenotypic selection were equal. Although the power and resolution of GWAS and the

Table 4 CIMMYT wheat germplasm combining high yield and stem rust resistance (R, APR categories) in international nurseries (based on highest disease severity recorded in four seasons of field-testing at KALRO, Njoro, Kenya and seedling tests)

Germplasm identification no.	Cross name/Pedigree	Selection history	Stem rust severity/%	Resistance genes/Category1
8237333	BECARD/ND643/2*WBL1/3/SWSR22T.B./2*BLOUK #1//WBL1*2/KURUKU	CMSS13Y00149S-099Y-099M-099NJ-099NJ-8Y-0WGY	5	<i>Sr22/SrND643</i>
8234886	MISR 1/3/SWSR22T.B./2*BLOUK #1//WBL1*2/KURUKU	CMSS13B00039S-099M-099NJ-099NJ-10Y-0WGY	15	<i>Sr25/Sr22</i>
8235073	ND643/2*WBL1/4/WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBL1/5/BORL14	CMSS13B00139S-099M-099NJ-099NJ-50Y-0WGY	5	<i>Sr25/SrND643</i>
8235528	WBL1*2/BRAMBLING*2//BAVIS/3/SWSR22T.B./2*BLOUK #1//WBL1*2/KURUKU	CMSS13B00381S-099M-099NJ-099NJ-5Y-0WGY	5	<i>Sr22/Sr13</i>
8235657	KRONSTAD F2004/KENYA SUNBIRD//WHEAR/KRONSTAD F2004/3/WBL1*2/BRAMBLING*2//BAVIS	CMSS13B00453S-099M-099NJ-099NJ-25Y-0WGY	10	<i>Sr13/SrND643</i>
8236725	DANPHE #1*2/SHORTENED SR26 TRANSLOCATION/3/SWSR22T.B./2*BLOUK #1//WBL1*2/KURUKU/4/SWSR22T.B./2*BLOUK #1//WBL1*2/KURUKU	CMSS13B01575T-099TOPY-099M-099NJ-099NJ-2Y-0WGY	10	<i>Sr22/Sr26</i>
8236942	MUTUS*2//ND643/2*WBL1/3/2*SWSR22T.B./KACHU//2*KACHU	CMSS13B01701T-099TOPY-099M-099NJ-099NJ-29Y-0WGY	1	<i>Sr22/SrND643</i>
8236956	WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBL1*2/4/NIINI #1*2/5/SWSR22T.B./2*BLOUK #1//WBL1*2/KURUKU	CMSS13B01707T-099TOPY-099M-099NJ-099NJ-14Y-0WGY	5	<i>SrNini/Sr22</i>
8236960	SWSR22T.B./FRANCOLIN #1//2*FRNCLN/5/WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBL1*2/4/NIINI #1/6/BORL14	CMSS13B01709T-099TOPY-099M-099NJ-099NJ-11Y-0WGY	5	<i>Sr22/SrNini</i>
8248316	WBL1*2/BRAMBLING//TAM200/TUI/3/VILLA JUAREZ F2009/4/2*BORL14	CMSS13B01705T-099TOPY-099M-099NJ-099NJ-9Y-0RGY	5	<i>Sr1A.1R</i>
8249245	BABAX/LR42//BABAX/3/ER2000/4/BAVIS/5/SWSR22T.B./2*BLOUK #1//WBL1*2/KURUKU	CMSS14Y00716S-099Y-099M-0S9Y-19M-0RGY	10	<i>Sr13/Sr22</i>
8238251	KFA/2*KACHU/3/2*ATTILA*2/PBW65*2//MURGA	CMSS13Y01093T-099TOPM-099Y-099M-099NJ-099NJ-18Y-0WGY	5	APR_NIR
8238893	TOB/ERA//TOB/CNO67/3/PLO/4/VEE#5/5/KAUZ/6/FRET2/7/PASTOR//MILAN/KAUZ/3/BAV92/8/ATTILA*2/PBW65*2//TNMU/9/ATTILA*2/PBW65*2//MURGA	CMSS13Y01437T-099TOPM-099Y-099M-099NJ-099NJ-32Y-0WGY	5	APR_NIR
8239063	CORRELL/3/PBW343*2/KUKUNA//TECUE #1/4/PBW343*2/KUKUNA*2//FRTL/PIFED	CMSS13Y01496T-099TOPM-099Y-099M-099NJ-099NJ-19Y-0WGY	10	APR_R
8234995	KACHU/DANPHE//KFA/2*KACHU	CMSS13B00105S-099M-099NJ-099NJ-41Y-0WGY	10	APR_R
8235423	KACHU//KIRITATI/2*TRCH/3/KFA/2*KACHU	CMSS13B00118S-099M-099NJ-099NJ-8Y-0WGY	5	APR_NIR
8235262	SUP152/2*DANPHE #1//BORL14	CMSS13B00270S-099M-099NJ-099NJ-6Y-0WGY	10	APR_R
8235936	BECARD//ND643/2*WBL1/3/KACHU/DANPHE	CMSS13B00700S-099M-099NJ-099NJ-5Y-0WGY	5	APR_NIR
8236909	WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBL1/4/PAURAQUE #1/5/WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBL1/6/2*KACHU/DANPHE	CMSS13B01680T-099TOPY-099M-099NJ-099NJ-14Y-0WGY	5	APR_NIR
8236918	CHYAK1/VILLA JUAREZ F2009//WBL1*2/BRAMBLING/7/PRL/2*PASTOR/4/CHOIX/STAR/3/HE1/3*CNO79//2*SERI/5/KIRITATI/2*TRCH/6/PRL/2*PASTOR/4/CHOIX/STAR/3/HE1/3*CNO79//2*SERI/8/KACHU/DANPHE	CMSS13B01683T-099TOPY-099M-099NJ-099NJ-10Y-0WGY	10	APR_R

