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Review

Status of genetic research for resistance to Ug99 race of *Puccinia graminis* f. sp. *tritici*: A review of current research and implications

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Stem rust, caused by *Puccinia graminis* f. sp. *tritici (Pgt)*, is one of the most serious diseases of bread (*Triticum aestivum* L.) and durum (*Triticum durum* Desf.) wheat worldwide. The discovery of new *Pgt* races in Africa, Ug99 and its variants, brings a new threat to global wheat production. Currently, the research of stem rust in wheat is focusing on identifying further resistance genes to control Ug99 and its derivatives. Some resistance genes, which were identified from wild relatives and chromosomal regions conferring resistance to stem rust, were also detected using QTL analysis and genome wide association studies. Additionally, development of molecular markers linked to stem rust resistance (*Sr*) genes is one of the focus areas of current research. These molecular markers play a key role in the genetic characterization of the new sources of resistance as well as in stacking two or more resistance genes in a single line. Pyramiding several, major and minor, stem rust resistance genes into adapted varieties as opposed to breeding varieties with a single resistance gene is considered a more effective method to combat new races. Therefore, recent progress on molecular marker development and improved donor sources are accelerating the pyramiding and deployment of cultivars with more durable resistance to stem rust.

Key words: Molecular markers, resistance, *Sr* genes, stem rust, Ug99.

INTRODUCTION

Stem rust caused by the fungus *Puccinia graminis* f. sp. *tritici* (*Pgt*) is one of the major factors that limit wheat production worldwide. Stem rust can cause severe yield losses in susceptible cultivars of wheat in environments favourable for disease development (Leonard and Szabo, 2005). According to Singh et al. (2011) most of the major wheat production areas worldwide are favourable environments for disease development and prone to severe losses. That is why stem rust has been also a major problem historically in all of Africa, the Middle East, all of Asia (except Central Asia), Australia, New Zealand and Europe (Saari and Prescott, 1985). In the mid 20th century, yield losses reached 20 to 30% in eastern and central Europe (Zadoks, 1963) and many other countries, including Australia, China and India (Roelfs, 1977; Leonard and Szabo, 2005). Major epidemics result in dramatic losses in the United States occurred in the mid 1930s and again in the 1950s (Roelfs, 1978). In Ethiopia, losses incurred due to stem rust were estimated up to 70% on susceptible wheat cultivars at times of disease epidemics (Bechere et al., 2000; Admassu, 2010).

Although the last major stem rust epidemic occurred

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In Ethiopia during 1993/94 (Shank, 1994; Badebo, 2002) when a popular wheat variety 'Enkoy' fell out of production, the rest of the world had practically remained unhurt from stem rust for over three decades (Singh et al., 2008a).

Stem rust resistance genes were successfully deployed in commercial cultivars worldwide from the middle 1950s, effectively controlling the disease. However, in 1999, a new race of stem rust, Ug99, also called TTKS, emerged in Uganda (Pretorius et al., 2000). Later, it was also found in Kenya, Ethiopia and Yemen (Singh et al., 2006). It has been predicted that the route of spread of Ug99 could follow that of a *Yr9*-virulent pathotype of *P. striiformis* which, in the late 1980s, originated in Africa and subsequently spread to the Arabian peninsula, Syria, and eastward to Pakistan and India (Singh et al., 2006). Similar trajectories from Ug99 sites in Iran indicate that Iran can be gateway for Ug99 migration to other Asian countries (Singh et al., 2008a, b). More recently, Ug99 has spread throughout much of Africa, the Middle East and West Asia (Yu et al., 2012). Approximately 1 billion people reside in the predicted path of Ug99. Many of the people present in this region are in countries that consume all the wheat produced within their borders (Olson, 2012). Therefore, stem rust has again become a major threat to global wheat production and food security (Singh et al., 2011).

