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Studies of the genetics of inheritance of stem rust resistance in bread wheat

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Pgt race TTKSK (Ug99) has a wide virulence range with respect to currently grown wheat cultivars worldwide. Aspects of migration, mutation, recombination and selection in the pathogen have led to previously deployed stem rust resistance genes being ineffective. Race TTKSK has further evolved to acquire virulence for resistance genes such as Sr24 (race Ug99 + Sr24) and Sr36 (Ug99 + Sr36). Five resistant wheat lines (KSL-2, KSL-3, KSL-5, KSL-12 and KSL-19) which were resistant in tests during 2008, 2009 and 2010 were used as parents in crosses with stem rust susceptible line CACUKE to develop genetic populations for determining the inheritance of resistance to stem rust. F_3 populations were evaluated at KARI Njoro in the 2012 off season and 2012 to 2013 main season. The adult plant stem rust responses were scored using the modified Cobb's scale. The $F_{2:3}$ lines of population(s) exhibiting qualitative variation were grouped as homozygous resistant (HR), segregating (Seg) and homozygous susceptible (HS). Heavy disease pressure was present during the cropping seasons with the check CACUKE displaying 90% susceptibility. Chi square analysis revealed that the segregation data in the parent KSL-2 did not deviate significantly from the single gene model (1:2:1) suggesting that the resistance to stem rust is conditioned by a single dominant gene. The Chi square test also revealed that the stem rust resistance in the parents KSL-3, KSL-5, KSL-12 and KSL-19 was conditioned by two genes. The families from the KSL-2 and KSL-3 crosses also segregated for the presence of the pseudo black chaff implying that the *Sr2* gene could be present in the background of these wheat parents. The superior transgressive segregants identified in these crosses will be used in breeding.

Key words: Genetic, wheat, gene, resistance.

INTRODUCTION

The current global inflation has led to increased food prices worsening the situation in the sub Saharan Africa which has continuously faced drought, civil strife, mal-nutrition, poverty, extreme hunger and even death. The increased production of wheat could help to ensure food and nutritional security while lifting the standard of living of the small scale farmers (Singh et al., 2011). However, wheat production of 350 000 tons is far below the current wheat consumption of 900 000 tons annually.

The stem rust disease caused by *Puccinia graminis forma specialis* tritici has currently threatened wheat production after a race virulent to stem rust resistance gene Sr31 was detected in Uganda in 1999. The Sr31/SrR stem rust resistance gene located on rye translocation 1B.1R was introgressed into wheat on a short chromosomal segment from rye (Secale cereale) (Mago et al., 2004). This race was later designated as Ug99 (TTKSK) and has also evolved into more virulent forms, TTKST

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and TTTSK showing more virulence to Sr24 and Sr36, respectively. The Ug99 race has also spread from Uganda to other East African countries then to Middle East and West Asia (Rouse et al., 2012). The stem rust fungus could affect the entire wheat crop, especially during the early growth stages leading to the blocking of the vascular system hence stunting and lodging of weak stalks eventually causing yield losses of even 100% due to shriveled grain and damaged tillers (Kokhmetova et al., 2011; Boukhatem et al., 2002). The major stem rust resistance genes previously deployed in wheat varieties have succumbed to the Ug99 race. Up to date, more than 50 stem rust resistance genes have been reported in wheat and its wild relatives of which most of these genes confer race specific resistance except the Sr2 gene which is a non race specific gene (McIntosh et al., 2008).

The resistance to stem rust includes seedling and adult plant resistance (Kaur et al., 2009; Messmer et al., 2000). Seedling resistance is usually expressed throughout the plant growth stages. It is also characterized by hypersensitive responses (Navabi et al., 2004) and follows the gene for gene concept. Due to the short life cycle and large population sizes of plant pathogens, rapid selection of rare but virulent alleles occur leading to very high disease epidemics (Prakash and Heather, 1988). The strong selection pressure on the pathogen to avoid its detection either through a single mutation event or deletion of the effector molecule of the host plant could lead to a change from avirulent to virulent forms. The selection of sexual progeny which do not contain recognized effector genes also leads to virulent races of the *P. graminis* as it is hypothesized for the Ug99 or TTKSK race (Ayliffe et al., 2008). However, the use of single resistance genes has been considered a threat to wheat production due to erosion of the few resistance genes effective against the Ug99 due to the arms race between the pathogens and the host. The use of the race specific resistance is also harboured by the presence of known or unknown Sr genes, in the adapted germplasm making disease assessment difficult due to confounding effects (Jin et al., 2007). Thus, breeders need to continuously replace cultivars and continually introgress new resistance genes, a process referred to as boom and bust cycle.

