

Field Resistance to the Ug99 Race Group of the Stem Rust Pathogen in Spring Wheat Landraces

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Abstract

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Wheat landraces provide a source of genetic variability for breeding. The emergence and spread of highly virulent races of the stem rust pathogen (Ug99 race group of *Puccinia graminis* f. sp. *tritici*) threaten wheat production globally. Spring wheat landraces were screened for resistance in eight field seasons at the Kenya Agricultural Research Institute, Njoro, where the Ug99 race group has become endemic. Accessions showing resistance in one season were retested and screened with molecular markers associated with resistance genes *Sr2*, *Sr24*, *Sr36*, and *Lr34/Yr18*; two height-reducing genes; and a photoperiod insensitivity allele. Of 2,509 accessions tested, 278 were categorized as resistant based on results from at least two seasons. Of these

resistant accessions, 32 were positive for one or more markers for *Sr2*, *Sr36*, *Rht-B1b*, or *Rht-D1b*, indicating that they do not fit the definition of “landrace” because these genes were likely introduced via modern breeding practices. Thus, 246 resistant “landrace” accessions were identified. Of countries with more than five tested accessions, Afghanistan, Iran, Portugal, Ethiopia, Uzbekistan, Greece, Tajikistan, Bosnia and Herzegovina, and Serbia had at least 10% of tested accessions that were resistant to the Ug99 race group. Future research will characterize the resistance to determine its novelty and incorporate novel genes into improved lines.

Plant disease epidemics causing severe economic loss are often associated with a narrow genetic base of resistance in the host plant (9,56). Recently, wheat production worldwide has been threatened by the emergence and long-distance migration of a newly detected race of *Puccinia graminis* f. sp. *tritici*, the cause of stem rust disease of wheat (*Triticum aestivum* subsp. *aestivum*). A key element of this new threat is the narrow genetic base for stem rust resistance in most of the wheat-producing areas of the world. Race TTKSK (16), commonly referred to as “Ug99”, was reported in Uganda in 1999 (38) and has spread to Kenya, Ethiopia, Sudan, Yemen, (47), Tanzania (12), and Iran (31). Several races related to Ug99 have been reported in South Africa (37) and Zimbabwe (29). The broad and unique combination of virulences found in the Ug99 race group, including *Sr31* virulence, has led to estimates that 90% of the wheat cultivars grown globally are susceptible to the new races (46). Hence, stem rust may cause severe yield loss if the new races spread further to major production regions, such as South Asia, where they have not yet been reported (34,46).

To broaden the genetic base of stem rust resistance in wheat, breeders must have access to genetically diverse resistance sources,

such as those maintained in germplasm banks worldwide. The importance of conserving plant genetic diversity has been recognized for decades, and for wheat there are between 410,000 (49) and 800,000 accessions maintained in approximately 80 germplasm banks around the world (34). For genetic diversity to be put to practical use, though, it not only needs to be conserved but also must be characterized to identify its potential (14,49). Presently, phenotypic evaluation of important traits is a limiting factor for the movement of genes from germplasm banks into breeding programs. Phenotypic evaluation of diverse genetic resources can be particularly challenging due to variation in phenology and growth habit (14). Rapid molecular assessments can complement physiologic and phenotypic data (24). However, it is unlikely that evaluations in field environments can be replaced in efforts to make resources from germplasm banks available to breeders.

Landraces of wheat provide a useful source of genetic variability for breeding. Landraces are associated with traditional farming systems, were developed without formal plant breeding processes, and are believed to be genetically diverse (55,56). In most wheat-producing areas, wheat landraces have been replaced with varieties that are the product of intentional breeding practices. However, in marginal environments where subsistence farming predominates, landraces are still grown and provide a source of genetic variability that may not be currently available in germplasm banks (55).

In response to recent awareness of the threat posed by the Ug99 stem rust race group, the global wheat community has formed international collaborations to quickly and effectively screen wheat germplasm for new sources of stem rust resistance (15,32,40, 41,43). The United States Department of Agriculture–Agricultural Research Service (USDA-ARS) National Small Grains Collection (NSGC) in Aberdeen, ID maintains nearly 10,000 spring-habit common wheat landraces among the 59,442 *Triticum* accessions within the collection. This germplasm has been acquired from

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around the world through collections and donations. Our objective was to screen a subset of the wheat landraces from the NSGC for field resistance to the Ug99 stem rust race group for the purpose of identifying new sources of resistance. Through a collaborative effort, landraces were grown in a field nursery in Kenya, where the Ug99 race group is now endemic. Resistant accessions were further characterized by surveying with molecular markers for genes with known breeding origins, including *Sr36* and *Sr2*, which are effective against the new races.

Materials and Methods

Plant materials. Common wheat, spring-habit landraces from the NSGC were selected for screening for adult-plant field resistance to the Ug99 group of races of *P. graminis* f. sp. *tritici* at the Kenya Agricultural Research Institute, Njoro, beginning in 2007. Because space was limited in the nursery, screening priority was given to accessions most likely to be resistant to the new races. The first 1,000 entries were selected either by geographic origin based on previous analysis of NSGC data (5), adult field resistance to a composite of stem rust races in a Minnesota nursery (data from the Germplasm Resources Information Network [GRIN]), or randomly. Subsequent selections were limited to landraces with seedling resistance to *P. graminis* f. sp. *tritici* race QFCSC, the predominant race found in the United States since 2003 (17), based on an assumption that resistance to QFCSC might be associated with resistance to the new races. In general, accessions with no previous field data on their reaction to Ug99 were selected for testing each June-to-October growing season (main season). Resistant accessions were validated in the following December-to-April season (off-season) and, in some cases, again in subsequent seasons.

