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Race non-specific resistance to rust diseases in CIMMYT spring wheats

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Abstract Rust diseases continue to cause significant losses to wheat production worldwide. Although the life of effective race-specific resistance genes can be prolonged by using gene combinations, an alternative approach is to deploy varieties that posses adult plant resistance (APR) based on combinations of minor, slow rusting genes. When present alone, APR genes do not confer adequate resistance especially under high disease pressure; however, combinations of 4–5 such genes usually result in "near-immunity" or a high level of resistance. Although high diversity for APR occurs for all three rusts in improved germplasm, relatively few genes are characterized in detail. Breeding for APR to leaf rust and stripe rust in CIMMYT spring wheats was initiated in the early 1970s by crossing slow rusting parents that lacked effective race-specific resistance genes to prevalent pathogen populations and selecting plants in segregating populations under high disease pressure in field nurseries. Consequently most of the wheat germplasm distributed worldwide now possesses near-immunity or adequate levels of resistance. Some semidwarf wheats such as Kingbird, Pavon 76, Kiritati and Parula show high levels of APR to stem rust race Ug99 and its derivatives based on the *Sr2*-complex, or a combination of *Sr2* with other uncharacterized slow rusting genes. These parents are being utilized in our crossing program and a Mexico-Kenya shuttle breeding scheme is used for selecting resistance to Ug99. High frequencies of lines with near-immunity to moderate levels of resistance are now emerging from these activities. After further yield trials and quality assessments these lines will be distributed internationally through the CIMMYT nursery system.

Keywords *Triticum aestivum* · Leaf rust · Stripe rust · Stem rust · *Puccinia triticina* · *Puccinia striiformis* · *Puccinia graminis tritici* · Ug99 · Shuttle breeding · Durable resistance

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Introduction

The three rusts, stem (or black), leaf (or brown) and stripe (or yellow) caused by fungi *Puccinia graminis* f. sp. *tritici*, *P. triticina* and *P. striiformis* f. sp. *tritici*, respectively, continue to cause losses, often major, in various parts of the world and hence receive high attention in breeding. The rust fungi are highly specialized pathogens and significant variations exist in their populations for avirulence/virulence to specific resistance genes. Evolution of new races through migration, mutation and recombination among existing genotypes, followed by selection is also frequent. Therefore, breeding for resistance has always been a dynamic process. Erosion of race specific resistance genes, or their combinations, has led to search for alternative approaches to resistance management. Van der Plank (1963) was the first epidemiologist to clearly define a theoretical basis of the concepts of resistance. This approach was widely recommended for breeding for leaf rust resistance by Caldwell (1968), for stem rust resistance by Borlaug (1972), and for stripe-rust resistance by Johnson (1988). The application of such concepts in breeding for leaf rust resistance, commonly known as slow rusting, has been a dominant force in CIMMYT's bread wheat improvement program for almost 40 years with major impacts (Marasas et al. 2003). Today, we understand better the genetic basis of race non-specific or durable resistance to rust diseases and this knowledge is being routinely applied in breeding. We firmly believe that development and deployment of wheat cultivars with such resistance will provide a long-term genetic solution to rust control.

Slow rusting APR to leaf rust and stripe rust

Varying levels of slow rusting resistance are commonly found in wheat germplasm; however, the level of observed adult plant resistance (APR) in field trials is often inadequate. The most studied, and possibly the most effective, now cloned slow rusting leaf rust resistance gene *Lr34* located on chromosome arm 7DS, has maintained its moderate effectiveness for over 60 years of use (Dyck 1987; Krattinger et al. 2009). This gene was traced to the Italian variety 'Mentana' using a gene based DNA-marker (Kolmer et al. 2008). *Lr34* is also common in Chinese landraces including 'Chinese Spring', and tall varieties 'Frontana' and 'Chris' from Brazil and U.S.A., respectively. 'Yaqui 50', the first Mexican stem rust resistant tall variety released by N.E. Borlaug in 1950 under the Mexican-Rockefeller Program, also carries *Lr34* probably from the U.S.A. breeding line 'Frontana/Kenya 58//Newthatch' used in its development. Subsequently, several first generation semidwarf wheats, such as 'Penjamo 62', 'Torim 73', and 'Kalyan/Bluebird', possessed *Lr34*. Distinct from the NBS-LRR structure underlying many race specific resistance genes, *Lr34* is a novel ABC Transporter gene belonging to the PDR (pleiotropic drug resistant) family and the mechanism of resistance seems unlike a typical gene-for-gene interaction. Moreover, the same resistance gene is also implicated in slow rusting to stripe rust and slow mildewing to powdery mildew even though specifically designated as *Yr18* and *Pm38*, respectively (McIntosh 1992; Singh 1992a; Spielmeyer et al. 2005). *Lr34* is also associated with the expression of post-flowering leaf tip necrosis (LTN) in some environments and the expression of LTN is enhanced under high leaf rust pressure (Singh 1992b).

