

The Emergence of Ug99 Races of the Stem Rust Fungus is a Threat to World Wheat Production

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Abstract

Race Ug99 of the fungus *Puccinia graminis tritici* that causes stem or black rust disease on wheat was first detected in Uganda in 1998. Seven races belonging to the Ug99 lineage are now known and have spread to various wheat-growing countries in the eastern African highlands, as well as Zimbabwe, South Africa, Sudan, Yemen, and Iran. Because of the susceptibility of 90% of the wheat varieties grown worldwide, the Ug99 group of races was recognized as a major threat to wheat production and food security. Its spread, either wind-mediated or human-aided, to other countries in Africa, Asia, and beyond is evident. Screening in Kenya and Ethiopia has identified a low frequency of resistant wheat varieties and breeding materials. Identification and transfer of new sources of race-specific resistance from various wheat relatives is underway to enhance the diversity of resistance. Although new Ug99-resistant varieties that yield more than current popular varieties are being released and promoted, major efforts are required to displace current Ug99 susceptible varieties with varieties that have diverse race-specific or durable resistance and mitigate the Ug99 threat.

INTRODUCTION

Recurrent food crises, volatile energy prices, natural resource depletion, and climate change undercut and threaten the livelihoods of millions of poor people. Accounting for a fifth of humanity's food, wheat is second only to rice as a source of calories in the diets of developing-country consumers and is first as a source of protein. Wheat provides 21% of the food calories and 20% of the protein to more than 4.5 billion people in 94 developing countries (1). Wheat is grown on approximately 215 million hectares worldwide, from the equator to latitudes of 60°N and 44°S and at altitudes ranging from sea level to more than 3,000 m. Approximately 630 million tons of wheat are produced annually, roughly half in developing countries. Demand for wheat in the developing world is projected to increase 60% by 2050; at the same time, climate change-induced temperature increases are expected to reduce wheat production in developing countries by 29% (40). This scenario is worsened by stagnating yields, increasing irrigation and fertilizer costs, and virulent new disease and pest strains such as race Ug99 of the stem rust fungus.

Stem rust, or black rust, of wheat caused by the fungus *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. has severely devastated wheat crops historically, becoming the most feared disease in wheat-growing countries on all continents. Hexaploid common bread wheat (*Triticum aestivum*), tetraploid durum wheat (*Triticum turgidum* var. *durum*), barley (*Hordeum vulgare*), triticale (*X Triticosecale*), and wheat progenitors are primary hosts of the stem rust fungus (39). Several major wheat production areas worldwide are favorable environments for disease development and prone to severe losses. According to Saari & Prescott (41), stem rust has been a major problem historically in all of Africa, the Middle East, all of Asia (except Central Asia), Australia, New Zealand, Europe, and the Americas (both North and South). The last major stem rust epidemic occurred in Ethiopia in 1993 and 1994 (42), when Enkoy, a popular wheat variety, suffered

major losses; however, the rest of the world has remained unhurt by stem rust for over three decades. In contrast, worldwide epidemics of the other two rust diseases, leaf (or brown) rust caused by *Puccinia triticina* and stripe (or yellow) rust caused by *Puccinia striiformis*, have been frequent, especially in recent years.

Severe stem rust infections were observed on CIMMYT (International Maize and Wheat Improvement Center) wheat nurseries planted in Uganda in 1998. Because these materials were known to be resistant to stem rust, the susceptibility of a large number of entries in the nursery drew attention, and urediniospores were collected from field nurseries for avirulence/virulence phenotyping, or race-analysis, in a greenhouse in South Africa in early 1999 on a set of wheat differentials carrying designated race-specific resistance genes. A new race with novel virulence on resistance gene *Sr31* was detected and designated as Ug99 (36). The importance of Ug99 was recognized in 2005 when Nobel Laureate Dr. Norman E. Borlaug raised the alarm and warned the world about the serious threat it could pose to food security if proper actions were not taken (4). The world wheat community and certain donor organizations responded positively, and various research and developmental projects are now underway to mitigate the Ug99 threat in a coordinated manner under the umbrella of the Borlaug Global Rust Initiative (<http://www.globalrust.org>). The objective of this review paper is to explain why the Ug99 group of races is a major threat to food security and describe the measures being undertaken to mitigate the threat.

RACES BELONGING TO THE UG99 LINEAGE AND THEIR DISTRIBUTION

Race Ug99 is the first known race of *P. graminis tritici* that has virulence to resistance gene *Sr31* located on translocation 1BL.1RS from rye (*Secale cereale*) (36). Collections of Ug99 gathered in Kenya were designated as TTKS based on the North American nomenclature

Table 1 Origin and usefulness of cataloged *Sr* genes in conferring seedling and/or adult plant resistance to *Puccinia graminis* f. sp. *tritici* races belonging to the Ug99 lineage

Origin of <i>Sr</i> genes	Stem rust resistance (<i>Sr</i>) genes	
	Ineffective	Effective
<i>Triticum aestivum</i>	5, 6, 7a, 7b, 8a, 8b, 9a, 9b, 9f, 10, 15, 16, 18, 19, 20, 23, 30, 41, 42, 49, McN, Wld-1	28, ^a 29, ^{b,c} 48, <i>Tmp</i> , ^a <i>AC-Cadillac</i> , <i>Sba7</i> , ^b <i>Huvv234</i> , ^b <i>ND643</i> ^b
<i>Triticum turgidum</i>	9d, 9e, 9g, 11, 12, 17	2, ^b 13, ^{a,b} 14 ^a
<i>Triticum monococcum</i>	21	22, 35
<i>Triticum timopheevi</i>	36	37 ^c
<i>Aegilops speltoides</i>		32, ^c 39, ^c 47 ^d
<i>Aegilops tauschii</i>		33, ^b 45, ^{a,b} 46 ^{a,d}
<i>Triticum comosum</i>	34	
<i>Triticum ventricosum</i>	38	
<i>Triticum araraticum</i>		40 ^c
<i>Thinopyrum elongatum</i>	24	25, ^a 26, 43 ^c
<i>Thinopyrum intermedium</i>		44 ^c
<i>Secale cereale</i>	31	27, ^a 50, <i>1A.1R</i> ^{a,b}

^aVirulence for the gene is known to occur in other races.

^bLevel of resistance conferred in the field usually inadequate under high disease pressure.