Field nursery. Entries were hand planted in double-row plots, 1 m in length. Double-row plots of the stem rust susceptible 'Red Bobs' were planted every 50 entries. Perpendicular to the entry plots, a mixture of Kenyan cultivars with *Sr31* and *Sr24* were planted in rows of hill plots as spreader rows. To select for *Sr31* and *Sr24* virulence in the inoculum source, inoculum was increased in field plots of wheat varieties with *Sr31* and *Sr24*. At the jointing growth stage, the spreader rows were inoculated with spores collected from the inoculum-source plots. Only the spreader rows were inoculated, and experimental plots were exposed to spores that dispersed from the inoculated plants and also to any background inoculum present.

Disease ratings and data summarization. The optimal plant growth stage for stem rust rating is considered to be soft dough,

because the disease has had maximum time to develop yet symptoms and signs are unaffected by host senescence. Efforts were made to stagger ratings over the period when the landraces reached soft dough, the timing of which varied among accessions. Experimental plots and Red Bobs checks were rated for stem rust severity on a scale of 0 to 100% stem area affected, following a modified Cobb scale (36), and for infection response using categorical scores based on the size of stem rust pustules and amount of associated chlorosis and necrosis. Infection response categories included the following, either singly or in combination: resistant (R), moderately resistant (MR), intermediate (M), moderately susceptible (MS), and susceptible (S) (39). Combinations of categories were recorded when two distinctly different infection responses occurred on a single stem (i.e., MR-MS ratings indicated MR pustules on the same stem as MS pustules). The predominant category was listed first, such that MR-MS differed from MS-MR. Within a season, the rating for an accession taken closest to soft dough stage was chosen for subsequent data analysis.

The disease severity for each accession in a test was calculated relative to that of the Red Bobs checks for that test and the mean relative disease severity values were calculated across tests. Infection responses for each accession were summarized by calculating the median infection response across tests. The infection responses comprised 15 categories, accounting for all recorded infection responses, including both single and combined ratings. The mean relative severities and median infection response values were used to categorize accessions as either resistant or susceptible. Resistance was defined as infection response categories R, MR-R, MR, MR-M, MR-MS, M-MR, and M, and infection responses M-MS and MS when the mean relative severity was less than 30% (Fig. 1). Including accessions with M-MS and MS infection responses and low disease severity allowed detection of rate-reducing forms of resistance that resulted in both lower severities and susceptible-type pustules.

To map the geographic origin of resistant and susceptible accessions, latitude and longitude data from GRIN for the original collection site were available for 1,615 accessions. For the remaining accessions, the center of the state or province ($N = 393$) or country ($N = 498$) was used, depending on the information available. Maps of the origin of resistant and susceptible accessions were constructed with JMP Genomics 5.1 (SAS Institute Inc.).

Molecular marker screening. Accessions that showed field resistance after initial testing were surveyed for eight genes or alleles using molecular markers (Table 1). These eight genes were se-

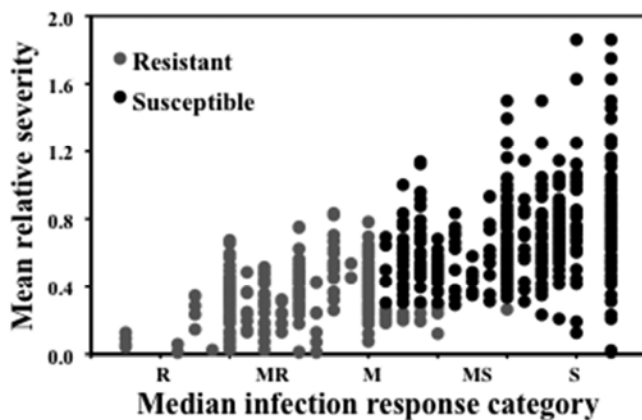


Fig. 1. Mean stem rust severity on a scale of 0 to 100, relative to susceptible checks, with 1 equaling the rating of the checks, plotted against the median infection response category for 2,253 spring-habit common wheat accessions screened for resistance to the Ug99 race group of *Puccinia graminis* f. sp. *tritici* during eight field seasons in Kenya. Each data point represents the mean rating of a single accession. Resistance was defined as either infection response categories intermediate (M) and more resistant, or categories M-MS and moderately susceptible (MS), where the mean severity was less than 30% of the susceptible checks.

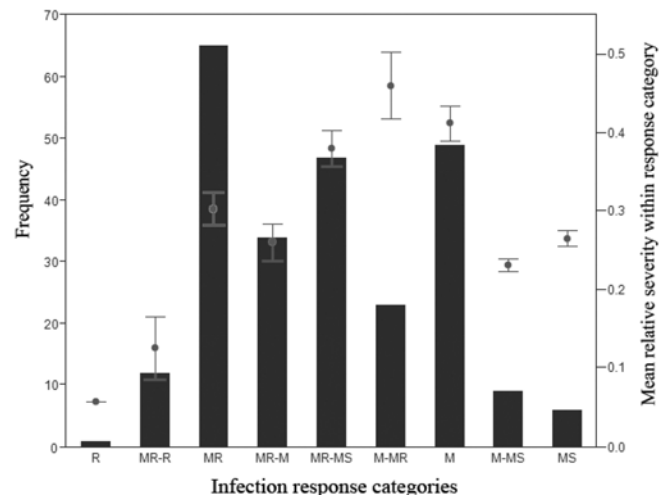


Fig. 2. Number of accessions in each stem rust infection response category and mean relative stem rust severity within each category for 246 spring-habit common-wheat landraces classified as resistant based on Kenya field tests. For each infection response category, bars indicate the frequency of accessions, points represent the mean relative stem rust severity, and error bars represent \pm one standard error of the mean.

lected for molecular marker screening to provide information about the genetic background of an accession and the likelihood that the field resistance was novel. For example, *Sr2* is effective to some degree in adult plants against Ug99 and *Sr24* and *Sr36* are effective in all growth stages against Ug99 and some of its variants; therefore, the presence of markers for these genes decreases the probability that an accession possesses novel Ug99 resistance. Similarly, the presence of markers for other genes originating from wide crosses or otherwise commonly found in modern cultivars indicates that the accession was likely developed through formal breeding and is not a landrace. Such accessions are more likely to possess known genes for Ug99 resistance compared with true landrace accessions. Marker selection was based on the combined factors of (i) tight linkage of the marker with the allele and (ii) alleles known to have originated from a source outside of the species or region from which the landraces were collected (28).