A second designated slow rusting resistance gene, *Lr46*, located on chromosome 1BL (Singh et al. 1998; William et al. 2003), was first identified in the CIMMYT-derived Mexican variety 'Pavon 76'. This gene is widely distributed in germplasm from CIMMYT and other countries. It also confers slow rusting to stripe rust and slow mildewing to powdery mildew and is designated as *Yr29* and *Pm39*, respectively (Singh et al. 1998; William et al. 2003; Lillemo et al. 2008). *Lr46* is also associated with slight post-flowering LTN.

Wheat genotype 'RL6077' developed in Canada was believed to carry *Lr34* due to the expression of APR and LTN, and because of lack of allelism, was thought to be due to a translocation to a different chromosome (Dyck et al. 1994). However, absence of the gene-based DNA marker for *Lr34* ruled out the presence of *Lr34* in RL6077, and subsequent studies located genes *Lr67* for leaf rust resistance and *Yr46* for stripe rust resistance on chromosome 4DL (Herrera-Foessel et al. 2010; Hiebert et al. 2010). The frequency of this gene in wheat germplasm is not yet known. A fourth slow rusting resistance gene located on chromosome arm 7BL and temporarily designated as *LrP*, present in CIMMYT wheat

'Parula', is likely to be distributed widely in CIMMYT spring bread wheat germplasm.

There are other uncharacterized slow rusting genes in CIMMYT and other wheat germplasm with smaller effects than the genes described above and without the association of LTN. The diversity for such resistance genes appears to be higher for stripe rust than for leaf rust. These genes are easier to detect in mapping populations in the presence of large effect slow rusting genes like *Lr34* and *Lr46* due to their often additive interaction effects enhancing the levels of resistance. However, phenotyping of mapping populations segregating for single slow rusting genes with minor effect remains a challenge and therefore finding tightly linked molecular markers will be very difficult using current approaches. These minor genes play an important role in enhancing the effectiveness of slow rusting genes with large effect, such as *Lr34*, in achieving high levels of resistance comparable to immunity (Singh et al. 2000).

Genetic analyses of several CIMMYT wheats possessing high or near-immune levels of slow rusting resistance to leaf rust and stripe rust worldwide indicated additive interaction of genes such as *Lr34* or *Lr46* and three to four additional slow-rusting genes (Singh and Rajaram 1992; Navabi et al. 2003, 2004; Zhang et al. 2008). Various genetic studies conducted at CIMMYT and elsewhere led to the establishment of a simple relationship between disease progress and the number of slow rusting resistance genes present in a wheat line (Singh and Trethowan 2007). A more precise relationship is not possible because each slow rusting resistance gene has a different phenotypic effect and the expression of individual genes is also influenced by the environment. However, the combined effect of 4–5 resistance genes is more stable across environments.

Slow rusting APR to stem rust

The APR gene *Sr2*, transferred to Hope and H44-24a from Yaroslav emmer wheat by E.S. McFadden in the U.S.A. and possibly to 'Khapstein' from 'Khapli' emmer wheat by W.L. Waterhouse in Australia, confers slow rusting to stem rust. Combinations of *Sr2* with other unknown slow rusting resistance genes possibly originating from Thatcher and the Thatcher-derived Chris, commonly known as the "*Sr2*-complex", provided the foundation of durable resistance to stem rust in germplasm from the U.S.A., Canada and Australia, and spring wheat germplasm developed in Mexico (McIntosh 1988; Rajaram et al. 1988). *Sr2* can be detected through its complete linkage with the pseudo-black chaff (PBC) phenotype; however, excessive expression of PBC is considered to be an undesirable trait and leads to the elimination of lines in breeding programs. Although the expression of PBC is enhanced under humid conditions, especially in the highlands, lines with negligible expression of PBC can be found in advanced breeding materials indicating that selection of lines with *Sr2* and negligible PBC is possible. Knott (1982, 1988) showed that adequate levels of multigenic resistance to stem rust could be achieved by accumulating approximately five minor resistance genes. *Sr2* is either tightly linked, or pleiotropic, with *Yr30*, a minor effect APR gene that confers slow rusting to stripe rust.

Unfortunately, with the exception of *Sr2*, not much is known about the other resistance genes involved in the *Sr2* complex or their interactions. However, earlier work by Knott (1982, 1988) and recent characterization in Kenya with Ug99 of various mapping populations involving crosses of APR wheats with a susceptible parent (unpublished CIMMYT studies) indicates that inheritance of complex APR is similar to that described earlier for leaf rust and stripe rust (Singh and Trethowan 2007). The accumulation of about 4–5 minor genes is therefore likely to delay stem rust progress to negligible disease levels at maturity even under high disease pressure. Although some of the old tall varieties from Kenya, Canada and U.S.A. continue to be resistant in Ug99 nurseries in Kenya, it is important to identify and utilize improved semidwarf wheat materials with APR to continue making breeding progress and to develop new wheat materials that have potential to replace current popular varieties in the shortest possible timeframe.