^cUnsuitable for utilization due to linkage with undesirable traits in the translocation.

^dNot tested for resistance to Ug99 in field trials to determine effectiveness.

system (52) and redesignated as TTKSK after adding a fifth set of differentials in the nomenclature system (13). Race Ug99 carries virulence to gene *Sr31*, but this unique virulence is present together with virulence to a majority of the genes of wheat origin, as well as virulence to gene *Sr38* introduced into wheat from *Triticum ventricosum* (Table 1) (15). This striking virulence combination in Ug99 explains the widespread susceptibility of wheat varieties and germplasm worldwide.

Singh et al. (43) summarized the known status of race Ug99 up to 2007. By then, Ug99 had been confirmed in Uganda, Kenya, Ethiopia, Sudan, and Yemen. Occurrence in Yemen was considered particularly significant, as it provided strong evidence that Ug99 was moving toward the important wheat areas of the Middle East and Asia. The subsequent confirmation of Ug99 (race TTKSK) in Iran, announced by FAO (Food and Agriculture Organization) in March 2008 (7), supported these predictions. Positive Iranian Ug99 isolates

were actually collected in 2007 from two sites, Borujerd and Hamadan, in northwestern Iran, but underwent extensive testing to confirm the race (31). Detection in Iran in 2007 was followed by drought conditions, and no reports of Ug99 were received from Iran in 2008. However, in 2009 Ug99 was found in the southern Iranian province of Khuzestan, where spring wheat is grown and growing conditions are favorable. Given the regular northeasterly airflows out of Yemen (43), the possibility that this was a new incursion from Yemen is considered likely. Alternatively, Ug99 may have been introduced into Khuzestan in 2007 but remained undetected and migrated to the northwest, where facultative and winter wheats are grown and mature approximately two months later. There is no evidence that the Ug99 lineage has become well established in Iran, and no crop losses have been reported so far. Also, to date it is not known to have spread beyond Iran. Reports of the unusual occurrence of stem rust in Pakistan in 2009

Table 2 Ug99 group of races identified until 2010 in various countries and their key virulence differences

Race ^a	Common alias	Key virulence difference				Confirmed countries (year)
		<i>Sr31</i>	<i>Sr21</i>	<i>Sr24</i>	<i>Sr36</i>	
TTKSK	Ug99	Vir	Vir	Avir	Avir	Uganda (1998), Kenya (2001), Ethiopia (2003), Sudan (2006), Yemen (2006), Iran (2007)
TTKSF		Avir	Vir	Avir	Avir	South Africa (2000), Zimbabwe (2009)
TTKST	Ug99+Sr24	Vir	Vir	Vir	Avir	Kenya (2006)
TTTSK	Ug99+Sr36	Vir	Vir	Avir	Vir	Kenya (2007)
TTKSP		Avir	Vir	Vir	Avir	South Africa (2007)
PTKSK		Vir	Avir	Avir	Avir	Kenya (2007), Ethiopia (2007)
PTKST		Vir	Avir	Vir	Avir	Kenya (2008), South Africa (2009)

^aRace designation follows the North American nomenclature system described by Jin et al. (13).

prompted some fears of a Ug99 incursion, but greenhouse phenotyping of samples on differentials and DNA analysis of dead spores indicated conclusively the absence of Ug99 and presence of another important race (29).

Within Africa, several significant changes have occurred in both the pathogen population and distribution. Loss of key additional resistance genes, notably *Sr24* and *Sr36*, was detected in Kenya in 2006 and 2007, respectively (13, 16). The pathogen is changing rapidly; seven variants are now recognized as being part of the Ug99 race lineage. All are closely related, having nearly identical DNA fingerprints, but differ slightly in their avirulence/virulence profiles (13, 48, 50). In contrast, these races are very different from other known races in the United States and South Africa. Simple sequence repeats marker similarity of Ug99 races indicates their evolution from a common ancestor. A summary of known races in the Ug99 lineage is given in **Table 2**.

Pathogen monitoring indicates that the recognized variants in the Ug99 lineage are expanding their geographic distribution in Africa over time. Most of the key variants were initially identified in Kenya. Notable recent events have included the confirmation of combined virulence to *Sr31* and *Sr24* (race PTKST) in South Africa from isolates collected in 2009 (35) and the same race in Ethiopia from isolates collected in 2007 (T. Fetch, unpublished results). Continued spread of the new variants is expected,

as is the identification of further variants within the Ug99 race lineage. At present, Ug99 (race TTKSK) is the only known pathotype in the lineage confirmed outside of Africa, but the eventual appearance of other variants outside of Africa is considered likely. An overview of the confirmed distribution of the Ug99 race lineage is given in **Figure 1**. Reports from several countries in Africa are undergoing confirmation.

Airflows out of Yemen during the 2009–2010 winter season exhibited the same general pattern as in previous years, with air moving from Yemen to southern Iran on a regular basis. One slight deviation in modeled airflows in 2009–2010 compared with other years was a tendency for air to move in a more northwesterly direction out of Yemen towards Israel and Jordan. Reports of stem rust were received from Israel and Lebanon in 2010; however, it is not known if Ug99 was present. Given the updated potential migration routes proposed by Singh et al. (43), any occurrence of Ug99 or its variants in this region may have future significance for Egypt's wheat areas.

The current situation does little to change the overall hypothesis that the pathogen will continue to push into the Middle East, and onward movement following predominant west-east airflows is a real possibility. The exact timing or nature of any such future events cannot be predicted with certainty, as disease outcomes will depend on prevailing environmental conditions, host susceptibility,

Race	Country (year of 1 st detection)
TTKSK	Uganda (1998), Kenya (2001), Ethiopia (2003), Sudan (2006), Yemen (2006), Iran (2007), Tanzania (2009)
TTKSF	South Africa (2000), Zimbabwe (2009)
TTKST	Kenya (2006), Tanzania (2009)
TTTSK	Kenya (2007), Tanzania (2009)
TTKSP	South Africa (2007)
PTKSK	Kenya (2009), Ethiopia (2007)
PTKST	Ethiopia (2007), Kenya (2008), South Africa (2009)