Due to these limitations of race specific genes, the identification and combination of several stem rust resistance genes to offer durable resistance to stem rust remains the only feasible alternative. With durable resistance, a pathogenic race which overcomes an allele of minor effect does not have a selective advantage since the host has more resistance alleles (Polanda et al., 2011). Adult plant resistance or non race specific resistance appears susceptible at seedling stage but resistant at the adult plant stage (Imtiaz et al., 2011). Furthermore, a compatible interaction between the plant and pathogen is displayed by having partially resistant adult plants. It is also characterized by genes with additive effects and non hypersensitive responses (Singh et al., 2009; Navabi et al., 2004).

However, major gene resistance and minor gene resistance are mutual. This complicates efforts aimed at selection for minor or non race specific gene resistance, the estimation and studying of any genetic variation during inheritance studies. Moreso, the recessive nature of some resistance genes and confounding effects of genes in the wheat germplasm background aggravate the problem (Babiker et al., 2009). This calls for the proper understanding of the genetics of disease resistance and use of appropriate crosses in order to identify any new resistance sources, broaden the genetic diversity and also help in marker assisted selection (Imtiaz et al., 2011). Previous studies have led to identification of seedling and adult plant resistance genes (Bai et al., 2009; Eversmeyer and Kramer, 2000; Liu and Kolmer, 1998). Further, the investigation of the mode of inheritance has broadened the genetic diversity of available wheat germplasm by possibly using genes with small additive effects (Parlevliet, 1993). Other studies have reported new resistance genes: the leaf rust resistance gene, *Lr50* (Brown-Guedira et al., 2003) and *SrD51* (Yin et al., 2008). To ensure breeding efficiency, the knowledge of number of genes controlling a trait is important. This could be achieved by comparing observed and expected Mendelian ratios. However, the determination of number of genes for quantitative traits is very difficult. This has been attributed to the fact that quantitative resistance is complex in nature, heterogeneous and the inability to transmit resistance in the subsequent progenies (Vanegas et al., 2007). The alternative lies in the possibility to estimate the minimum number of effective factors. An effective factor comprises a chromosome segment which acts as an inheritable unit and is separated from other units by an average recombination frequency of 50% (Naghavi et al., 2007).

However, given the major threat of stem rust (Ug99) facing wheat production, the genetic analysis of elite wheat germplasm remains a priority. Thus, this study aimed to determine the number and mode of inheritance of the stem rust resistance genes among five promising wheat parents or genotypes.

MATERIALS AND METHODS

Host material

Among 25 wheat lines tested for resistance to stem rust in the growing seasons 2008, 2009 and 2010, five wheat lines: KSL-2, KSL-3, KSL-5, KSL-12 and KSL-19 displayed good levels of stem rust resistance (Table 1). These five resistant lines were used as parents in a partial diallel with the susceptible parent CACUKE. The parent CACUKE is a fully susceptible line making it a suitable parent in this study to minimize the confounding effects of race specific hypersensitive resistance factors (Rubiales and Nicks, 2000). Furthermore, CACUKE is also used as a spreader row at Kenya Agricultural Research Institute (KARI), Njoro during international wheat screening experiments.

Development of the wheat crosses

Four seeds of each F_1 were planted in 15 cm plastic pots and placed in the growth chamber of the greenhouse at room temperature at KARI, Njoro. The F_1's were then transplanted in the crossing block in 2010. The F_1's were self pollinated and then harvested from individual plants in each cross. The parents and 200 to 250 F_2 seeds of each F_1 cross were space planted at 10 cm in two row plots each measuring 12.5 m and advanced to the F_3 generation through single seed descent under disease free conditions and no selection was done (Vanegas et al., 2007; Liu and Kolmer, 1998).