Breeding for slow rusting APR to leaf rust and stripe rust

Breeding for slow rusting resistance based on minor additive genes has been challenging and often slow, for several reasons:

(1) a sufficient number of minor genes may not be present in a single source genotype,
(2) a source genotype may be poorly adapted,
(3) there may be confounding effects from the segregation of both major and minor genes,
(4) crossing and selection schemes and population sizes commonly used by breeding programs are more suitable for selecting major genes,
(5) reliable molecular markers for several minor genes are unavailable,
(6) high costs associated with identifying and utilizing multiple markers.

A successful example of breeding for resistance based on minor genes is the resistance to leaf rust and stripe rust now present in many CIMMYT wheats. This achievement took about 30 years of effort. In the early 1970s, S. Rajaram, influenced by the concept of slow-rusting resistance in wheat proposed by R. Caldwell (1968) and of partial resistance to potato late blight championed by J. Niederhauser (Niederhauser et al. 1954), made a strategic decision to initiate selection for slow-rusting resistance to leaf rust in CIMMYT spring wheat germplasm. In the early phase of breeding he selected plants and lines in segregating populations showing 20–30% rust severities with susceptible infection types. This strategy led to the release of several wheat cultivars, such as 'Pavon 76', 'Nacozari 76', 'Rayon 89' and 'Tarachi 2000', in Mexico and other countries. These slow-rusting lines were used heavily in the crossing program and resulted in the wide distribution of minor genes within CIMMYT spring wheat germplasm.

In the early 1990s, once the genetic bases and diversity of slow rusting resistances became clearer, high-yielding lines that combined four or five additive, minor genes for both leaf rust and stripe rust resistances showing near-immune levels of resistance were developed through 3- and 4-way crosses involving lines carrying different minor genes (Singh et al. 2000). Plants were selected from large segregating populations under artificially created rust epidemics. As far as possible, races of pathogens that had virulence for race-specific resistance genes present in the parents were used to create the epidemics. The resulting highly resistant lines formed the basis of further resistance breeding and were included in recent international trials, such as ESWYT (Elite Spring Wheat Yield Trial) and IBWSN (International Bread Wheat Screening Nursery). Figure 1 summarizes the adult plant leaf rust severities of 360 recently developed advanced lines under high disease pressure in field trials at El Batan, Mexico, during 2009. Over 80% of lines had between 1 and 5% severities at mid to late dough stages compared to the necrotic leaves of the susceptible checks. These near-immune lines were susceptible as seedlings in greenhouse tests with the same race as used in the field trial indicating that complex APR was the basis of resistance.

A similar result was observed for the stripe rust responses of 504 recent advanced lines in field trials conducted in Mexico, Ecuador and Kenya (Fig. 2). Although seedling reaction data are not available, it can be predicted from the pedigrees that at least half of the lines showing 1–5% disease severities carry genes for near-immune levels of APR. Selection of materials with low disease severities in Mexico, Kenya and Ecuador is expected to reduce the temperature sensitivity of APR and thus identify lines with stable performance.

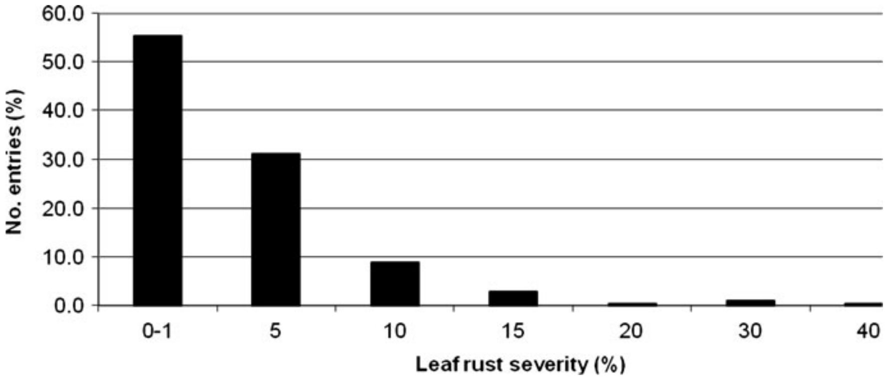

Fig. 1 Adult-plant leaf rust severities of 360 recently developed seedling susceptible wheat lines (effective race-specific resistance genes absent) evaluated at El Batan, Mexico, in 2009 when susceptible checks were defoliated by leaf rust