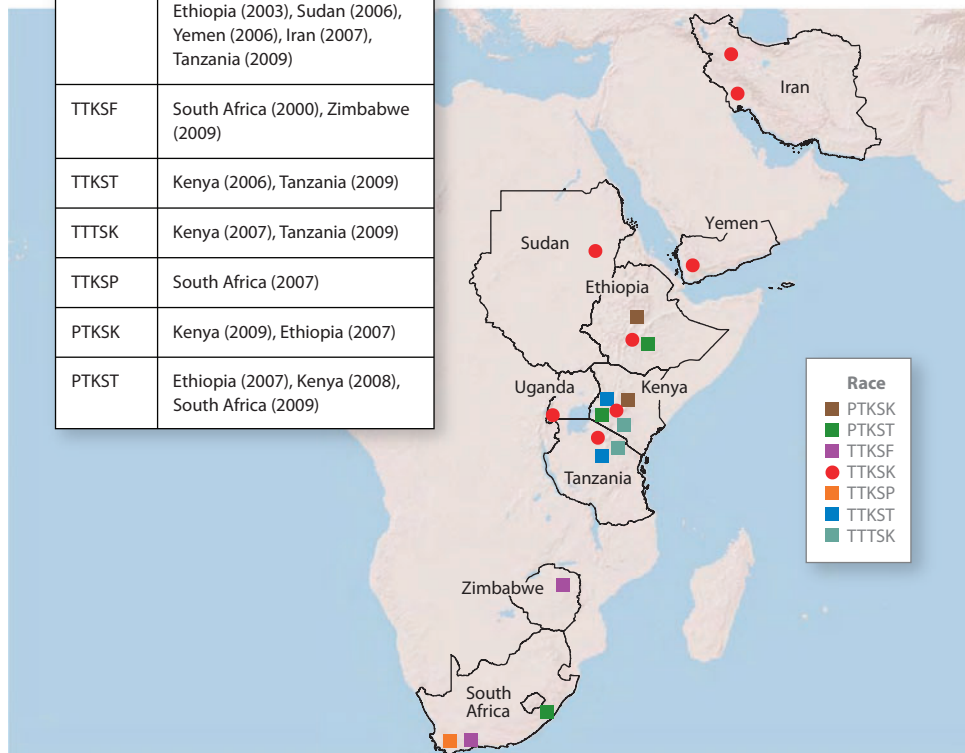


Figure 1

Current status and distribution of the Ug99 group of races. [The races of stem rust fungus are designated by following a five letter code as described by Jin et al. (13)].

and a range of other factors. Outputs from the HYSPLIT trajectory model (5), using the confirmed 2007 Ug99 Iranian sites as sources, supported the idea that airflows would likely move towards the east, but also indicated the possibility of more northerly movements into the Caucasus and Central Asia (**Figure 2**).

Confirmed race data indicate that movements of Ug99 variants are now occurring within Africa. Detection of race TTKSF in South Africa in 2000 [and subsequent confirmation that it is part of the Ug99 lineage (51)] was the first indication of the interchange between eastern African and southern African stem rust populations. The *Sr31*-avirulent race TTKSF is presumed to be an exotic introduction into South Africa. Race TTKSP is considered to

have evolved locally within South Africa and to have acquired virulence to *Sr24* through mutation (49). Southern Africa was considered to be a single epidemiological zone (41) and the recent detection of race TTKSF in Zimbabwe supports the spread of common races within the region. Identification of race PTKST, virulent to both *Sr31* and *Sr24*, during 2009 in South Africa (35) was a further indication of the connection between eastern and southern African stem rust populations. Race PTKST was previously detected in Kenya from isolates collected in 2008 and, more recently, from back-dated analysis of isolates collected in Ethiopia in 2007.

The precise mechanism of movement between eastern and southern Africa are unknown, but there are at least two possibilities.