The importance of Ug99 was recognized by the world wheat community and certain donor organizations (such as Melinda and Bill Gates Foundation) responded positively, and various research and developmental projects are now underway to combat Ug99 under the coordination of the Borlaug Global Rust Initiative (http://www.globalrust.org). For example, a primary focus of pre-breeding research supported as part of the Durable Rust Resistance in Wheat (DRRW) (Pumphrey, 2012) project is to search effective sources of resistance from readily accessible gene pools, introgression and cytogenetic manipulation of new sources of resistance from alien gene pools, genetic mapping and development of diagnostic DNA markers for desirable sources of resistance, determination of optimal combinations of resistance genes, and germplasm development. The objective of this review paper is to indicate the current research activities undertaken to mitigate the threat from Ug99 and its derivatives.

STEM RUST RESISTANCE GENES

Stem rust has been successfully brought under effective control through the use of host resistance in the past several decades until the occurrence of race TTKSK and its variants which have defeated most stem rust resistance (*Sr*) genes existing in commercial varieties. A number of stem rust resistance genes, designated as *Sr* genes in wheat and its close relatives, were described and cataloged, and monogenic lines carrying the individual *Sr* genes are available in several wheat backgrounds. High levels of stem rust adult plant resistance (APR) should be achievable by combining multiple APR genes as achieved for leaf rust and stripe rust (Rutkoski et al., 2011). Most of the *Sr* genes have been characterized for their reactions to specific races of *P. graminis f. sp. tritici* including reactions at the seedling stage. To date, 55 genes have been designated for resistance to wheat stem rust (McIntosh et al., 1995, 2011). Over the last century, these genes have been identified within common wheat and wild relatives (Olson, 2012). According to the report of Pumphrey (2012), about 30 major genes conferring resistance to Ug99-complex races, and about five designated adult plant resistance genes that contribute to stem rust resistance have been identified.

In the past 50 years, a number of *Sr* genes have been identified and incorporated into wheat genomes through chromosome engineering. Some of these, including *Sr22*, *Sr25*, *Sr27, Sr32, Sr33, Sr35, Sr37, Sr39, Sr40, Sr44, Sr45, Sr46* and a few unnamed genes are still resistant to Ug99 and its derivatives (Xu et al., 2008). *Sr* genes shown to be effective against Ug99 are given in Table 1. However, most of these genes are derived from wild relatives of wheat and are located on chromosome translocations that include large donor segments that harbour genes possibly deleterious to agronomic and quality traits (Dundas et al., 2007). Thus, they are virtually unusable in their current form. To enhance the utility of genes in wheat breeding, ccurrently there are ongoing research efforts to eliminate the deleterious linkage drag and to produce lines with smaller chromosome segments containing the resistance genes.

These genes have been introduced into wheat but have not been deployed in commercial cultivars (Yu et al., 2011). Among the wheat relatives, *Ae. speltoides* has been an excellent source of genes for stem rust resistance. *Sr* genes, for example, *Sr32*, *Sr39*, and *Sr47* have been transferred into common wheat and durum wheat and all three confer resistance to TTKSK (Jin et al., 2007; Faris et al., 2008; Xu et al., 2009). Efforts to reduce the size of alien chromatins containing diverse *Sr* genes are currently underway (Pumphrey, 2012). Dundas et al. (2007) produced a number of lines with shortened or modified alien chromosome segments carrying *Sr32*, *Sr37*, *Sr39*, and *Sr40.* Similarly, Singh et al. (2008a) recommended that sizes of alien chromosome segments must be reduced before these genes can be used successfully in breeding because the successful use of alien genes is mostly determined by the ability of the introduced alien chromosome segments to substitute for homoeologous chromosome segments of wheat.

Translocations with small alien fragments have less likelihood of a linkage drag, which can depress essential agronomic and end-use quality traits (Liu et al., 2011). Wheat-rye 1RS recombinants that break the linkage

Table 1. Chromosomal location, description, linked markers and citation for stem rust resistance genes effective against *Puccinai graminis* f. sp. *tritici* race of Ug99 and its variants.