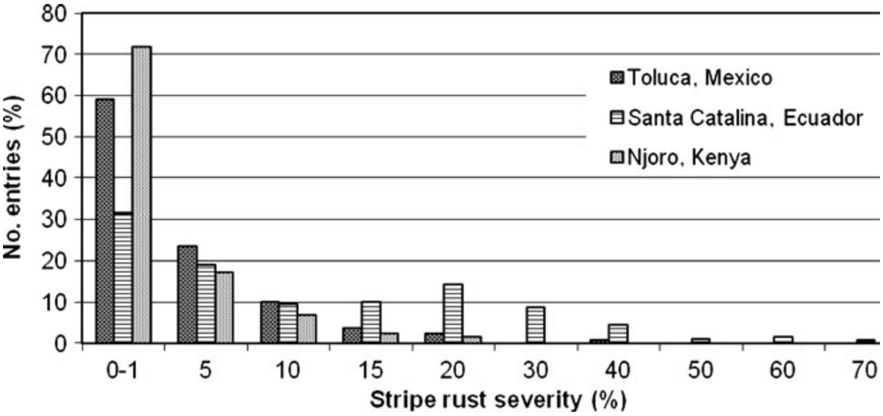

Fig. 2 Adult plant stripe rust severities of 504 recently developed advanced breeding lines at Toluca (Mexico), Santa Catalina (Ecuador) and Njoro (Kenya) in 2009. Data were recorded when the Avocet S check was defoliated in Mexico and Ecuador, and 80% severity in Kenya

Table 1 Stem rust responses of entries included in 31st ESWYT, 43rd IBWSN and 4th SRRSN when evaluated at Njoro, Kenya, in 2008

Resistance category	4th SRRSN		31st ESWYT		43rd IBWSN	
	No	%	No	%	No	%
Adult-plant response[a]						
R-MR (20–30% severity)	20	27.4	15	32.6	5	2.8
MR (40% severity)	29	39.7	7	15.2	19	10.7
MR-MS (50–60% severity)			11	23.9	56	31.5
MS (70% severity)					37	20.8
MS-S (80–90% severity)			3	6.5	39	21.9
S (100% severity-necrotic)					8	4.5
Race-specific resistance gene						
Sr25	12	16.4	5	10.9	8	4.5
SrTmp	10	13.7	2	4.3	5	2.8
SrHuw234	1	1.4	2	4.3		
SrUnknown	1	1.4	1	2.2	1	0.6

[a] Stem rust severities were recorded on adult plants when susceptible check 'Cacuke' had become necrotic following 100% stem rust severity

Breeding for slow stem rusting APR to the race Ug99 group

Characterization of existing spring wheat breeding materials for resistance to Ug99 and its derivatives in field trials in Kenya and as seedlings in the greenhouse at the USDA-ARS Cereal Disease Laboratory, St. Paul, MN, U.S.A. during 2005–2009 resulted in identification of several wheat lines with varying levels of APR. The best sources for APR in semidwarf wheat backgrounds were included in the 1st to 4th Stem Rust Resistance Screening Nurseries (SRRSN) annually distributed since 2006. Results for the 1st to 3rd SRRSN are available at www.globalrust.org and also summarized by Njau et al. (2010). Wheat lines 'Kingbird', 'Kiritati', 'Pavon 76', 'Muu', 'Parula' and a few others carry high levels of APR. The stem rust responses for the most recent CIMMYT International trials, 4th SRRSN, 31st ESWYT and 43rd IBWSN, are given in Table 1. The frequencies of wheat lines with moderate, but likely adequate, levels of APR and race-specific resistance have increased significantly since screening was initiated in Kenya.

Because a large proportion of high-yielding spring wheat varieties and germplasm do not carry effective race-specific resistance to Ug99, the availability of genotypes with moderate to high levels of APR provide opportunities to reconstitute high levels of

APR in more recent hybrid populations. In the absence of molecular markers for APR genes and the absence of Ug99 in Mexico, a shuttle breeding scheme between Mexican field sites (Ciudad Obregon in northwestern Mexico during winter, and Toluca or El Batan in the highlands near Mexico City during summer) and Njoro, Kenya, was initiated in 2006 to build APR in modern semidwarf wheats. Two crop seasons per year in both Mexico and Kenya halve the number of years required to generate and test advanced breeding lines. The "single-backcross, selected-bulk" breeding approach (Singh and Trethowan 2007) is being applied for transferring multiple minor genes to adapted backgrounds. Simple and three-way crosses, where one or more parents carry adult-plant resistance, are being used to breed new high-yielding, near-immune wheat materials to all three rusts. The flow of breeding materials in the "Mexico-Kenya Shuttle" is described in Table 2.

In the single-backcross approach, resistance sources are crossed with adapted, high yielding wheats. A single backcross is made with the recurrent parent to obtain 350–400 BC_1 seeds. Alternatively, 3-way or top crosses are often made to a second adapted parent. The BC_1 plants are selected for desired agronomic features and resistance to leaf rust and stripe rust, and harvested as bulks in Mexico. F_2 plants derived from the BC_1, simple, and top crosses with desired agronomic features and resistance to leaf rust and stripe rust are selected for agronomic traits and resistance to other diseases at Cd. Obregon or Toluca and harvested as bulks. The selected-bulk selection scheme allows selection of unlimited numbers of plants in each population. If the F_2 populations were grown at Cd.