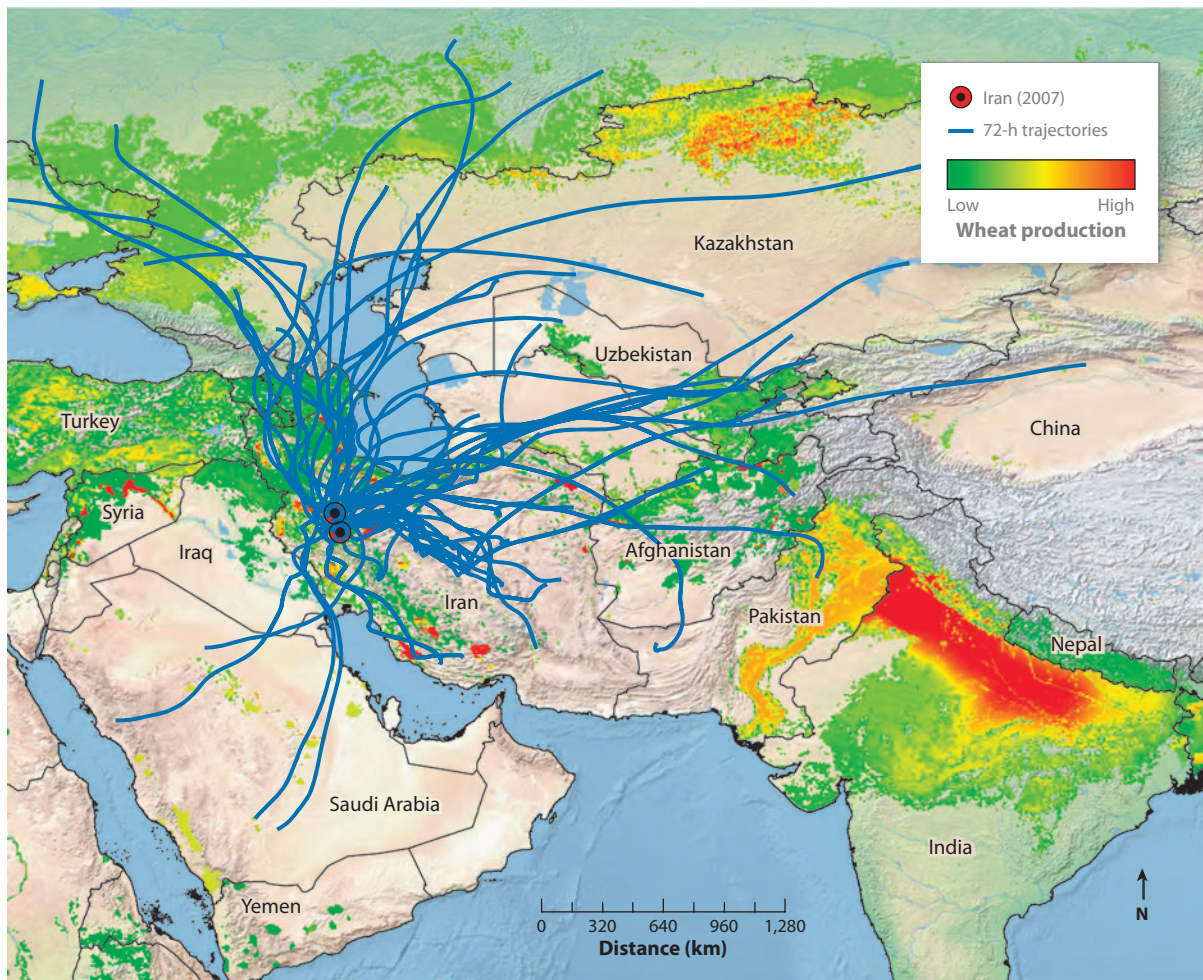


Figure 2

Airborne particle trajectories (blue lines), derived from the HYSPLIT model, originating from the confirmed Ug99 sites of Borujerd and Hamadan, Iran (trajectories represent selected 72-h movements for the period January-July 2008).

Firstly, a natural movement on air currents is potentially feasible. Asian soybean rust (*Phakopsora pachyrhizi*) provides a possible analogous situation. *P. pachyrhizi* was first identified in Uganda in 1996, thereafter it was considered to be wind dispersed to Rwanda, Zimbabwe, and Zambia by 1998 and onto southern Mozambique by 2000 and eastern South Africa by 2001 (22). For the Ug99 group of races one possible hypothesis for movement is via a series of stepping stone jumps between the islands of wheat and barley that exist in the eastern

and southern African countries of Tanzania, Malawi, Mozambique, Zambia, and Zimbabwe. Modeled wind trajectories indicate that air movements out of Kenya pushing into southern Tanzania are a regular occurrence, notably from January to March. Infected wheat areas in the southern highlands of Tanzania may then act as a source of rust spores for onward movement into Zambia or Malawi/Mozambique and subsequent movement into Zimbabwe and then into South Africa. Wind trajectories from October 2009 onward do indicate the

possibility of airflows from known stem rust infected sites in eastern Zimbabwe and the confirmed PTKST sites in KwaZulu-Natal. The second mechanism that cannot be discounted as the means of arrival of race PTKST in South Africa is accidental human-mediated transmission. Extensive trade and travel linkages between Kenya and South Africa, coupled with high levels of stem rust inoculum in Kenya, make this an unproven but feasible mechanism. With increased globalization, accidental exotic incursions of plant pathogens, including the rusts, are increasing (11).

The presence of Ug99 variants in southern Africa has potential implications for other wheat-growing regions. The main concern is the region's potential as a source for onward movement to either Australia or the Americas, although with a very low probability. Watson & De Sousa (53) provide strong evidence for three wind-borne transmission events of *P. graminis tritici* races from southern Africa to Australia during the period 1925–1983. Brown & Hovmöller (2), Nagarajan & Singh (30), and Prospero et al. (37) all cite convincing examples, supported by high altitude balloon data, wind trajectory model data, and sample analysis, of cross-continental rust or bacteria movements originating in southern or western Africa and going to South America or Australia. Sturman et al. (46) demonstrated the existence of inter-regional air transfer between southern Africa and Oceania, estimating that in July, 54% of air originating over the central interior of South Africa reaches coastal waters just south of Australia after approximately 15 days.

GLOBAL CEREAL RUST MONITORING SYSTEM

Within the framework of the Borlaug Global Rust Initiative (BGRI), and focused on the Ug99 race lineage, an international coalition of partners [Consultative Group on International Agricultural Research (CGIAR) centers, advanced research labs, national agricultural programs, and UN-FAO] is now implementing the Global Cereal Rust Monitoring System

(GCRMS). In its current form, the GCRMS integrates and disseminates up-to-date information on stem rust incidence and severity, as well as races. A rapidly expanding, coordinated international rust surveillance network is now emerging. In 2007, the system was in its infancy, with only two countries reporting rust survey information. By 2009, 15 countries were reporting standardized field survey information on rust disease incidence and severity, and this number is expected to rise to over 20 countries by 2011. International sampling and race analysis carried out under strict biosafety regulations by advanced labs have yielded most of what is currently known about the Ug99 race lineage. Intensive efforts are also underway to increase the in-country race-analysis capacity of several priority countries. All available information is now being disseminated in three UN languages (English, Arabic, and Russian) via a Web portal, Rust SPORE (<http://www.fao.org/agriculture/crops/rust/stem/en/>), released in June 2010 (8). Future development of the GCRMS is likely to include information on available sources of resistance and disease suitability modeling, as well as expansion to cover other cereal rusts.

PERFORMANCE OF GLOBAL WHEAT VARIETIES AND GERmplASM AGAINST UG99

Over 200,000 wheat varieties, germplasm collections, and advanced breeding materials were screened during 2005–2010 for resistance to Ug99 and its derivative races at Njoro, Kenya, and to a lesser extent, at Kulumsa and Debre Zeit, Ethiopia (43, 44). The disease response data of varieties and information on the areas planted were used to estimate the genetic vulnerability of a wheat crop to Ug99. By 2007, screening data were available for varieties sown on an estimated 75–80 million ha in 22 main wheat-producing countries of Africa and Asia, including China. Varieties exhibiting adequate resistance to Ug99 accounted for only 5%–10% of the total estimated area in these 22 countries. The huge susceptible areas

in Pakistan, India, and China result from the predominance of either mega-varieties such as PBW343 in India and Inqualab 91 and Seher 2006 in Pakistan, or the susceptibility of most varieties in China. Approximately 85%–95% of breeding materials from various countries were also found to be susceptible to the Ug99 group of races. With a view to improving its spring wheat materials, in 2010 CIMMYT began identifying advanced breeding lines from its stem rust resistance breeding efforts by utilizing a Mexico-Kenya shuttle breeding scheme that includes two generations per year.