(Continued)

Germplasm identification no.	Cross name/Pedigree	Selection history	Stem rust severity/%	Resistance genes/Category I
8236943	SUP152*2/TINKIO #1/4/FRET2*2/SHAMA//KIRITATI/2*TRCH/3/BAJ #1/5/SUP152*2/TINKIO #1	CMSS13B01703T-099TOPY-099M-099NJ-099NJ-15Y-0WGY	5	APR_NIR
8244588	KACHU/SAUAL/3/TACUPETO F2001/BRAMBLING//KIRITATI/4/COPIO	CMSS14Y00648S-099Y-099M-0SY-13M-0WGY	5	APR_NIR
8245010	KACHU/DANPHE*2//BORL14	CMSS14Y01482T-099TOPM-099Y-099M-0SY-24M-0WGY	15	APR_R-MR
8245012	KACHU/DANPHE*2//BORL14	CMSS14Y01482T-099TOPM-099Y-099M-0SY-34M-0WGY	5	APR_NIR
8241262	KACHU/BECARD//WBL1*2/BRAMBLING*2/5/ATTILA/3*BCN*2//BAV92/3/KIRITATI/WBL1/4/DANPHE	CMSS14B01373T-099TOPY-099M-0SY-37M-0WGY	10	APR_R
8248604	CHIPAK*2//TRCH/HUIRIVIS #1	CMSS13Y01097T-099TOPM-099Y-099M-099NJ-099NJ-6Y-0RGY	5	APR_NIR
8249240	NGL/4/PFAU/MILAN/3/BABAX/LR42//BABAX/5/KFA/2*KACHU	CMSS14Y00712S-099Y-099M-0SY-5M-0RGY	5	APR_NIR

Note: ¹ Resistance categories for adult plant resistance (APR) are: NIR = near-immune resistant, R = resistant, and R-MR = resistant-moderately resistant.

accuracy of GS can be generally improved by large data sets; for quantitative disease resistance, greater selection intensities under GS and better prediction models may be needed to surpass phenotypic selection. Combining GWAS and GS with MAS will accelerate breeding cycles^[103] and rationalize the design of breeding programs. Irrespective of whatever molecular techniques are used, there is a strong need to maintain the greenhouse and field phenotyping facility to verify that the desired level of resistance is expressed in the selected lines.