Table 2 Flow of breeding materials in the Mexico-Kenya shuttle scheme, utilizing two crop seasons per year, for developing high-yielding wheat germplasm combining adult plant resistance to stem rust with other traits

Year	Location[a]	Activities
1	Cd. Obregon	New crosses made.
	El Batan	F_1 grown, BC_1 and F_1-Top made on selected F_1
2	Cd. Obregon	BC_1 and F_1-Top (350 plants), F_2 (1000 plants from simple crosses) grown and selected for agronomic traits and leaf rust resistance. Spikes from selected plants harvested as bulks and plump grains retained
	Toluca	F_2 (1000 plants from BC_1 and F_1-Top) and F_3 (350 plants from F_2 simple) grown and selected for agronomic traits and resistance to stripe rust and Septoria tritici blotch. Spikes from selected plants harvested as bulks and plump grain retained
3	Njoro	F_3 and F_4 (800 plants) grown in stem and stripe rust nurseries. Plants with high to adequate resistance tagged and harvested as bulks. Plump grains retained
	Njoro	F_4 and F_5 (800 plants) grown, spikes from short plants resistant to stem and stripe rust selected and harvested as bulk. Plump grains retained
4	Cd. Obregon	F_5 and F_6 (350 plants) grown and selected for agronomic traits and resistance to leaf rust. Plants harvested individually and those with plump grains retained
	El Batan and Toluca	Advanced lines grown as small plots, selected for agronomic traits and resistance to stripe rust and Septoria tritici blotch at Toluca and leaf rust at El Batan. Best lines harvested in El Batan and those with plump grains promoted to yield trials
5	Cd. Obregon, Njoro and Santa Catalina	Advanced lines grown as replicated yield trials at Cd. Obregon and as small plots at all three sites and phenotyped for leaf rust, stem rust and stripe rust at Cd. Obregon, Njoro and Santa Catalina, respectively. Best lines retained
	El Batan, Toluca and Njoro	Seed of candidates for International Nurseries multiplied at El Batan. Lines also grown at all sites and phenotyped for leaf rust, stripe rust, stem rust, Septoria tritici blotch, Fusarium head blight. Quality analysis conducted using Obregon grain.
6	Cd. Obregon, Mexicali and Njoro	2nd year yield trials conducted in 5 environments at Obregon, seed multiplication for international distribution at Mexicali and phenotyped for stem rust response at Njoro
	El Batan	International Yield Trials and Screening Nurseries prepared and distributed
7	International	Countries with wheat seasons April-December
8	International	Countries with wheat seasons October-June

[a] Cd. Obregon, Toluca, El Batan and Mexicali are in Mexico, Njoro is in Kenya and Santa Catalina is in Ecuador

Obregon, where the quarantine disease Karnal bunt may be present, the F_3 populations are grown at Toluca for another round of selection. About 1,000 seeds of each F_3 and F_4 population obtained from the Toluca harvest are grown at Njoro for selection under high stem rust pressure during the off-season. Populations not carrying sufficient resistant plants are discarded. Selection of plants with high to adequate resistance is carried out, selected plants are bulk-harvested and plump grains are selected for establishing F_4 and F_5 populations of about 1,000 plants during the main season at Njoro under high stem rust pressure. Because stem rust affects grain filling, we expect plants with insufficient resistance to have shriveled grains. Selection in the main season is carried out in the same manner as off-season and about 400 plump seeds harvested from selected plants are returned to Mexico and grown at Cd. Obregon under high leaf rust pressure for final selection as individual plants in the F_5 and F_6 generations. Small plots of advanced lines obtained by selecting individual plants in Cd. Obregon are grown at El Batan and Toluca to select for agronomic characteristics and resistance to leaf rust and stripe rust.

Figure 3 summarizes the stem rust responses of 761 ‘Mexico-Kenya Shuttle Breeding’ advanced lines under high disease pressure during the 2010 off-season at Njoro, Kenya. The parents of the lines lacked effective race specific resistance genes based on their pedigrees and field reactions. Around 25% of the lines derived from about 60 different crosses displayed near-immune levels of resistance with stem rust severities of 1–5% compared to 100% for the susceptible check Cacuke. An additional 25% of the lines displayed 10–15% stem rust severities. These lines are under yield evaluation in Mexico and stem rust resistance will be verified again during the 2010 main-season in Kenya. Our goal is to develop high-yielding lines that would sustain up to 10% stem rust severities at the late dough stage under high disease pressures. In most commercial fields this would mean practically clean crops and negligible losses.