Wheat varieties from other wheat-growing regions also display a similar situation to that described for wheat varieties from Africa and Asia. Information on European wheat varieties and germplasm is scarce. Breeding for stem rust resistance is not considered a high priority in Europe because systemic, broad-spectrum fungicides are used routinely in commercial fields. Unfortunately, information on Russian wheat varieties and germplasm is also limited. In 2005 and 2006, through screening with the original Ug99 (TTKSK) in Kenya, approximately 10% of resistant wheat materials from South America, Australia, the United States, and CIMMYT were identified as possessing the stem rust resistance gene *Sr24*. The presence of this gene in adapted genetic backgrounds was encouraging to researchers combating the Ug99 threat (14). *Sr24* is linked to leaf rust resistance gene *Lr24*. TTKST, a Ug99 derivative race with virulence to *Sr24*, was detected in low frequency in Kenya during 2006 (13). However, by 2007 it had built up sufficiently to cause an epidemic on the *Sr24*-carrying variety Mwamba, which occupied approximately 30% of the wheat area in Kenya. TTKST is now the predominant stem rust race in Kenyan fields, and a majority of wheats carrying *Sr24*, including many hard red winter wheats that were resistant to the original Ug99, are now showing high susceptibility to TTKST in field screening nurseries.

Another frequently used resistance gene is *Sr36*, known to be present in high frequency in soft winter wheats from the United States

(14) and some spring wheats from Australia; it became ineffective against the Ug99 variant race TTTSK detected in 2007. Ineffectiveness of these two resistance genes, *Sr24* and *Sr36*, against the Ug99 lineage has enhanced the genetic vulnerability of global wheat varieties and increased the potential threat posed by stem rust.

In contrast to bread wheat, a greater proportion of durum wheat varieties and germplasm (40%–60%, depending on the origin) show resistance to races of the Ug99 lineage. This difference is largely attributed to resistance gene *Sr13*, present in high frequency in durum wheat germplasm. A single mutation could endow the Ug99 lineage with virulence to *Sr13*. Unfortunately, virulence to *Sr13* is known to occur in races TRTTF and JRCQC, which are predominant in durum growing areas of Ethiopia, and only approximately 5% of durum wheats remained resistant when screened at Debre Zeit, Ethiopia (33). Races very similar to TRTTF have also been identified from collections originating in Yemen and Pakistan (29); this group of races possesses virulence to resistance genes provisionally designated as *SrTmp* (from Triumph) and *Sr1A.1R* (a gene present in wheat-rye translocation 1A.1R), which are effective against the Ug99 group of races. Identification of the TRTTF group of races in Africa, the Middle East, and Asia, with virulence to *Sr13*, *SrTmp*, and *Sr1A.1R*, reduces the focus in the utilization of these resistance genes in breeding efforts. The Debre Zeit field site in Ethiopia is being used by BGRI to screen durum wheats and bread wheats identified in Kenya as being resistant to the Ug99 group of races.

In most wheat-growing regions of the world, existing environmental conditions will favor stem rust infection, which could lead to epidemic buildup. This situation, plus the fact that susceptible wheat varieties are grown over large areas and that a large proportion of current breeding materials are susceptible to Ug99 and other newly identified races, means that these pathogens have the potential to cause a wheat production disaster that would affect food

security worldwide. Although it is difficult to predict where and when a major epidemic will occur, an epidemic of Ug99 would seriously affect extremely large numbers of wheat-farming families in Africa and Asia—especially those who have few alternative livelihoods. Large production losses also have implications for rural and national economic growth rates and could increase wheat prices.

RESISTANCE TO UG99 AND OTHER IMPORTANT RACES

Reaction of Race-Specific Resistance Genes

Approximately 50 different stem resistance genes are cataloged, and multiple alleles are known for three gene loci (**Table 1**). Increased research in recent years has identified additional resistance genes that are likely different from designated genes. Several stem rust resistance genes were transferred into wheat from wheat relatives (**Table 1**). All designated genes, except *Sr2*, are race specific and expressed in both seedling and adult plants. Race specificity derives from the gene-for-gene relationship between the host plant resistance gene and corresponding avirulence genes in the pathogen. With avirulent races, a majority of stem rust resistance genes allow the formation of tiny-to-medium-sized uredinia, with limited sporulation, which are surrounded by necrosis or chlorosis (28). Genes that allow development of only microscopic or macroscopic hypersensitive reactions include *Sr5*, *Sr17*, *Sr27*, *Sr36*, and *Sr6* at cooler temperatures. A majority of stem rust resistance genes, for which the Ug99 group of races lacked virulence, conferred varying levels of intermediate resistance both in seedlings and adult plants, and some genes did not confer adequate protection in field trials in Kenya (**Table 1**) (15). Although several resistance genes listed in **Table 1** confer high-to-intermediate resistance to races belonging to the Ug99 lineage, only *Sr22*, *Sr26*, *Sr35*, and *Sr50* are known to be effective against all current important races and have

the potential to be utilized successfully. An important activity of BRGI is to reduce the size of various alien translocations that carry effective resistance genes with the hope of eliminating the undesirable linkage drag.

Resistance gene *Sr25*, located on a *Thinopyrum elongatum* translocation, together with leaf rust resistance gene *Lr19* on chromosome 7DL, is not used widely because it is linked to a gene associated with the accumulation of undesirable levels of yellow pigment. A white-floured mutant of the translocation (18) was recently transferred into some Australian and CIMMYT wheat backgrounds. *Sr25* conferred a high level of resistance only in some genetic backgrounds, especially when the adult plant resistance gene *Sr2* was also present, e.g., in recently released Ug99-resistant varieties Misr 1 in Egypt and Muquawin 09 in Afghanistan. Race PKTSC, which possesses virulence to *Sr25* and several other resistance genes and was detected in the Nilgiri Hills of India in 2007 (12), reduces the utility of *Sr25* in future breeding efforts.

Gene *Sr26*, transferred to wheat chromosome 6AL from *T. elongatum*, was used successfully in Australia and remains effective despite its large-scale deployment in the 1970s, 1980s, and once again recently (28). It is not known to be present in cultivars from other countries. Because of its availability in adapted genetic backgrounds and the existence of a reliable DNA marker, *Sr26* is likely to be utilized by many breeding programs. Gene *Sr27* of rye origin has not been used in wheat improvement. Its deployment in triticale in Australia resulted in a rapid evolution of virulence (27). This gene has also become ineffective in South Africa. Strategically, this gene should be used for triticale improvement in areas where virulence is not known.