The *Sr* genes evaluated were all originally derived from species other than *T. aestivum* (28), and *Rht* dwarfing alleles are common in modern cultivars (11). Positive results for *Lr34/Yr18* (21 positives) and *PpdD-1a* (36 positives) markers were not considered inconsistent with a landrace classification. These genes are associated with multiple haplotypes that have arisen independently (*Lr34/Yr18*) (19) and a deletion mutation (*PpdD-1a*) (3), making it possible that the alleles could have arisen multiple times (3,7). Moreover, it is known that landraces from China frequently have the photoperiod insensitivity allele *PpdD-1a* (57).

Genomic DNA was extracted from leaf tissue harvested from a single seedling per accession. The leaf tissue was collected into 1.5-ml strip tubes in boxes of 96, lyophilized, and ground into powder using a shaker (Mixer Mill MM 300; Retsch) with steel beads placed in each sample. DNA was extracted using a cetyltrimethylammonium bromide method.

Molecular marker assays were conducted at the USDA-ARS Eastern Regional Genotyping Lab, Raleigh, NC. The presence of the short arm of rye chromosome one (1RS) was assayed with the rye-specific simple sequence repeat (SSR) for the *Xscm9* locus (44). SSR markers *Xbarc71* and *Xwmc477* were used to detect the *Lophopyrum elongatum*-derived segment carrying *Sr24* (20) and the *Sr36* gene derived from *T. timopheevii* (51), respectively. Protocols for polymerase chain reaction (PCR) and thermocycling were as reported by Olson et al. (33). Sizing of PCR products was performed by capillary electrophoresis using an ABI3130xl Genetic Analyzer (Applied BioSystems). Analysis of PCR fragments was performed using GeneMarker 1.60 software (SoftGenetics). Alleles at the *Sr2*, *Lr34/Yr18*, *Rht-B1*, and *Rht-D1* loci were assessed using allele-specific primers based on single nucleotide polymorphisms (SNPs) reported in the genes (11,19) or closely linked markers (21). The SNPs were assayed using the KASP technology (KBiosciences).

Results

In total, 2,509 landrace accessions maintained in the NSGC were screened for field resistance to the predominant races (gener-

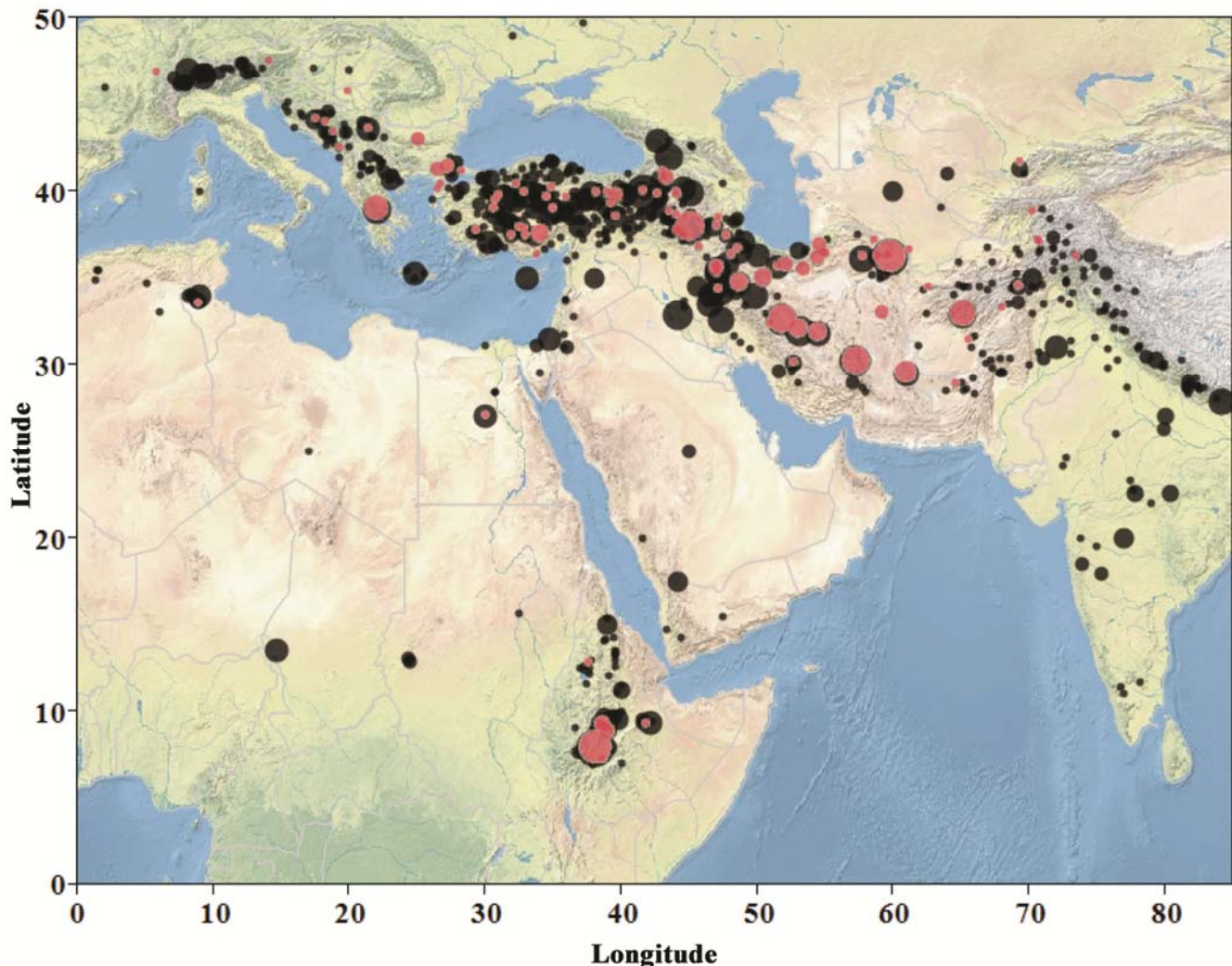


Fig. 3. Geographic origin of 2,470 spring-habit common-wheat landraces screened in Kenya and found to be either resistant (red circles) or susceptible (black circles) to the Ug99 race group of *Puccinia graminis* f. sp. *tritici*. Circle radius is a function of the number of accessions originating from each location.