Experimental site

The experiments were carried out at Kenya Agricultural Research Institute (KARI), Njoro. KARI Njoro lies at 0 20'S; 35° 56' E, and 2185 m above sea level (Ooro et al., 2009). It has minimum and maximum temperatures of 9.7 and 23.5°C, respectively and mean rainfall of 900 mm. This site is also used for large scale field-screening nursery for stem rust, established by KARI in collaboration with the International Maize and Wheat Improvement Centre (CIMMYT) and the Global Rust Initiative (Singh et al., 2009). It is known to have the currently known *P. graminis* pathotypes especially the *Ug99* (TTKSK) and derivative pathotypes.

Assessment of adult plant stem rust resistance

The parents and about 150$F_{2:3}$ lines were grown on two 0.5 m rows unreplicated plots seeded 20 by 70 cm apart (15 to 20 seeds per plot) in 2012 off season and 2012 to 2013 main season. After every 20 plots, the susceptible check CACUKE was also included. Spreader rows which comprised of seven *Sr31* and *Sr24* gene carrying wheat lines were grown perpendicular to the plots and in the perimeter of the experimental plots. The spreader rows were repeatedly inoculated by injecting the pre-emergent leaves with a water suspension of urediniosores collected from the trap nurseries to create an artificial stem rust epidemic in the field (Hickey et al., 2012; Khanna et al., 2005).

The modified Cobb's scale (Peterson et al., 1948) was used to assess the wheat genotypes for adult plant stem rust resistance based on the percentage of the leaf area covered with stem rust pustules. The disease scoring began when the susceptible check displayed about 30% susceptible responses during the evaluation seasons. The observations in the $F_{2:3}$ families were genetically grouped into homozygous resistant, segregating and homozygous susceptible. Those displaying disease severity equal to or higher than the susceptible parent CACUKE were considered susceptible (Khanna et al., 2005). The presence of the pseudo black chaff was also noted among these $F_{2:3}$ families and parents.

Other agronomic traits

The maturity of the parents and the families were also noted during the two seasons of evaluation. This was achieved by recording the days to 50% flowering in each two row plots. The parents and their families were also evaluated for the presence of the pseudo black chaff (PBC) phenotype.

Data analysis

To estimate the number of genes conditioning resistance of the stem rust resistance among these populations, a Chi square test was done (Babiker et al., 2009). The Chi square analysis was used to test the goodness of fit of observed segregations to the expected genetic ratios of 1 homozygous resistant, 2 segregating and 1 homozygous susceptible line as shown on Equation 1:

$$\chi^2 = \frac{\sum (\text{Observed} - \text{Expected})^2}{\text{Expected}}$$

Equation 1: Chi square formula

RESULTS

There was heavy disease pressure in the field during all the growing seasons. The five wheat lines namely: KSL-2, KSL-3, KSL-5, KSL-12 and KSL-19 displayed stem rust severity and infection responses ranging from trace responses (TR) to 25MRMS (M) responses during the 2008, 2009, 2010, 2012 and 2013 screening experiments at KARI (Table 1). When compared with the check CACUKE, the five parents were considered resistant and were thus chosen for this genetic study. When these parents and their F_3 families were evaluated for adult plant resistance in the field in 2012 and 2013 season, a varied response was noted (Table 1). In 2012 off season, the parents: KSL-2, KSL-3, KSL-5 had resistant responses of 5R, while the parents KSL-12 and KSL-19 had stem rust severity of 10MR-15M and R-20MSS, respectively. During the 2012-2013 season, disease responses ranging from TR to 5M were observed among the five parents. The susceptible line, CACUKE had susceptible responses ranging from 60S to 90S (Table 1). It was also characterized by shriveled or no grains at all and broken stems at physiological maturity. In 2012 to 2013 season, a heavy stem rust disease pressure was observed with the stalks, sheaths and leaves of the susceptible check CACUKE heavily covered with stem rust pustules.

The $F_{2:3}$ families were grouped into three distinct classes based on their field responses: homozygous resistant (HR), segregating (SEG) and homozygous susceptible (HS) responses. The Chi square tests revealed that the segregation data did not deviate significantly from the expected ratio of 1:2:1 for a single gene model among the parents KSL-2, KSL-5 and KSL-12 at 1% significance level in the 2012 off season (Table 2). However, the segregation data of the parents KSL-3 and KSL-19 followed a genetic ratio of 12:3:1 in the 2012 season. During the 2012-2013 season, only the segregation data of KSL-2 fitted a 1:2:1 genetic ratio (Table 2). The segregation data of the parents KSL-3 and KSL-19 still conformed to the 12:3:1 genetic ratio, while the parents KSL-5 and KSL-12 fitted the genetic ratios of 7:08:01 and 9:04:03, respectively. In this study, segrega-tion was noted among the crosses involving resistant by resistant parents implying that these wheat parents carry different stems rust resistance genes (Table 3).