Genes *Sr22* and *Sr35*, derived from *Triticum monococcum* and located on chromosomes 7AL and 3AL, respectively, are both highly effective against Ug99 and can be backcrossed to modern wheats. Virulence to *Sr35* was identified in a laboratory culture in Australia (28). Although race Ug99 is avirulent to gene *Sr28*, numerous races virulent to this gene are known to occur

worldwide. Genes *Sr33*, *Sr45*, and *Sr46*, derived from *Aegilops tauschii*, confer moderate resistance levels that are inadequate under stem rust pressure in screening nurseries in Kenya. Genes *Sr29*, *Sr32*, *Sr37*, *Sr39*, *Sr40*, and *Sr44* have not been tested widely for their effectiveness to other races and thus are not used in breeding. The size of the alien chromosome segments carrying these genes have to be (and are being) reduced before these genes can be used successfully. The translocation carrying resistance gene *Sr50*, previously known as *SrR*, introduced into wheat from Imperial rye in chromosomes 1BL.1RS and 1DL.1RS (23), is effective against race Ug99 and is being used in an Australian wheat breeding program; however, no variety has been released to date.

A resistance gene temporarily designated as *SrCad*, located on chromosome 6DS and present in Canadian wheat varieties AC Cadillac and Peace, confers moderate resistance to the Ug99 group of races when present alone and a high level of resistance when present together with slow rusting leaf rust resistance gene *Lr34* (10). Similarly, a few other temporarily designated genes (*SrSha7* derived from Chinese cultivar Shanghai#7, *SrND643* from ND643, and *SrHuw234* from HUW234) are present in improved wheat materials and, when present alone, confer moderate levels of resistance to the Ug99 group of races. How these resistance genes perform against other races is not yet known.

When evaluating wheat relatives, Y. Jin and coworkers (Y. Jin, M. Rouse, P.D. Olivera, M. Pumphrey, and B.J. Steffenson, unpublished results) readily found resistance to Ug99 and other important races, but frequencies of resistance varied among the species. Approximately 96% of the 92 *Aegilops speltoides* accessions were resistant to all races used in testing. Other species having high frequencies of resistance include *Triticum urartu* (96.8% of 205 accessions) and *T. monococcum* (61% of 1020 accessions). Also resistant were 15% of *A. tauschii* (456 accessions), 15% of *Triticum timopheevii* (298 accessions), and 17% of *T. turgidum* ssp.

dicoccoides (157 accessions). Based on specific infection types caused by several races, it is likely that novel genes for resistance to TTKSK are present in some of these species. Resistance from accessions with putative novel resistance genes is being transferred to hexaploid wheat, and mapping populations are being developed for determining their genomic locations and identifying linked molecular markers. These putative novel sources are likely to contribute additional genetic diversity for resistance to Ug99 and other races of the stem rust pathogen.

Adult Plant Resistance with Complex Inheritance

Resistance in this category is associated with compatible host reactions in both seedlings and adult plants, leading to moderately susceptible to susceptible host reactions. Resistance is therefore measured based on the reduction in number of pustules, or disease severity. This results in a type of resistance known as slow rusting (3). The adult plant resistance gene *Sr2*, transferred to hexaploid wheat Hope and H44-24 from tetraploid emmer wheat Yaroslav by McFadden (24), was shown to confer slow rusting (47). *Sr2* is known to be linked with pseudoblack chaff (PBC) expression in glumes and near nodes of the stems (25). However, the degree of PBC expression is variable and dependent on genotype and environment (43). Evaluation in field trials in Kenya confirmed previous observations that *Sr2* confers inadequate protection when present alone. Attempts to break the linkage between *Sr2* and PBC have failed (21). The combination of *Sr2* with other unknown slow rusting resistance genes (possibly originating from tetraploid wheat Iumillo and transferred to hexaploid wheats Thatcher and Chris) is commonly known as the *Sr2* complex (43). The *Sr2* complex is believed to have provided the foundation for durable resistance to stem rust in germplasm from the University of Minnesota in the United States, Sydney University in Australia, and the spring wheat germplasm developed

by Dr. N. E. Borlaug at CIMMYT in Mexico (26, 38).

Thatcher and Chris displayed moderate and high levels of resistance, respectively, against Ug99 in field trials in Kenya and are believed to lack the *Sr2* gene because of the absence of PBC expression in North American environments. Similarly, by accumulating approximately five minor genes, Knott (19, 20) developed wheat lines that carried adequate levels of adult plant resistance to stem rust but lacked PBC based on phenotyping done in Canada. The adult plant resistance of Thatcher and Chris is believed to be derived from Iumillo, which remains resistant to Ug99 and *Sr13*-virulent races present in Ethiopia. Iumillo, Thatcher, and its isolines, developed for leaf rust resistance genes, showed low intensity of PBC on glumes and occasionally on peduncles and internodes when examined at CIMMYT's El Batan Research Station in Mexico during the 2010 crop season. Similarly, Chris and the adult plant resistant lines developed by Knott (19, 20) showed PBC when examined at Njoro, Kenya.

Sr2 was detected in several highly resistant old, tall Kenyan varieties, including Kenya Plume (45), and CIMMYT-derived semidwarf wheats Pavon 76, Parula, Kritati, and Kingbird (32, 43). These CIMMYT wheats were susceptible in seedling greenhouse tests with Ug99 but showed high levels of adult plant resistance to Ug99 in field trials conducted since 2005 in Kenya and Ethiopia. Characterization of mapping populations for adult plant resistance and initial molecular mapping indicate a complex inheritance of resistance that involves the presence of *Sr2* and other minor genes at various genomic regions (S. Bhavani, J. Huerta-Espino, P. Njau, R.P. Singh, unpublished CIMMYT studies). Pleiotropic slow rusting resistance genes *Lr34/Yr18/Pm38*, *Lr46/Yr29/Pm39*, and *Lr67/Yr46*, which are known to confer slow rusting/mildewing to leaf rust, stripe rust, and powdery mildew, are also implicated in complex adult plant resistance to stem rust (6, 9, 10). Several ongoing mapping studies are expected to enhance the understanding of adult plant resistance to stem rust in coming years.