Gene	Location	General description	Linked markers	Source	Citation
Major genes (race-specific resistance)					
Sr1A.1R	1A.1R	- Confers moderate resistance to Ug99. - Present in several hard red winter wheat cultivars.	*SCM9* *BARC28*	*Secale cereale*	Saal and Wricke, 1999; Mago et al., 2005; Jin and Singh, 2006
Sr13	6AL	- Frequent gene in durum varieties. - Current virulent *Pgt* race on durum wheat in Ethiopia is reported.	*BARC104* *WMC580* *DUPW167* *CK207347* *CD926040* *BE403950*	*Triticum turgidum*	Klindworth et al., 2007; Admassu et al. 2011; Simons et al., 2011; Haile et al., 2012, Olivera et al., 2012
Sr22	7AL	- Confers resistance to Ug99 and other important races. - Limited use due to chromosome translocations harbouring a yield penalty and a delay in heading date.	*WMC633* *CFA2123* *CFA2019* *BARC121*	*Triticum monococcum*	Gerechter-Amitai et al., 1971; Kerber and Dyck, 1973; Khan et al., 2005; Olson et al., 2010; Periyannan et al., 2011; Singh et al., 2011
Sr25	7DL , 7AL	- Conferred a high level of resistance only in some genetic backgrounds. - Linked with another *Th. ponticum* derived gene causing undesirable yellow flour.	*BF145935* *GB* *PSY-D1* *PSY-E1*	*Thinopyrum elongatum*	Ayala-Navarrete et al., 2007; Liu et al., 2010; Singh et al., 2011
Sr26	6AL	- Confers resistance to Ug99 and other races. - Not widely deployed in commercial varieties due to yield penalty.	*Sr26#43* *BE518379*	*Aegilops elongatum*	Knott et al., 1961; The et al., 1988; Mago et al., 2005; Dundas et al., 2007; Liu et al., 2010, Singh et al., 2011
Sr27	3A	- Effective against Ug99. - Has not been used in wheat improvement.	-	*Secale cereale*	Singh et al., 2011
Sr28	2BL	- APR for most known races. - Seedling stage resistance for races BCCBC, TTKSK and TTKST.	*WMC332*	*Triticum aestivum*	Jin et al., 2007; Rouse et al., 2011, 2012
Sr32	2A, 2B, 2D	Effective against Ug99.	*STM773* *BARC55*	*Aegilops speltoides*	McIntosh et al., 1995; Friebe et al., 1996; Bariana et al., 2001; Singh et al., 2006; Dundas et al., 2007; Jin et al., 2007; Yu et al., 2009
Sr33	1DS	Confers only moderate levels of resistance.	-	*Aegilops tauschii*	Jones et al., 1991; Sambasivam et al., 2008; Jin et al., 2007; Singh et al., 2008a
Sr35	3AL	Effective against race TTKSK (Ug99) and its variants (TTKST and TTTSK).	*GWM480* *GWM271* *WMC169* *WMC559* *BARC51* *CFA2193* *CFA2170* *CFA2076* *BE423242* *BF485004* *AK335187* BE405552	*Triticum monococcum*	Jin et al., 2007; Babiker et al., 2009; Yu et al., 2009; Zhang et al., 2010; Singh et al., 2011
Sr37	4BL	- An effective gene against Ug99. - Because of linkage drag, it has not been used in wheat breeding.	-	*Triticum timopheevi*	McIntosh, 1991; Zhang et al., 2012
		- Moderately to highly resistant to Ug99 in seedling	*Sr39#22r* *Sr39#50s*	*Aegilops speltoides*	Kerber and Dyke, 1990; Friebe et al., 1996; Knox et al., 2000; Jin et

Table 1. Contd.