Additionally, a trait of great importance noted among these materials was the presence of the pseudo black chaff in the parents KSL-2 and KSL-3. However, the PBC was not expressed among the parents KSL-5, KSL-12,

Table 1. Stem rust disease severity of the wheat parents used in the genetic studies across the years of testing.

Genotype	Pedigree	Origin	[a]Field rust severity (%) and [b]field responses across the years of testing					[c]PBC
			2008	2009	2010	2012	2013	
KSL-2	CWANA 1st SR RESIS. ON - ETH - OS71	Syria	10M	12.5M	5RMR	5R	5M	+
KSL-3	MON'S'/ALD'S'//TOWPE'S'	CWANA	10R	12.5M	5RMR	5R	5MR	+
KSL-5	THELIN#2/ TUKURU CGSS02Y00118S-099M-099Y-099M-16Y-OB	Mexico	TR	17.5M	15MR	5R	R	_
KSL-12	PBW343*2/KUKUNA//PBW343*2/KUKUNA/3/PBW343	Mexico	5R	25RMR	25M	10MR -15M	5MR	_
KSL-19	SUNCO//TNMU/TUI	Mexico	TR	TR	TR	R-20MSS	TR	_
CACUKE	CANADIAN/CUNNINGHAM//KENNEDY		90S	90S	90S	90S	90S	_

[a]Field rust severity was based on modified Cobb's scale where 0: immune and 100: completely susceptible; [b]Field responses based on Roelfs et al. (1992) scale where TR = trace responses assumed to give a disease severity of 1; RMR, resistant to moderately resistant; MR, moderately resistant; M, moderately resistant to moderately susceptible; S, susceptible; [c]PBC = pseudo black chaff where a plus (+) implies presence and a minus (–) means absence of the pseudo black chaff.

Table 2. Segregating data for adult plant resistance to stem rust in F_2 derived F3 families from crosses involving the five wheat genotypes during the 2012 off season and 2012 -2013 main season at KARI Njoro, Kenya.

Cross	Parentage	Season	Number of F_2 derived f_3 families			Total	Chi square (X^2)	Genetic ratio	Number of genes
			Resistant	Segregating	Susceptible				
CACUKE/KSL-2	CACUKE X CWANA 1st SR RESIS. ON - ETH - OS71	2012-2013	17	63	28	108	5.2	1:02:01	1
		2012	34	62	18	114	5.37	1:02:01	1
CACUKE/KSL-3	CACUKE X MON'S'/ALD'S'//TOWPE'S'	2012-2013	118	34	2	154	7.0	12:03:01	2
		2012	121	47	12	180	6.0	12:03:01	2
CACUKE/KSL-5	CACUKE X THELIN#2/ TUKURU CGSS02Y00118S-099M-099Y-099M-16Y-OB	2012-2013	56	75	18	149	7.7	7:08:01	2
		2012	56	73	37	166	6.76	1:02:01	1
CACUKE/KSL-12	CACUKE X PBW343*2/KUKUNA//PBW343*2/ KUKUNA/3/PBW343	2012-2013	32	20	25	77	6.8	9:04:03	2
		2012	25	41	19	85	0.95	1:02:01	1
CACUKE/KSL-19	CACUKE X SUNCO//TNMU/TUI	2012-2013	80	25	3	108	3.2	12:03:01	2
		2012	79	38	9	126	3.36	12:03:01	2

[b]X^2 at 2df and at probability level p = 0.01 was 9.21.

Table 3. Segregation data among the resistant crosses of the F_2 derived F_3 families tested during the 2012 off season.