Enhanced expression of moderately effective race-specific resistance genes in the presence of slow rusting APR genes

There are studies demonstrating interaction between moderately effective race specific and slow rusting APR genes. For example, German and Kolmer (1992) showed that *Lr34* enhanced the expression of several moderately effective race specific resistance genes by lowering the seedling infection types to races avirulent to the race specific genes. Singh and Huerta-Espino (1995) reported that although *Lr16* only conferred moderate levels of leaf rust resistance in field trials in Mexico, the near-immune level of resistance in wheat varieties ‘Ciano 79’ and ‘Papago 86’ was based on the interaction of *Lr16* with two additional slow rusting genes. Similarly, immunity to stripe rust in wheat variety ‘Pastor’ involved the moderately effective race specific resistance gene *Yr31* and slow rusting genes *Yr29*, *Yr30* and possibly one additional minor gene (Singh et al. 2003). Detection of a new race in 2008 in Mexico with virulence to *Yr31* changed the near-immunity of Pastor to a moderate level of resistance.

Several known race specific stem rust resistance genes confer moderate to inadequate levels of resistance under high disease pressure in field trials (McIntosh et al. 1995; Jin et al. 2007). Singh and McIntosh (1986, 1987) showed that *Sr7a*, known to confer only slight resistance in seedlings, conferred high levels of seedling resistance in several wheat backgrounds including ‘Chris’ and ‘Kenya Plume’.

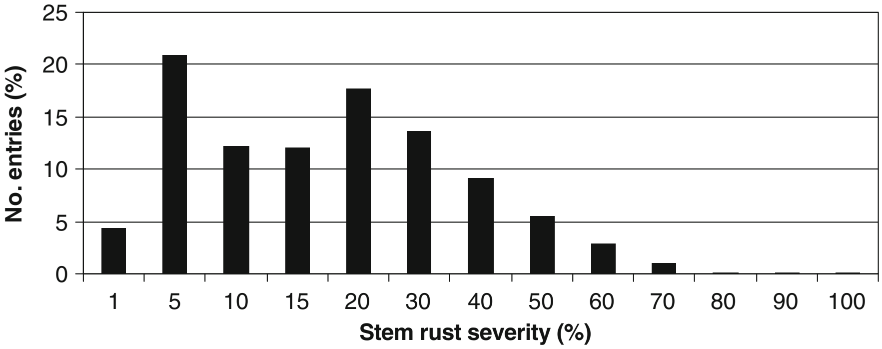

Fig. 3 Adult plant stem rust responses of 761 ‘Mexico-Kenya shuttle breeding-2008’ wheat lines from crosses targeted for incorporating APR into high yielding wheat backgrounds and evaluated at Njoro, Kenya, during the 2010 off-season. Data were recorded when ‘Cacuke’ displayed 100% stem rust severity

Interestingly both of these varieties also displayed high levels of complex APR in Australia and resistance in both varieties remain effective to Ug99 in Kenya. Several of the Ug99-effective characterized and uncharacterized race specific genes confer only intermediate levels of resistance. Adequate protection under high stem rust pressure will require enhanced expression. Enhanced expression of *Sr25* in the field, possibly due to the presence of slow rusting gene *Sr2*, in CIMMYT spring bread wheat backgrounds was reported by Njau et al. (2010). The variation in stem rust severities recorded for wheat lines that likely carry provisionally designated resistance genes *SrTmp* and *SrSha7* is summarized in Fig. 4. The postulations for the presence of these resistance genes were based on the pedigrees and infection types observed in the field trials and are under verification through seedling greenhouse tests. Stem rust severities for lines varied from 5 to 60% for *SrTmp* and 1–30% for *SrSha7*. A similar result was obtained for another moderately effective gene *SrHuw234* (data not presented). It is therefore important that slow rusting APR genes are accumulated to enhance the level of protection provided by moderately effective race specific genes under high disease pressures.

Grain yield performance of new Ug99 resistant CIMMYT wheats in target countries

Twenty-nine, high-yielding wheats identified to carry adequate levels of resistance to stem rust at Njoro in 2008 (both off- and main-seasons) were included in the 4th Elite Bread Wheat Yield Trial (4th EBWYT). Twenty-four entries had APR whereas the resistance of 4 entries was based on *Sr25* and one on *SrHuw234*. Fifty-one sets of the trial were distributed to various countries for planting during 2008–2009. Results for six countries are summarized in Table 3.

Twenty-eight entries on average yielded 100–114% of the local checks used at 10 sites in India. Five entries, including 'Munal#1' (CIMMYT check) yielded 10–14% higher than the checks. Ten sites represented diverse environments in the North-Western Plain Zone (NWPZ), North-Eastern Plain Zone (NEPZ), and Central and Peninsular Zone (CPZ). Considering only the NWPZ (6 sites), all entries yielded more than the local check and 11 entries were 10–19% higher yielding than the checks (PBW343 used at most sites). 'Wheatear/Sokoll' (entry 529) with *Sr25* was the best yielder, 19% higher than the check in NWPZ. This was followed by 'Neloki#1' (entry 527) with 17% higher yield and APR to stem rust. NWPZ is the main wheat zone in India. The CIMMYT check Munal#1 has shown significant superiority over the checks in India for 3 years of testing and has potential to become a successful variety.