ally races TTKSK and TTKST) in the Njoro stem rust nursery during eight consecutive seasons from 2007 to 2011. Of these, 278 accessions (Tables 2 and 3; Supplementary Table 1) were categorized as resistant, based on results from at least two seasons (mean = 3.8 seasons, SD = 1.8 season). In all, 85 of the resistant accessions exhibited low infection responses of R ($N = 4$), MR-R ($N = 12$), or MR ($N = 69$) (Tables 2 and 3). There were 2,231 accessions categorized as susceptible, in some cases based on a result from a single season.

In total, 39 accessions were positive for one or more of the molecular markers diagnostic for stem rust resistance genes *Sr2* (21 positives) and *Sr36* (6 positives) and height-reducing genes *Rht-B1b* (12 positives) and *Rht-D1b* (7 positives). Markers for *Sr24* and the IRS rye translocation were not detected among the accessions tested. The 39 accessions positive for one or more of the markers for *Sr2*, *Sr36*, *Rht-B1b*, or *Rht-D1b* were originally classified as landraces based on the information available from NSGC accession passport data. Considering the molecular marker results, these accessions do not appear to be landraces because they carry alleles that were likely introduced via modern breeding practices. Of the 39 accessions that appear to be misclassified as landraces, 32 were categorized as resistant (Table 3). Thus, 246 landraces with resistance to the TTKS race group were identified. Of the 246 resistant landraces, 78 were highly resistant, with infection responses of R ($N = 1$), MR-R ($N = 12$), or MR ($N = 65$) (Table 2).

Among the nine categories of infection responses for 246 landraces classified as resistant, the most common response was MR ($N = 65$), followed by M ($N = 49$) and MR-MS ($N = 47$) (Fig. 2). The average relative severity within each response category (Fig. 2) increased from R to MR-R to MR. Accessions within categories M-MS and MS were classified as resistant because they showed relative mean disease severities less than 30% in the field trials. These 15 accessions (9 M-MS and 6 MS) could have slow rusting resistance, with low relative severities but susceptible infection response types. Further work using larger field plots and within-season replication would be necessary to confirm such resistance.

Among the 32 resistant accessions considered misclassified as landraces (Table 3), the most common infection response category was MR-M ($N = 8$), followed by M ($N = 6$), MR and M-MS ($N = 4$ each), R and MS ($N = 3$ each), and MR-MS and M-MR ($N = 2$ each). Five accessions from Ethiopia and one from Pakistan having *Sr36* exhibited low disease ratings during most seasons (Table 3). The quantitative rust resistance genes *Sr2* and *Lr34/Yr18* were the most common resistance genes detected among accessions determined to be misclassified. The field responses of accessions having these genes varied (Table 3). There were seven misclassified susceptible accessions, all with infection response MS.

The landrace accessions screened in the Njoro nursery were originally collected from 67 countries, of which 37 countries had more than 5 tested accessions and 4 had more than 100 tested accessions (Table 4). Among the countries with more than five

tested accessions, Afghanistan, Iran, Portugal, Ethiopia, Uzbekistan, Greece, Tajikistan, Bosnia and Herzegovina, and Serbia exhibited resistance in at least 10% of the accessions screened (Table 4). Twenty countries with more than five tested accessions had no detected resistant accessions, of which India had the largest sample size ($N = 80$). There were 195 accessions tested from the contiguous region that includes India, Nepal, Bhutan, and most of Pakistan, except the far northwest border, and all were susceptible to Ug99. The largest geographic area with the highest density of resistant accessions is in the contiguous region that includes parts of Afghanistan, Iran, and Uzbekistan (Fig. 3).

Discussion

We evaluated common wheat landraces for resistance to the Ug99 race group over eight field seasons and identified 246 resistant accessions, or approximately 10% of the 2,470 tested, that fit the “landrace” classification. This percentage of resistance in spring wheat landraces is similar to the 12.6% rate of field resistance reported by Rouse et al. (43) from screening spring wheat breeding lines and cultivars developed before 1990. Of the 246 landrace accessions in which we detected some level of resistance, 78 (3% of the total tested) had median infection responses of MR, MR-R, or R and could be characterized as having strong field resistance to Ug99.

All of the resistant landrace accessions were tested in the field at least twice, with an average of 3.8 tests. Stem rust ratings varied greatly across seasons, possibly in relation to the health of the stand, intensity of stem rust disease pressure, interactions with other diseases, and growth stage at the time of the rating. Variation among landrace accessions in flowering dates, resistance to other pathogens, and propensity to lodge affected the stem rust ratings and increased the importance of repeat tests. The summary values for mean relative severity and median infection responses from all tests across seasons were used to classify accessions as either resistant or susceptible, partially accounting for the seasonal variability.

Examination of the disease severity and infection response scores for accessions positive for *Sr2* provides a gauge for assessing the reliability of the testing methodology, because the response conferred by *Sr2* has been assessed in other studies. When *Sr2* is the only stem rust resistance gene present in a cultivar, it is not expected to be highly effective against Ug99 (46). The *Sr2*-positive accessions in the present study were frequently classified as resistant in the final summary ratings (17 of 22). In addition, the resistant *Sr2*-positive accessions tended to be close to the susceptible cut-off, as might be expected because *Sr2* confers only partial resistance in adult plants (23).