Cross	Pedigree	Number of F_2 derived f_3 families			
		Resistant	Segregating	Susceptible	Total
KSL-5 X KSL-2	THELIN#2/ TUKURU CGSS02Y00118S-099M-099Y-099M-16Y-OB X CWANA 1st SR RESIS. ON - ETH - OS71	99	8	25	132
KSL-5 X KSL-3	THELIN#2/ TUKURU CGSS02Y00118S-099M-099Y-099M-16Y-OB x MON'S'/ALD'S'//TOWPE'S'	59	45	4	108
KSL-12 X KSL-2	PBW343*2/KUKUNA//PBW343*2/KUKUNA/3/PBW343 x CWANA 1st SR RESIS. ON - ETH - OS71	85	21	17	123
KSL-12 X KSL-3	PBW343*2/KUKUNA//PBW343*2/KUKUNA/3/PBW343 x MON'S'/ALD'S'//TOWPE'S'	79	38	5	122
KSL-12 X KSL-5	PBW343*2/KUKUNA//PBW343*2/KUKUNA/3/PBW343 x THELIN#2/ TUKURU CGSS02Y00118S-099M-099Y-099M-16Y-OB	97	34	9	140
KSL-19 X KSL-3	SUNCO//TNMU/TUI X MON'S'/ALD'S'//TOWPE'S'	69	16	28	113
KSL-19 X KSL-5	PBW343*2/KUKUNA//PBW343*2/KUKUNA/3/PBW343 x THELIN#2/ TUKURU CGSS02Y00118S-099M-099Y-099M-16Y-OB	82	19	1	102

KSL-19 and the check CACUKE.

DISCUSSION

The wheat lines involved in this genetic study have shown promising resistance even after five years of field testing at KARI Njoro. These lines were selected for crossing based on their promising stem rust resistance during the 2008, 2009 and 2010 growing season at KARI Njoro; a hot spot for stem rust with all known *P. graminis forma speciales tritici* races. Despite the fact that heavy stem rust disease pressure characterized all the wheat growing seasons, these five wheat lines have consistently exhibited resistance to stem rust. This implies that these lines are important sources of stem rust resistance and could be used to improve and broaden the genetic base for stem rust resistance among the wheat germplasm in Kenya.

During the 2012 to 2013 main season, only the segregation data for the parent KSL-2 conformed to the single dominant gene model. Chi square analyses done by several authors have revealed the presence of a single dominant gene conditioning the stem rust resistance in wheat (Babiker et al., 2009; Yin et al., 2008). The genetic ratios 9:4:3, 12:3:1 and 7:8:1 implied that two different genes contributed to the enhanced stem rust resistance. From this study, it was also noted that parents with moderately resistant (MR) to moderately susceptible (MS) or M responses had low disease severities thus these parents could be carrying some level of partial resistance. The partial resistance is associated with non hypersensitive, non race specific, moderately and highly heritable additive genes and is thought to confer durable resistance in wheat. The partial resistance could also be attributed to either additive or epistatic genes.

Epistasis is a form of gene interaction, whereby one gene interferes with the phenotypic expression of another non-allelic gene or genes. Thus, the combined phenotypic effect of two or more

genes is either less than (negative epistasis) or greater than (positive epistasis) the sum of effects of individual genes. Further studies involving the dissection of the genomic regions harbouring the resistance genes will be helpful in elucidating the exact gene effects involved especially in KSL-2 which exhibited the PBC trait. These resistance genes could also be isolated and further characterized in order to enhance durability of the available Kenyan wheat germplasm. Further, the diversity revealed in these wheat parents could be exploited effectively in breeding programs if the loci associated with the high resistance could be identified and also used in combinations with other effective stem rust resistance genes, especially in the Ug99 race high risk areas (Khanna et al., 2005). The further development of genetic linkage maps and repeat phenotyping is also imperative to reduce the possibility of recombinants.

Segregation for the expression of the pseudo black chaff was also noted in this experiment among the crosses with KSL-2 and KSL-3 during the 2012 and 2013 field tests. The pseudo black chaff phenotype which develops around stem internodes and the heads is completely linked with the *Sr2* gene; a non race specific stem rust resistance gene (Kaur et al., 2009). The non race specific genes are associated with non hypersensitive responses which lead to reduced sporulation and infection frequency. In its presence, there is slow disease progression and less selection pressure is exerted on the pathogen population leading to durability with respect to rust resistance in wheat (Prakash and Heather, 1988).