Cloning of some wheat rust resistance genes in the recent years offers scope to pyramid multiple genes as *Cis*-gene cassettes for enhancing resistance durability^[25]. These gene stacks or cassettes developed on a single construct would be inherited as a single locus, thus facilitating rapid transfer into different genetic backgrounds without the fear of losing stacks due to segregation, hence making it easier to retain multiple gene combinations. Designing cassettes carrying combinations of both R and APR genes in high yielding lines by transformation in addition to other useful traits which are difficult to combine through conventional breeding can be accomplished through this process and offering scope of adding or replacing genes to generate new gene stacks. Although this technology is promising, the feasibility of developing varieties is limited by regulatory and consumer acceptance issues as transgenic wheat cultivars are not grown currently anywhere in the world.

Genome editing technology in the recent years has shown great potential to overcome the limitations of conventional resistance breeding. This technology offers the advantage of modifying specific target genes in elite varieties, thus bypassing the whole process of crossing.

Genome editing being site-specific avoids the potential problems of linkage drag and does not require genetic crosses and selection in segregating generations that can accelerate breeding for disease resistance and breeders can focus on more critical issues such as increasing yield potential. Genome editing was found to be effective in improving powdery mildew resistance in wheat^[104] and can be used for modifying targets for a range of traits within polyploid genomes. To become a routine procedure, however, sequences of the resistance genes for editing need to be known, but these remain limited in wheat.

8 Future of rust resistance breeding

Stem rust is still one of the major threats to wheat production because of the extreme level of damage the disease causes to susceptible varieties. Although it is under control in the world's major production areas, serious genetic vulnerability exists and active steps are being taken to incorporate new effective resistance into most wheat breeding programs. However, evolution and faster spread of more virulent pathogen races and selection for fungicide resistance due to excessive use necessitate reinforcing breeding strategies to develop adequate durable resistance to multiple diseases for enhancing wheat productivity, while simultaneously reducing the cultivation of susceptible varieties in disease prone regions.

Cultivars carrying single race specific genes for resistance have resulted in boom and bust cycles and breeding programs should ensure multiple gene combinations through MAS to enhance the resistance durability. On the other hand APR genes like *Sr2* and *Sr55*, *Sr57* and

Sr-58 can be combined with other R or APR genes (due to their multi-pathogen and additive effects) resulting in higher levels of resistance. Even though only a few APR genes have been characterized in the past, with newer tools many such genes with broad-spectrum resistance should become available for use in breeding.

Maintaining diversity for stem rust resistance within breeding germplasm and identifying and characterizing new genes in the breeder's toolbox will greatly reduce the vulnerability of cultivars and provide options for immediate replacement. Active survey and surveillance in understanding the variation in pathogen populations, their evolution and migration can help in pre-emptive breeding and coupled with forecasting models can help in reducing the disease impacts in many wheat-growing regions. Breeding strategies such as GWAS and GS will greatly enhance identification and selection of superior individuals based on GEBV, which take into account the effects of multiple genes controlling a target trait. Promising new technologies such as *Cis*-gene cassettes, gene editing, GM technology and additional genetic analysis will provide the tools for understanding and developing durable rust resistance. Finally, breeders and farmers should discourage growing stem rust susceptible varieties thereby reducing the inoculum build up, evolution of new virulences and spread to other wheat growing regions. This strategy can largely contain the disease, preventing it from developing into devastating epidemics.

9 Concluding remarks

The rapid evolution and spread of both the Ug99 and Digalu race groups of stem rust fungus over a decade in several countries of Africa, Middle East and Europe, causing localized epidemics, reconfirms the famous observation of Borlaug that “rust never sleeps”. Research to mitigate the threat of stem rust started with the launch of the Borlaug Global Rust Initiative in 2005. Major achievements include surveillance, including understanding pathogen diversity and its spread, evolution and migration, as well as the establishment of phenotyping platforms to facilitate the testing of global wheat germplasm and the identification and characterization of new sources of race-specific and APR genes. All of this has led to the development of rust-resistant cultivars and their rapid deployment in target countries. CIMMYT breeding over the last decade has provided improved high-yielding wheat germplasm carrying high to adequate resistance to the currently predominant races in Africa and the Middle East. More than 100 Ug99 resistant cultivars have been deployed both in primary and secondary risk regions, mitigating the potential threat even in countries where Ug99 is not yet present. However, emerging concerns of

new race groups migrating into Europe and across several countries in Africa highlights the importance of breeding and continuous deployment of resistant germplasm in target environments to limit future epidemics.

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