Trials were grown in Pakistan at 5 diverse sites from north to south. Four entries, 508, 515, 519 and 530, on average yielded 7–11% higher than the means of the local checks (different check at each site). Similarly, in Iran trials were grown at 5 diverse sites including those where facultative wheats are grown. On average eight entries had 100–108% yields compared to the checks. The best line was entry 527, Neloki#1, the entry rated 2nd in India.

Fifteen lines yielded 9–21% higher in Afghanistan based on means for three sites. One site data set was

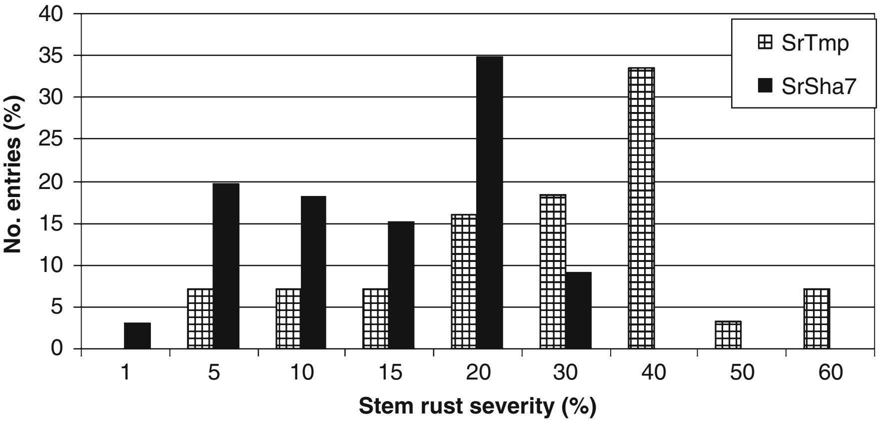

Fig. 4 Adult plant stem rust severities of 125 and 66 wheat lines carrying resistance genes *SrTmp* and *SrSha7*, respectively, at Njoro, Kenya, in 2010. Data were recorded when 'Cacuke' displayed 100% stem rust severity and reaction of lines varied from R to MR

Table 3 Yield performance of entries in 4th EBWYT in six countries

Entry	Cross	Resistance	India (10 sites)		Pakistan (5 sites)		Iran (5 sites)		Afghanistan (3 sites)		Nepal (1 site)		Ethiopia (1 site)	
		Category[a]	kg/ha	% Ck	Kg/ha	% Ck	kg/ha	% Ck	Kg/ha	% Ck	kg/ha	% Ck	kg/ha	% Ck
501	Local check		3460	100	3193	100	6916	100	4437	100	3644	100	3106	100
502	Munal #1	APR-MR	3828	111	3077	96	6750	98	4760	107	4519	124	3463	112
503	Kiritati/4/2*Seri.1B*2/3/Kauz*2/Bow//Kauz	APR-MR	3466	100	3272	102	6838	99	5108	115	3148	86	3001	97
504	Tarachi *2//Pfau/Weaver	APR-MR	3567	103	2670	84	7092	103	4830	109	3963	109	3270	105
505	Saar/2*Waxwing	APR-MRMS	3577	103	2912	91	6643	96	4556	103	4000	110	3490	112
506	Seri.1B*2/3/Kauz*2/Bow//Kauz*2/5/Cno79//PF70354/Mus/3/Pastor/4/Bav92	APR-MR	3504	101	3164	99	6662	96	4674	105	3852	106	2747	88
507	PBW343*2/Kukuna/3/Pastor//Chil/Prl/4/PBW343*2/Kukuna	APR-MRMS	3700	107	3334	104	6331	92	4990	112	4082	112	2992	96
508	Whear//Inqualab91*2/Tukuru	*Sr25*	3385	98	3615	113	7105	103	5385	121	4074	112	3422	110
509	PBW343*2/Kukuna//PBW343*2/Kukuna	APR-MR	3705	107	3180	100	6173	89	4617	104	2933	80	3236	104
510	PBW343*2/Kukuna//PBW343*2/Kukuna	APR-MR	3823	110	3285	103	6736	97	4705	106	3585	98	3233	104
511	PBW343*2/Kukuna//PBW343*2/Kukuna	APR-MR	3625	105	3276	103	6286	91	5041	114	3111	85	3129	101
512	Cndo/R143//Ente/Mexi_2/3/Ae.Sq./4/Weaver/5/2*Pastor/6/SKauz/Parus//Parus	APR-MRMS	3533	102	3236	101	6977	101	5072	114	3496	96	2955	95
513	Mino/898.97	APR-MR	3590	104	3045	95	6179	89	4360	98	3459	95	2962	95
514	Picaflor#2	APR-RMR	3609	104	2801	88	7129	103	5134	116	3889	107	3271	105
515	Webill1*2/Brambling	APR-MRMS	3647	105	3447	108	6777	98	5059	114	4037	111	3502	113
516	Becard	APR-MR	3857	111	3157	99	6941	100	4758	107	4185	115	2808	90
517	Becard	APR-MR	3616	105	3251	102	6959	101	5081	115	4148	114	2782	90
518	Becard	APR-MR	3581	104	3319	104	6838	99	4388	99	3259	89	3287	106
519	Prl/2*Pastor//PBW343*2/Kukuna	APR-MR	3655	106	3431	107	6454	93	4912	111	4000	110	2962	95
520	PBW343/Huites/4/Yar/Ae.Sq(783)//Milan/3/Bav92	APR-MR	3372	97	2965	93	5736	83	4602	104	3341	92	2493	80
521	Kauz//Altar84/Aos/3/Pastor/4/Milan/Cupe//SW89.3064/5/Kiritati	APR-MR	3444	100	3142	98	5968	86	4776	108	3704	102	2813	91
522	SW89.5277/Borl95//SKauz/3/Prl/2*Pastor/4/Heilo	APR-MR	3631	105	3228	101	6807	98	4676	105	3526	97	3167	102
523	Seri.1B*2/3/Kauz*2/Bow//Kauz/4/PBW343*2/Tukuru/5/C80.1/3*Batavia//2*Wbill	*Sr25*	3652	106	3286	103	6039	87	4270	96	3852	106	3303	106
524	Pfau/Seri.1B//Amad*2/3/PBW343*2/Kukuna	APR-MR	3641	105	2928	92	6502	94	4372	99	3563	98	3386	109
525	Pfau/Seri.1B//Amad*2/3/PBW343*2/Kukuna	APR-MR	3758	109	2992	94	6117	88	4578	103	3778	104	3156	102