In this study, it was also noted that there was segregation for stem rust resistance among the resistant by resistant crosses. It is also worth noting that during crop improvement, the nature of population and crosses are crucial in determining the segregation pattern of germplasm (Xian et al., 2006). The segregation distortion noted among these crosses suggested non allelism among the resistance genes carried by the different parents (Williams and Miller, 1982). The genes conditioning the stem rust resistance among these parents are supposedly different or are non allelic and it is probable that other important stem rust resistance genes could be in the wheat genotypes' background. However, allelism test should be done to investigate this finding.

Conclusions

Since these wheat genotypes have exhibited enhanced resistance to stem rust, they are elite parents to be integrated in breeding for durable resistance to stem rust in wheat. The knowledge of the nature and the number of genes revealed among the wheat parents forms a core component of the wheat breeding program in ensuring efficient breeding strategy. These parents could be involved in more biparental crosses and also production of recombinant inbred lines (RILs). These RILs when used for QTL mapping will help to identify the genes which are conditioning the resistance in these crosses and their chromosomal locations. The identified stem rust resistance genes could be pyramided with other genes of minor effects into the adapted but susceptible Kenyan varieties to combat food and nutritional insecurity, given the imminent global threat due to the Ug99 and its derivative pathotypes.

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REFERENCES

Ayliffe M, Singh R, Lagudah E (2008). Durable resistance to wheat stem rust needed. Current Opinion in Plant Biol. 11:187-192

Babiker E, Ibrahim AMH, Yen Y, Stein J (2009). Identification of a microsatellite marker associated with stem rust resistance gene *Sr35* in wheat. Austr. J. Crop Sci. 3 (4):195-200

Bai G, Wu S, Pumphrey M (2009). Molecular Mapping of Stem Rust Resistance Gene Sr40 in Wheat. Crop breeding and genetics. Crop Sci. 49:1681-1686.

Boukhatem N, Baret PV, Jacquemin D, Mingeot JM (2002). Quantitative trait loci for resistance against Yellow rust in two wheat-derived recombinant inbred line populations. Theor Appl Genet. 104:111-118

Brown-Guedira GL, Singh S, Fritz AK (2003). Performance and mapping of leaf rust resistance transferred to wheat from *Triticum timopheevi* subspecies *armeniacum*. Phytopathology. 93:784-789

Eversmeyer MG, Kramer CL (2000). Epidemiology of wheat leaf and stem rust in the central great plains of the USA. Annu Rev Phytopathol. 38:491-513

Hickey LT, Wilkinson PM, Knight CR, Godwin ID, Kravchuk OY, Aitken EAB, Bansal UK, DeLacy IH, Dieters MJ (2012). Rapid phenotyping for adult plant resistance to stripe rust in wheat. Plant Breeding. 131: 54-61

Imtiaz M, Cromey MG, Hampton JG, Ahmad M (2011). Inheritance of durable adult plant resistance to stripe rust (*Puccinia striiformis* f.sp. *tritici*) in Otane wheat (*Triticum aestivum*). New Zealand J. Crop Hortic. Sci. 31 (1):23-31

Jin Y, Singh RP, Ward RW, Wanyera R, Kinyua M, Njau P, Fetch T, Pretorius ZA, Yahyaoui A (2007). Characterization of seedling infection types and adult plant infection responses of monogenic *Sr* gene lines to race TTKS of *Puccinia graminis* f. sp. *tritici*. Plant Dis. 91:1096-1099.

Kaur J, Bansal UK, Khanna R, Saini GR, Bariana HS (2009). Molecular mapping of stem rust resistance in HD2009/WL711 recombinant inbred line population. Int. J. Plant Breeding. 3 (1):28-33

Khanna R, Bansal UK, Saini RG (2005). Genetics of durable resistance to leaf rust and stripe rust of an Indian wheat cultivar HD2009. J. Appl. Genet. 46 (3):259-263

Kokhmetova MAA, Rsaliev S, Rsaliev A, Yessenbekova G, Typina L (2011). Wheat Germplasm Screening for Stem Rust ResistanceUsing Conventional and Molecular Techniques**.** Czech J. Genet. Plant Breeding. 47:S146-S154

Liu JQ, Kolmer JA (1998). Genetics of stem rust resistance in wheat cultivars Pasqua and AC Taber. Phytopathology. 88 (2):171-176

Mago R, Spielmeyer W, Lawrence GJ, Ellis JG, Pryor AJ (2004). Resistance genes for rye stem rust (*SrR*) and barley powdery mildew (*Mla*) are located in syntenic regions on short arm of chromosome. Genome. 47:112-121.