Deploying Ug99-Resistant Wheats

Several actions have been undertaken to reduce the Ug99 risk in several countries of Africa, the Middle East, and Asia: (a) promoting Ug99-resistant varieties, (b) including resistant wheat materials in National Variety Registration Trials, and (c) testing and simultaneously multiplying seed of existing high-yielding, resistant wheats from international centers with potential to become varieties. An aggressive strategy to promote resistant varieties in farmers' fields is the only viable option because both resource poor and commercial farmers in most of Africa, the Middle East, and Asia cannot afford chemical control or may not apply chemicals in the event of large-scale epidemics due to their unavailability for timely application. If cropping of susceptible varieties decreases throughout the primary risk area, this should further reduce wind dispersal of spores from these areas to other regions.

To implement the above strategy, Ug99 resistance screening has been conducted in Kenya and Ethiopia since 2005 on wheat materials from 22 countries. Several varieties with adequate resistance to Ug99 were identified in India (list available at <http://www.dwr.in>). Iran released variety Morvarid and 10 additional lines are undergoing advanced stages of testing and simultaneous seed multiplication. Pakistan, Nepal, and Bangladesh released varieties Lasani 2008, BL3063, and Bari Gom 26, respectively, from wheat materials that were in advanced stages of registration trials. These varieties have moderate levels of resistance to Ug99. Because most target countries do not have Ug99, or (with the exception of Kenya) an epidemic has not occurred in countries where Ug99 occurs, it is not a simple task to promote resistant materials to farmers who have not seen stem rust devastation for a long time, unless these materials show additional advantages such as resistance to stripe rust or leaf rust and significantly higher yield performance than current varieties. CIMMYT initiated grain yield performance and adaptation trials of Ug99-resistant materials in the 2006–2007 crop season through a special

Table 3 Ug99-resistant wheat varieties released or in advanced stages of variety registration trials in eight countries of Africa and Asia with their reaction to Ug99 in Kenya during 2010 and likely resistance genes

Country released	Variety name	CIMMYT name or cross	Stem rust reaction ^a	Ug99 resistance
Afghanistan	Koshan 09	Quaiu #1	40 MR	<i>Sr2, SrTmp</i>
Afghanistan	Muqawim 09	Oasis/SKauz//4*Bcn/3/2*Pastor	10 R	<i>Sr2, Sr25</i>
Afghanistan	Baghlan 09	Picaflo#1	5 MS	APR ^b (<i>Sr2+</i>)
Afghanistan		Chonte#1	5 MS	APR (<i>Sr2+</i>)
Bangladesh		Frankolin#1	10 MS-S	APR (<i>Sr2+</i>)
Egypt	Misir 1	Oasis/SKauz//4*Bcn/3/2*Pastor	10 R	<i>Sr2, Sr25</i>
Egypt	Misir 2	Skauz/Bav92	10 R	<i>Sr2, Sr25</i>
Ethiopia	Danda	Danphe#1	1 MS	APR (<i>Sr2+</i>)
Ethiopia	Kakaba	Picaflo#1	5 MS	APR (<i>Sr2+</i>)
India	Super 152	Pfau/Seri.1B//Amad/3/Waxwing	30 MS-S	APR (<i>Sr2+</i>)
India	Super 172	Munal#1	15 MS-S	APR (<i>Sr2+</i>)
India	Baz	Waxwing/4/Sni/Trap#1/3/Kauz*2/Trap//Kauz	10 MR-MS	APR (<i>Sr2+</i>)
India	Ufan	Frankolin#1	10 MS-S	APR (<i>Sr2+</i>)
Kenya	Robin	Babax/Lr42//Babax*2/3/Tukuru	15 R-MR	<i>Sr2, SrTmp</i>
Kenya	Eagle 10	Emb16/Cbrd//Cbrd	10 R-MR	<i>SrCbrd</i>
Nepal		Frankolin#1	10 MS-S	APR (<i>Sr2+</i>)
Nepal		Picaflo#1	1 MS	APR (<i>Sr2+</i>)
Nepal		Danphe#1	1 MS	APR (<i>Sr2+</i>)
Pakistan	NR356	Oasis/SKauz//4*Bcn/3/2*Pastor	10 R	<i>Sr2, Sr25</i>

^aUg99 reaction recorded when susceptible check Cacuke became necrotic approximately one week after displaying 100 S reaction; it has two components, percent disease severity based on the modified Cobb Scale (34) and host response as described by Roelfs et al. (39). Abbreviations: R, resistant (small uredinia surrounded by necrosis or chlorosis); MR, medium-sized uredinia surrounded by necrosis or chlorosis; MS, medium-sized uredinia without chlorosis or necrosis; S, large-sized uredinia without chlorosis or necrosis.

^bAdult plant resistance based on the *Sr2* complex.

multi-location yield trial grown in various countries. This effort was successful and several varieties were released in eight countries (Table 3). Various seed production and promotion activities are underway in all of these countries with the collaboration of national programs, private seed companies, farmers, and international organizations, such as CIMMYT, ICARDA, and FAO (17). The primary seed multiplication objective is to ensure that at least 5% of all production environments in high-risk countries are occupied by Ug99-resistant varieties. Thanks to seed multiplication efforts, sufficient seed will be available to cover most of the area in case Ug99 is established. As they are released, additional resistant varieties will be promoted to ensure genetic diversity.

Breeding Ug99-Resistant Wheats

Breeding resistant wheat varieties that have superior yields than currently grown popular varieties is the best option and can be achieved by utilizing race-specific resistance genes or minor genes that confer adult plant resistance. The best practice for the utilization of the two types of resistance is described below.

Race-specific resistance. The fastest way to reduce the susceptibility of important wheat cultivars and the best new germplasm is to systematically incorporate combinations of diverse resistance genes through limited or repeated backcrossing. Because most of the useful Ug99-effective genes are of alien origin,

available cosegregating molecular markers can aid in their selection (43). Markers for additional effective race-specific resistance genes are also being developed. Molecular markers provide a powerful tool for identifying plants that carry combinations of resistance genes. Where the alien stem rust resistance genes are linked to leaf rust resistance genes, screening for leaf rust in seedlings or adult plants can also be practiced in countries where Ug99 is absent.