Table 3 continued

Entry	Cross	Resistance	India (10 sites)		Pakistan (5 sites)		Iran (5 sites)		Afghanistan (3 sites)		Nepal (1 site)		Ethiopia (1 site)	
		Category[a]	kg/ha	% Ck	Kg/ha	% Ck	kg/ha	% Ck	Kg/ha	% Ck	kg/ha	% Ck	kg/ha	% Ck
526	Prl/2*Pastor//PBW343*2/Kukuna/3/Tacupeto F2001*2/Kukuna	APR-MR	3808	110	3060	96	6604	95	4723	106	3556	98	2766	89
527	Neloki#1	APR-MR	3937	114	3160	99	7469	108	5047	114	4667	128	3722	120
528	HUW234 + Lr34/Prinia//PBW343*2/Kukuna/3/Roelfs F2007	*SrHuw234*	3623	105	3057	96	6570	95	4823	109	3556	98	3003	97
529	Wheatear/Sokoll	*Sr25*	3959	114	3370	106	6881	99	5287	119	4333	119	4077	131
530	Wheatear//2*Prl/2*Pastor	*Sr25*	3541	102	3535	111	7015	101	5202	117	3348	92	3476	112
	LSD ($P = 0.05$)		199		299		519		754		606		363	
	CV, %		8.8		4.8		8.9		7.9		8.0		5.7	
	Heritability		0.40		0.69		0.59		0.62		0.74		0.79	

[a] Adult plant resistance (APR) categories RMR = 15–20%, MR = 30–40%, MRMS = 50%. Stem rust severities were recorded on adult plants in Kenya in 2008 when susceptible check 'Cacuke' had become necrotic following 100% stem rust severity

returned from Bhairahwa, Nepal, and 10 lines yielded 10–28% higher than the check. Munal#1 was the 2nd best yielder (24% higher yielding than the check) and Neloki#1, entry 527, yielded 28% higher than the check.

One site data set was returned from Kulumsa, Ethiopia. Eight entries had 9–31% higher yields than the highly popular cultivar 'Kubsa'. The top two performers, Wheatear/Sokoll (entry 529) and Neloki#1 (entry 527) were also the top two performers in India. Munal#1 (entry 2), a derivative of Kubsa, had a 12% higher yield than Kubsa and is under seed multiplication in Ethiopia.

Entries included in the 4th EBWYT were selected based on visual agronomic and disease evaluations and grain-yield performance in a single yield trial at Ciudad Obregon in Mexico, the main breeding and testing site for the CIMMYT spring wheat program. The grain yield performances of new semidwarf wheat lines in various countries show that significant progress in yield potential has been made over time. Varieties such as PBW343 in India, and Kubsa in Ethiopia, or Chamran in Iran were bred about 15 years ago in Mexico. We believe that changing to new higher yielding Ug99 resistant wheat varieties should enhance wheat productivity and farmers' income in addition to genetic protection from all three rusts.

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