Mcintosh RA, Devos KM, Dubcovsky J, Rogers WJ, Morris CF, Appels R, Somers DJ, Anderson OA (2008). Catalogue of gene symbols for

wheat: 2008 Supplement. *Annual Wheat Newsletter*, vol. 54, p. 219. Available from Internet: http://wheat.pw.usda.gov/ggpages/wgc/2008upd.pdf.

Messmer MM, Seyfarth R , Keller M, Schachermayr G, Winzeller M, Feuillet SZC, Keller B (2000). Genetics analysis of durable leaf rust resistance in winter wheat. Theor. Appl. Genet. 100:419-432

Naghavi MR, Mohammadi V, Ghannadha MR (2007). Gene number and heredity of barley powdery mildew (Erysiphe graminis f.sp. hordei) resistance at adult plant stage. Int. J. Agric. Biol. 9 (2):239-241

Navabi A, Singh Ravi P, Tewari JP, Briggs KG (2004). Inheritance of High Levels of Adult-Plant Resistance to Stripe Rust in Five Spring Wheat Genotypes. Crop breeding, genetics and cytology. Crop Sci. 44:1156-1162.

Ooro PA, Bor PK, Amadi DOK (2009). Evaluation of wheat genotypes for improved drought tolerance through increased seedling vigour. African Crop Science Conference Proceedings. 9:49-53 (This is not the complete reference. Write the place of the conference, the date and the name of the editor(s).

Parlevliet JE (1993). What is durable resistance? A general outline. Durability of disease resistance. Th. Jacobs and J.E. Parlevliet (Eds). Kluwer Academic Publishers, Norwell, MA. 23-29.

Peterson RF, Campbell AB, Hannah AE (1948). A diagrammatic scale for estimating rust intensity on leaves and stems of cereals. Canadian J. Res. 26:496-500

Polanda JA, Bradbury PJ, Buckler ES, Rebecca JN (2011). Genome-wide nested association mapping of quantitative resistance to northern leaf blight in maize. www.pnas.org/cgi/doi/10.1073/pnas.1010894108

Prakash CS, Heather WA (1988). Inheritance of partial resistance to two races of leaf rust, *Melampsoram medusa* in Easrwen Cottonwood, Populous deltoids. Silvae genetica. 38:3-4

Rouse MN, Nava IC, Chao S, Anderson JA, Jin Y (2012). Identification of markers linked to the race Ug99 effective stem rust resistance gene Sr28 in wheat (Triticum aestivum L.). Theor Appl Genet. 125:877-885

Rubiales D, Nicks RE (2000). Combination of mechanism of resistance to rust fungi as a strategy to increase durability. CIHEAM –IAMZ. 333-339.

Singh D, Simmonds J, Park RF, Bariana HS, Snape JW (2009). Inheritance and QTL mapping of leaf rust resistance in the European winter wheat cultivar “Weaver”. Euphytica. 169:253-261

Singh RP, Hodson DP, Huerta-Espino J, Jin Y, Bhavani S, Njau P, Herrera-Foessel S, Singh PK, Singh S, Govindan V (2011). The Emergence of Ug99 Races of the Stem Rust Fungus is a Threat to World Wheat Production. Annu. Rev. Phytopathol. 49:465-81.

Vanegas CDG, Garvin DF, Kolmer JA (2007). Genetics of stem rust resistance in spring wheat cultivar Thatcher and the enhancement of stem rust resistance by *Lr34* stem rust resistance in TcLr34. Euphytica. 159:391-401

Williams ND, Miller JD (1982). Allelic and Linkage Relations among Genes for Stem Rust Resistance from *Triticum turgidum*, ‘Mindum,’ ‘Acme’ Selection, ‘Palestine,’ and ‘Khapli’. Crop Sci. 22:1203-1207

Xian L, Xue S, Tian ZZ (2006). Segregation distortion and its effect on genetic mapping in plants. J. Agric. Biotechnol. 14 (2):286-292

Yin J, Wang G, Ma F, Zhang H, Xiao J, Sun, Y, Diao, Y, Huang J, Guo Q (2008). Genetic analysis and SSR mapping of stem rust gene from mutant D51. Frontiers of Agriculture, China. 2 (2):131-136.