One major issue remains: Several currently effective resistance genes are already present in advanced breeding materials that are being tested or under development in various countries. For example, varieties have been released in Egypt, Afghanistan, and Pakistan whose resistance is based on single race-specific gene *Sr25* and slow rusting resistance gene *Sr2* (Table 3). The prospect of devoting resources during the next four to six years to developing combinations of genes that are already in the hands of many wheat breeding groups and the fact that there is no legislation or obligation to stop the release of cultivars carrying single resistance genes have prompted the CIMMYT wheat improvement group to focus their efforts on breeding adult plant resistance based on minor genes, especially for high-risk areas, i.e., areas where the pathogen is expected to survive for several years because of the presence of susceptible hosts and favorable environmental conditions. It is believed that this strategy will lead to more durable resistance and will allow other areas of the world, especially facultative and winter wheat areas, to use race-specific resistance genes more successfully in their breeding program.

Adult plant resistance. Breeding for complex adult plant resistance that requires accumulating four to five minor, slow rusting resistance genes to achieve high levels of resistance is a difficult task. This difficulty is compounded by the absence of disease pressure caused by race Ug99 at most breeding sites and the lack of molecular markers associated with genes contributing to resistance. Molecular markers or the phenotypic marker PBC, which is linked

to the slow rusting resistance gene *Sr2*, can be used in selection; however, selection of *Sr2* alone will not confer adequate resistance. Screening CIMMYT advanced breeding materials for stem rust in Kenya since 2005 has resulted in the identification of 15%–20% of tested lines that show adequate levels of resistance under heavy disease pressure. These lines have been distributed worldwide annually since 2006 through the first to fifth Stem Rust Resistance Screening Nurseries. The resistance of several lines in these nurseries is based on genes conferring adult plant resistance (32).

Because a large portion of CIMMYT's high yielding spring wheat germplasm does not carry effective race-specific resistance genes to Ug99 and several lines were identified as possessing moderate levels of resistance, this was viewed as an ideal opportunity to reconstitute high levels of adult plant resistance in newer wheat materials. A targeted shuttle breeding scheme between two Mexican field sites and a field site in Njoro, Kenya, was initiated in 2006 with the purpose of transferring adult plant resistance identified in semidwarf CIMMYT wheats to a range of important wheat materials. Two crops are sown per year in Mexico and Kenya to accelerate the breeding. Simple single backcrosses and three-way (top) crosses involving at least one parent with a high level of adult plant resistance to stem rust are performed, and large population sizes are managed in a selected-bulk selection scheme in BC₁/F₁-top through F₄/F₅ generations, followed by pedigree selection in F₅/F₆ generation (43). This strategy resulted in the successful identification of new high-yielding, near-immune wheat materials after the first breeding cycle (Table 4). Forty-one percent, or 298 entries, displayed near-immune or resistant categories of adult plant resistance under high stem rust pressure during the 2010 off- and main-crop seasons at Njoro, Kenya. These entries were included in extended grain yield performance trials under various conditions at CIMMYT's research station at Ciudad Obregon in northwestern Mexico during the 2010–2011 crop season. The best performing entries will be distributed

Table 4 Stem rust resistance responses of 728 high-yielding CIMMYT spring wheat entries derived from targeted Ug99 resistance breeding and retained after evaluating 1,258 entries for resistance to stem rust and stripe rust in Kenya, and for stripe rust, leaf rust, and other traits in Mexico, during the 2010 crop season

Resistance category	Stem rust Severity and reaction ^a	Entries	
		Number	Percent
Adult-plant resistance			
Near-immune resistant	1 MS-S	120	16.5
Resistant	5–10 MS-S	178	24.5
Resistant-moderately resistant	15–20 MS-S	199	27.3
Moderately resistant	30 MS-S	63	8.7
Moderately resistant–moderately susceptible	40 MS-S	34	4.7
Moderately susceptible	50–60 MS-S	27	3.7
Moderately susceptible-susceptible	70–80 MS-S	5	0.7
Susceptible	100 S	2	0.3
Race-specific genes			
<i>Sr25</i>	1–10 R-MR	17	2.3
<i>Sr26</i>	5–10 R-MR	9	1.2
<i>SrTmp</i>	1–40 MR-MS	49	6.7
<i>SrHw234</i>	30 MR-MS	1	0.1
<i>SrSha7</i>	1–10 R-MR	19	2.6
Other unknown genes	1–5 R-MR	5	0.7

^aUg99 reaction recorded when susceptible check Cacuke became necrotic approximately one week after displaying 100 S reaction; it has two components, percent disease severity based on the modified Cobb Scale (34) and host response as described by Roelfs et al. (39). Abbreviations: R, resistant (small uredinia surrounded by necrosis or chlorosis); MR, medium-sized uredinia surrounded by necrosis or chlorosis; MS, medium-sized uredinia without chlorosis or necrosis; S, large-sized uredinia without chlorosis or necrosis.

through international yield trials and screening nurseries in 2011. However, between 0.5 and 40 kg of seeds of a smaller set of entries were sent to seven countries for testing and seed multiplication. We expect that some of these new wheat materials showing a near-immune level of adult plant resistance to stem and other rusts, significantly superior yield potential, and end-use quality comparable to that of currently grown varieties will be released in countries to which CIMMYT-derived wheats are adapted.

CONCLUSION

The Ug99 group of races of the stem rust fungus is widely recognized as a threat to wheat production worldwide because of the races' fast

evolution and migration, and as a threat to the susceptibility of wheat varieties grown on over 90% of the world's wheat area. The Borlaug Global Rust Initiative was launched in 2005 to coordinate, support, promote, and advocate for a concerted global effort to mitigate the Ug99 threat. The evolution and migration of the Ug99 group of races are being monitored carefully to be able to provide early warning in case of an epidemic. This would allow farmers to apply chemical controls, if necessary, and guide decision making. Most popular varieties in Africa, the Middle East, and Asia are 10 to 15 years old, and it is appropriate that they be replaced by new, more productive resistant varieties now being released in various countries. Significant progress is made in breeding new superior yielding spring wheat germplasm that

has a high level of adult plant resistance to stem and other rusts. Reducing the area currently occupied by susceptible wheat varieties should become the highest priority. It is highly advisable to release and promote varieties that have

durable adult plant resistance or have effective race-specific resistance genes in combinations to prevent further evolution and selection of new virulences that lead to boom-and-bust cycles of production.

DISCLOSURE STATEMENT

All authors are active scientists contributing through their research and expertise to various objectives of the Borlaug Global Rust Initiative launched to mitigate the Ug99 threat and develop wheat germplasm and varieties with durable rust resistance.

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