Results from the molecular marker survey provided evidence that 39 of the 2,509 accessions included in this report are most likely the product of modern breeding. Although the definition of landrace (55) is relatively clear when the history of an accession is

Table 1. Wheat genes and linked molecular markers evaluated during a survey of common wheat landraces with field resistance to the Ug99 race group of *Puccinia graminis* f. sp. *tritici*

Gene	Chromosome arm	Source ^a	Marker type ^b	Marker name ^a
IRS translocation (<i>SrIRS^{Amigo}</i> and <i>Sr31</i>)	1RS:1AL, 1RS:1BL	Interspecific crosses between <i>Secale cereale</i> ‘Petkus’ introduced into ‘Kavkaz’ wheat and ‘Imperial’ rye into ‘Gabo’ wheat (22)	SSR	<i>scm9</i> (44)
<i>Sr2</i>	3BS	Interspecific cross between tetraploid emmer (<i>Triticum turgidum</i> subsp. <i>dicoccon</i>) and Marquis (26)	SNP	<i>csSr2</i> (21)
<i>Sr24</i>	3DL, 1BS	<i>Agropyron elongatum</i> (27,45)	SSR	<i>barc71</i> (20)
<i>Sr36</i>	2BS	Interspecific cross with <i>T. timopheevii</i> (1)	SSR	<i>wmc477</i> (51)
<i>Lr34/Yr18/Pm38</i>	7DS	‘Frontana’, Brazilian cultivar, originally from Italian ‘Mentana’ and ‘Ardito’ (18)	SNP	<i>cssfr6</i> and <i>cssfr7</i> (19)
<i>Rht-B1b</i>	4BS	‘Norin 10’, Japanese cultivar, originally from Shiro Daruma, a Japanese landrace (14)	SNP	(8)
<i>Rht-D1b</i>	4DS	Norin 10	SNP	(8)
<i>Ppd-D1a</i>	2DS	Akakomugi	STS	<i>Ppd-D1</i> (2Dins) (3)

^a Numbers in parentheses indicate literature citations.

^b SSR = simple sequence repeat and SNP = single nucleotide polymorphism.

Table 2. Stem rust ratings by season and molecular marker results for 78 spring-habit common-wheat landrace accessions with median infection responses of R, MR, or MR-R to the Ug99 race group of *Puccinia graminis* f. sp. *tritici* in Kenya field tests^a

Accession	Country	Fall 2007	Spring 2008	Fall 2008	Spring 2009	Fall 2009	Spring 2010	Fall 2010	Spring 2011	Mean severity ^b	Median response ^c	Marker positives
Red Bobs ^d	Check	40 (5.5) S	60 (1) S	72 (1.0) S	60 (0) S	48 (1.8) S	64 (4.0) S	43 (2.7) S	40 (2.1) S	1.0	S	...
PI 362698	Montenegro	R	10 M	5 R	10 MS	Tr R-MR	Tr R	0 R	0 R	0.05	R	<i>Lr34/Yr18</i> , <i>Ppd-D1a</i>
PI 387480	Ethiopia	Tr MR	0 R	0.01	MR-R	...
PI 480360	Ethiopia	Tr MR	0	0.01	MR-R	...
PI 480385	Ethiopia	Tr MR	0 R	0.01	MR-R	...
PI 480390	Ethiopia	Tr MR	0 R	0.01	MR-R	...
PI 480392	Ethiopia	Tr MR	0 R	0.01	MR-R	...
PI 480401	Ethiopia	Tr MR	0 R	0.01	MR-R	...
PI 554456	Turkey	5 MR	0 R	0.06	MR-R	...
PI 387254	Ethiopia	10 MR-MS	30 MS	5 R-MR	Tr R	5 MR	0 R	0.15	MR-R	...
PI 623538	Iran	30 R-MR	40 M	5 R-MR	5 MR	5 MR	Tr R-MR	0.23	MR-R	...
PI 479908	Ethiopia	40 MS	5 R-MR	Tr R	Tr MR	...	0.29	MR-R	...
PI 625471	Iran	15 MR	15 R-MR	0.34	MR-R	...
PI 626491	Iran	20 MR	...	20 R-MR	0.35	MR-R	...
PI 352163	Austria	Tr R	Tr MR-MS	0.02	MR	...
PI 387343	Ethiopia	Tr MR	Tr MR	0.02	MR	...
PI 387419	Ethiopia	Tr MR	Tr MR	0.02	MR	...
PI 470806	Ethiopia	Tr MR	Tr MR	0.02	MR	...
PI 480376	Ethiopia	Tr MR	Tr MR	0.02	MR	...
PI 480386	Ethiopia	Tr MR	Tr MR	0.02	MR	...
PI 480391	Ethiopia	Tr MR	Tr MR	0.02	MR	...
PI 625285	Iran	Tr MR	Tr MR	0.02	MR	...
PI 94439	Russian Federation	5 M	Tr R	Tr MR	0.04	MR	...
PI 479825	Ethiopia	5 MR	Tr MR	0.07	MR	...
PI 554450	Turkey	5 MR	Tr MR	0.07	MR	...
CItr 14626	Ethiopia	5 MR-MS	5 MR	0 R	...	0.09	MR	...
PI 625673	Iran	5 MR	5 MR	0.12	MR	...
PI 374670	Bosnia and Herzegovina	5 MR	10 M	10 R-MR	10 MR	20 MR-MS	0 R	Tr MR	Tr MR-MS	0.13	MR	...
CItr 14732	Ethiopia	20 MR	Tr R	5 MR	...	0.18	MR	...
PI 480388	Ethiopia	20 MR	...	5 R	30 M	10 MR	Tr R	Tr MR	Tr MR	0.19	MR	...
PI 181433	Afghanistan	10 MR	20 MS-S	5 R-MR	10 MR	5 MR	...	0.19	MR	...
PI 166303	Turkey	20 MR	Tr R	10 MS-S	0.20	MR	...
PI 624336	Iran	10 R-MR	10 MR	10 MR	...	0.20	MR	...
PI 178054	Turkey	15 MR-MS	15 MR	5 MR	...	0.22	MR	<i>Lr34/Yr18</i>
PI 623162	Iran	15 MR	10 MS-S	Tr R-MR	15 MR	15 MR	...	0.23	MR	...
PI 625661	Iran	10 MR	40 MS	15 R-MR	Tr R	5 MR	...	0.25	MR	...
PI 480384	Ethiopia	20 MR	50 MS-S	10 MR	Tr R	0 R	Tr MR	0.27	MR	...
PI 559962	Ethiopia	25 MS	10 MR	10 R	1 R	...	60 MS-S	5 MR	Tr MR	0.29	MR	...
PI 117755	Greece	20 MR	10 MR	40 MR-MS	...	10 MR	Tr	0.29	MR	...
PI 184639	Greece	30 MR	30 M	10 R-MR	10 MR	20 R-MR	Tr MR	0.30	MR	<i>Lr34/Yr18</i>
PI 101567	China	30 MR	10 R	5 MR	...	0.30	MR	...
PI 177906	Turkey	30 MR	10 MR	5 MR-R	...	0.30	MR	...
PI 625696	Iran	30 R-MR	30 MS	15 R-MR	5 MR	10 MR-M	...	0.31	MR	...
PI 184221	Serbia	40 MR	...	20 MR	5 MR	10 R-MR	...	0.32	MR	...
PI 243779	Iran	10 MR	30 M	5 MR	0.33	MR	...
PI 626573	Iran	10 MR	20 M	20 MR	40 M	Tr R-MR	30 MR	10 MR	15 MS	0.33	MR	...
PI 623757	Iran	20 MR-MS	30 M	20 R-MR	20 MR	5 MR	5 MR	0.33	MR	...
PI 626308	Iran	40 MR	...	5 MR	0.33	MR	...
PI 626409	Iran	20 MR	40 MS	15 R-MR	20 MR	5 MR	15 MR-MS	0.34	MR	...
PI 166675	Turkey	5 R-MR	15 MR	30 M	...	0.35	MR	...
PI 626074	Iran	30 MR	...	20 R-MR	...	10 M	...	0.36	MR	...
PI 117494	Greece	30 MR	40 M	20 MR	10 M	20 MR	Tr MR	0.36	MR	...
PI 116310	Portugal	15 MR	20 M	50 MS	30 MR	30 MR	5 MR	10 MR	Tr MR-MS	0.36	MR	...
PI 626252	Iran	40 MR	20 M	20 R-MR	10 MR	20 MR	10 MR-MS	0.36	MR	...
PI 626634	Iran	20 MS	15 M	40 MR	50 MS	30 R-MR	Tr R	5 MR	Tr MR	0.37	MR	...
PI 429407	Iran	40 MR	50 M	10 R-MR	...	5 MS	5 MR	0.37	MR	...
PI 623517	Iran	10 MR	40 S	30 R-MR	15 MR	5 MR	...	0.38	MR	...
PI 624149	Iran	20 MR	30 M	10 R-MR	30 MR	10 MR-M	...	0.38	MR	...
PI 623582	Iran	20 MR	30 R-MR	20 MR	10 MR	10 MR-MS	0.38	MR	...
PI 166758	Turkey	5 MR	10 R	40 M	...	0.40	MR	...
PI 165193	Turkey	20 MR	20 MR	20 M	...	0.40	MR	...
PI 177881	Turkey	20 MR	20 MS	20 MR	...	0.40	MR	...
PI 623164	Iran	40 MR	40 MS-S	15 R-MR	15 MR	10 MR	...	0.40	MR	...

(continued on next page)

^a Ratings included stem rust severity as percent stem area affected on a scale of 0 to 100, and infection response categories of resistant (R), moderately resistant (MR), intermediate (M), moderately susceptible (MS), and susceptible (S), either singly or in combination; Tr = trace. For Red Bobs, standard error of the mean is shown in parentheses.

^b Mean relative severity.

^c Median infection response.

^d Susceptible check.

Table 2. (continued from preceding page)

Accession	Country	Fall 2007	Spring 2008	Fall 2008	Spring 2009	Fall 2009	Spring 2010	Fall 2010	Spring 2011	Mean severity ^b	Median response ^c	Marker positives
PI 625315	Iran	0 R	15 MR	40 MR	0.40	MR	...
PI 166684	Turkey	20 MR	50 MS	20 MR	30 MR	5 MR	...	0.42	MR	...
PI 480375	Ethiopia	50 MS	20 MR	Tr R	Tr MR	...	0.43	MR	...
PI 623785	Iran	40 MR	50 M	10 R-MR	20 MR	10 MR-M	...	0.43	MR	...
PI 341431	Turkey	30 MR	15 MR	0 R	...	0.43	MR	...
PI 626389	Iran	60 MR	...	20 R-MR	20 MR	10 MR-M	...	0.45	MR	...
PI 623118	Iran	40 MR	50 M	15 R-MR	20 MR	10 MR	...	0.45	MR	...
PI 479828	Ethiopia	60 MR-MS	10 MR	50 MR-MS	10 MR	30 MR	15 S	10 MR	Tr MR	0.46	MR	...
PI 623197	Iran	40 R-MR	30 MS-S	30 R-MR	...	10 MR	15 MR-MS	0.46	MR	...
PI 181378	Afghanistan	20 R-MR	70 S	Tr R	15 MR-MS	0.46	MR	...
PI 178188	Turkey	20 MR	20 MS	30 R-MR	20 MR	30 S-MS	...	0.49	MR	...
PI 116226	Greece	50 MS	15 MR	5 MR	20 MR	...	0.53	MR	...
PI 623355	Iran	30 MR	50 MR	10 MR	15 MR	...	0.57	MR	...
PI 167531	Turkey	15 R-MR	20 MR	50 M	...	0.60	MR	...
PI 165700	Afghanistan	20 MR	40 S	20 MR	20 MR	60 S	...	0.66	MR	...
Cltr 15035	Afghanistan	50 MR	70 S	10 MR	5 R	0.68	MR	...

Table 3. Stem rust ratings by season and molecular marker results for 32 spring-habit common wheat accessions that were likely misclassified as landraces with field resistance to the Ug99 race group of *Puccinia graminis* f. sp. *tritici* in Kenya field tests^a

Accession	Country	Fall 2007	Spring 2008	Fall 2008	Spring 2009	Fall 2009	Spring 2010	Fall 2010	Spring 2011	Mean ^b	Median response ^c	Marker positives
PI 480270	Ethiopia	5 R	1 R	0 R	Tr R	...	0.04	R	<i>Ppd-D1a</i> mixed, <i>Sr36</i> mixed
PI 480280	Ethiopia	10 R-MR	10 MS-S	Tr R	5 R	0 R	Tr R	Tr R	...	0.09	R	<i>Ppd-D1a</i> , <i>Sr36</i>
PI 480278	Ethiopia	15 R-MR	10 M	Tr R	10 MR	0 R	Tr R	Tr R	...	0.13	R	<i>Ppd-D1a</i> , <i>Sr36</i>
PI 436218	Chile	5 MR	Tr MR	0.07	MR	<i>Rht-B1b</i>
PI 480274	Ethiopia	5 MR	15 S	0 R	0.19	MR	<i>Ppd-D1a</i> , <i>Sr36</i>
PI 625192	Iran	20 R-MR	20 MS	5 R-MR	10 MR	15 MR	Tr MR	0.21	MR	<i>Lr34/Yr18</i> , <i>Ppd-D1a</i> , <i>Rht-B1b</i>
PI 349471	Switzerland	15 MR	15 MS-S	20 R	50 MS-S	20 MR	20 MS-S	10 MR	...	0.39	MR	<i>Sr2</i>
PI 349458	Switzerland	5 R	10 MR	20 M	15 MR-M	...	0.25	MR-M	<i>Sr2</i>
PI 349505	Switzerland	5 R	50 MS-S	10 R-MR	40 S	15 MR-M	5 MR	0.37	MR-M	<i>Lr34/Yr18</i> mixed, <i>Sr2</i>
PI 470799	Ethiopia	5 MR	Tr MR-MS	0.07	MR-M	<i>Ppd-D1a</i> , <i>Rht-B1b</i>
PI 366079	Egypt	5 MR	5 MR-MS	0.12	MR-M	<i>Sr2</i>
PI 321947	Turkey	10 MR	5 MR-MS	0.18	MR-M	<i>Sr2</i>
PI 565239	Bolivia	5 MR	10 MR-MS	0.18	MR-M	<i>Lr34/Yr18</i> , <i>Ppd-D1a</i> , <i>Rht-D1b</i>
PI 349517	Switzerland	5 MR	15 M	5 R	60 MS-S	5 MR-MS	10 MR	10 MR	Tr MR-MS	0.25	MR-M	<i>Sr2</i> mixed
PI 381970	Iran	10 MR	15 MR-MS	0.30	MR-M	<i>Lr34/Yr18</i> , <i>Ppd-D1a</i> , <i>Rht-B1b</i> , <i>Sr2</i>
PI 349452	Switzerland	20 MR	15 S	20 R	40 MS	5 MR	20 MS-S	15 M-MR	5 MR	0.32	MR-MS	<i>Sr2</i> mixed
PI 223898	Afghanistan	10 MR	40 M	Tr MR-MS	0.37	MR-MS	<i>Lr34/Yr18</i> mixed, <i>Rht-D1b</i> mixed
PI 480279	Ethiopia	1 MS	0 R	0.01	M-MR	<i>Ppd-D1a</i> , <i>Sr36</i>
PI 349513	Switzerland	10 R-MR	60 MS-S	10 MR-MS	15 S	10 M-MR	...	0.36	M-MR	<i>Sr2</i>
PI 602440	Ethiopia	5 MR	10 MS	0.18	M	<i>Lr34/Yr18</i> , <i>Ppd-D1a</i> , <i>Rht-B1b</i>
Cltr 14811	Eritrea	S	20 MR	20 MS	Tr R-MR	...	0.25	M	<i>Ppd-D1a</i> mixed, <i>Rht-B1b</i> mixed
PI 478031	Pakistan	10 MS	20 MS-S	10 MR	...	10 MR	...	0.26	M	<i>Ppd-D1a</i> mixed, <i>Sr36</i> mixed
PI 119358	Turkey	5 R-MR	30 MS-S	10 R-MR	30 MS	20 MS	10 MS	10 MR	Tr MR	0.26	M	<i>Sr2</i>
PI 349509	Switzerland	5 R-MR	20 S	20 R	60 S	15 R-MR	40 MS-S	10 M	...	0.42	M	<i>Sr2</i>
PI 436341	Chile	10 MR	30 MS	0.44	M	<i>Ppd-D1a</i> , <i>Sr2</i>
PI 470794	Ethiopia	Tr MR	15 MS-S	0.20	M-MS	<i>Lr34/Yr18</i> , <i>Ppd-D1a</i> , <i>Rht-B1b</i>
PI 565210	Bolivia	10 MR	10 MS-S	0.24	M-MS	<i>Ppd-D1a</i> , <i>Sr2</i>
PI 381971	Iran	Tr MR	20 MS-S	0.26	M-MS	<i>Lr34/Yr18</i> , <i>Ppd-D1a</i> , <i>Rht-B1b</i> , <i>Sr2</i>
PI 626405	Iran	Tr MR-M	15 MS-S	0.20	M-MS	<i>Ppd-D1a</i> , <i>Rht-B1b</i> , <i>Rht-D1b</i> , <i>Sr2</i>
PI 124278	China	10 S	10 MR	...	0.19	MS	<i>Sr2</i>
PI 480100	Ethiopia	5 M-MR	5 MS-S	0.12	MS	<i>Lr34/Yr18</i> , <i>Ppd-D1a</i> , <i>Rht-B1b</i>
PI 321981	Turkey	10 MR	20 MS-S	10 MS	0.26	MS	<i>Sr2</i>

^a Ratings included stem rust severity as percent stem area affected on a scale of 0 to 100, and infection response categories of resistant (R), moderately resistant (MR), intermediate (M), moderately susceptible (MS), and susceptible (S), either singly or in combination; Tr = trace.

^b Mean relative severity.

^c Median infection response.

known, the classification based solely on passport information provided to a gene bank is subjective. Misclassified landraces were found most commonly among accessions from Ethiopia ($N = 10$) and Switzerland ($N = 8$). Many of the hexaploid wheat accessions from Ethiopia classified as landraces could, in fact, have been the product of modern breeding, because common wheat is predominantly introduced in Ethiopia whereas tetraploid wheat is indigenous and highly diverse (30,50). It is likely that many of the NSGC common wheat landrace accessions from Ethiopia, and possibly other regions where hexaploid wheat was introduced within the past 100 years, may be either cultivars or breeding lines. Further analysis of these accessions is warranted, including molecular marker and phenotypic descriptor evaluation, to determine whether the landrace category for this group of accessions should be dropped.

When rates of resistance were classified by geography, the distribution of resistance appeared to be nonrandom. However, the present study was not designed to compare resistance by location and, in fact, selection criteria were established which introduced deliberate bias. Nevertheless, the higher rates of resistance that appear to be present in Afghanistan and Iran (Table 4; Fig. 3), and also the absence of resistance in India, Nepal, Bhutan, and most of Pakistan, pose additional questions or hypotheses to test. Rouse et al. (42) found that resistance to Ug99 and related races in wheat relative *Aegilops tauschii* was most common in Caspian Iran, Turkmenistan, and Azerbaijan, a region similar to where we found stem rust resistance in common wheat landraces. The apparent concentration of resistant accessions in Ethiopia (Fig. 3) could be due to misclassification of cultivars as landraces, with the observed resistance conferred by stem rust resistance genes that were ac-

Table 4. Proportion of spring-habit common wheat landraces with field resistance to Ug99 in Kenya field tests by country of origin, excluding 39 accessions originally misclassified as landraces and including only countries with more than five tested landraces

Country	Proportion resistant	N
Afghanistan	0.23	74
Iran	0.18	595
Portugal	0.17	30
Ethiopia	0.15	324
Uzbekistan	0.14	7
Greece	0.14	43
Tajikistan	0.11	9
Bosnia and Herzegovina	0.10	29
Serbia	0.10	20
Turkey	0.08	546
Egypt	0.07	15
Austria	0.06	17
Russian Federation	0.06	35
Tunisia	0.05	21
Pakistan	0.04	53
China	0.02	103
Chile	0.02	61
Algeria	0	6
Armenia	0	21
Bhutan	0	8
Bolivia	0	25
Chad	0	6
Cyprus	0	6
Former Soviet Union	0	6
Georgia	0	29
India	0	80
Iraq	0	26
Macedonia	0	17
Nepal	0	56
Peru	0	25
Saudi Arabia	0	7
Spain	0	6
Sudan	0	9
Switzerland	0	59
Syria	0	6
Uruguay	0	9
Venezuela	0	7

tively bred into lines introduced into Ethiopia. Based on previous studies, a nonrandom geographic distribution of stem rust resistance is expected. Geographic clusters of stem rust resistance (5), or associations between stem rust resistance and environments and zones (2), were detected using resistance data for races other than Ug99 and its variants.

Whether or not the rates of field resistance to TTKS are higher among landraces collected from Afghanistan and Iran is a testable hypothesis. Moreover, it is intriguing because Vavilov in 1926 described the area of Afghanistan as one of the centers of origin for wheat based on the diversity of landraces (6). Although the concept of a center of origin of wheat is complicated, many researchers (13,52–54,58,59) agree that the Fertile Crescent (Iraq, portions of Iran near the Persian Gulf, Kuwait, Syria, Lebanon, Jordan, Israel, and Palestinian territories) is the center where agriculture originated and where the diploid progenitors of durum and bread wheat originated (48). This region overlaps with the region where higher densities of resistant landraces were detected (Fig. 3). Similarly, when data on resistance to dwarf and common bunts was summarized for wheat landrace accessions from the NSGC, the highest frequencies of dwarf bunt resistance were detected in Turkey and Iran, and common bunt in Serbia-Montenegro and Iran (4).

There are multiple possible explanations for the geographical differences in rates of field resistance to TTKS found in this study (Table 2; Fig. 3), including that the differences are an artifact of the selection criteria that defined which landraces were tested. Additional studies on geographical trends would increase our understanding of stem rust resistance. Landraces are believed to represent local genetic adaptation (55), and the geographic pattern of resistance among landraces may reflect the intensity of selection pressure by the stem rust pathogen on wheat hosts. There are several landscape features that could define regions of high selection pressure, including the distributions, types, and abundance of the *Berberis* alternate hosts; climatic variables such as humidity and temperature; and landscape connectivity of wheat hosts (10,25,35). Further research could address knowledge gaps related to the geographical distribution of resistance in landraces.

The present study identified 246 spring-habit common-wheat landraces with field resistance to Ug99. Further research is needed to (i) characterize the resistance to determine its novelty, including genetic mapping and testing against an array of races of *P. graminis* f. sp. *tritici*; (ii) identify markers linked to novel resistance that could be used to select resistance within segregating populations in the absence of the new races, and (iii) ultimately, transfer novel genes into genetic backgrounds that are useful to wheat improvement programs. The landraces surveyed in this work are maintained in the USDA-ARS NSGC and are available upon request. The genes conferring stem rust resistance are conserved within the germplasm collection. They must be recognized for their potential benefit and phenotypic value in order to be a resource for the public good. These results are a first step toward using this genetic resource to meet the global need for new sources of resistance to Ug99.

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