Sr39	2B	tests. - Negative agronomic effects due to linkage drag.	*WMC474* *RWGS27* *RWGS28* *RWGS29*		al. 2007; Singh et al., 2007; Mago et al., 2009; Yu et al., 2010; Niu et al., 2011
Sr40	2BS	Moderately to highly resistant to Ug99 in seedling tests.	*GWM344* *GWM319* *WMC477* *WMC661* *WMC474* *Sr39#22r*	*Triticum timopheevii* ssp. *armeniacum*	Dyck, 1992; Jin et al., 2007; Singh et al., 2007; Wu et al., 2009
Sr42	6DS	Confers resistant to TTKSK and variants TTKST and TTTSK.	BARC183 GPW5182	*Triticum aestivum*	Ghazvini et al., 2012
Sr43	7D	Resistant to TTKSK, TTKST and TTTSK.	-	*Aegilops elongatum*	Knot et al., 1977; Xu et al., 2009
Sr44	7DS	Moderately to highly resistant to Ug99 in seedling tests.	-	*Thinopyrum intermedium*	Jin et al., 2007; Singh et al., 2007
Sr45	1DS	- A locus more proximal to *Sr33.* - Confers moderate level of resistance.	-	*Aegilops tauschii*	Sambasivam et al., 2008; Singh et al., 2011; Olson, 2012
Sr46	2DS	Confers moderate level of resistance.	-	*Aegilops tauschii*	Rouse et al., 2011; Singh et al., 2011; Olson, 2012
Sr47	2BL	High level of resistance to Ug99 in tetraploid wheat.	*GPW4043* *GWM501* *GWM47* *GPW4165*	*Aegilops speltoides*	Faris et al., 2008; Klindworth et al., 2012
Sr50 (SrR)	1DL.1RS	Effective against Ug99.	-	*Secale cereale*	Mago et al., 2004; Anugrahwati et al., 2008
Sr52	6AL	Shows a temperature-sensitive resistance pattern to race Ug99.	*WMS570* *BE497099*	*Dasypyrum villosum*	Qi et al., 2011
Sr53	5DL	Effective against Ug99.	*BE443202* *BE442600*	*Aegilops geniculata*	Liu et al., 2011
SrCad	6DS	Provides high levels of resistance to stem rust only when combined with the leaf rust resistance gene *Lr34.*	*CFD49* *FSD_RSA*	*Triticum aestivum*	Kerber and Aung, 1999; Laroche et al., 2000; Hiebert et al., 2011
SrTmp	-	- Exists in several hard red winter wheat cultivars. - Low infection type to race Ug99.	-	*Triticum aestivum*	Roelfs and McVey, 1975; Singh et al., 2007
SrWeb	2BL	Has an allelic relationship with *Sr9* and *Sr28*	*GWM47* *WMC332* *WMC175*	*Triticum aestivum*	Hiebert et al., 2010
Adult Plant Resistance (APR) genes					
Sr2	3BS	- Conferred durable resistance against all virulent races of *Pgt* worldwide for more than 50 years (combined with other genes). - Deployed in many wheat cultivars worldwide. - Pseudo-black chaff (morphological marker).	*GWM533* *GWM389* *BARC133* *csSr2* *3B042G11* *3B028F08* *STM559TGAG*	*Triticum turgidum*	Hare and McIntosh, 1979; Rajaram et al., 1988; Roelfs, 1988; McIntosh et al., 1995; McIntosh et al., 1998; Spielmeyer et al., 2003; Hayden et al., 2004; McNeil et al., 2008; Mago et al., 2011a; Singh et al., 2011

between the stem rust resistance gene *SrR* and Sec-1 locus (encoding secalin seed storage proteins and their association with quality defects) were isolated by Anugrahwati et al. (2008). A yield penalty associated with the *T. monococcum* ssp*. boeoticum* chromosome segment carrying *Sr22* has limited the use of this gene in wheat breeding programs (The et al., 1988). But, recently, lines with *Sr22* and reduced *T. monococcum* segments have been developed (Olson et al., 2010). Three new markers, *RWGS27, RWGS28,* and *RWGS29,* were recently developed for *Sr39* using RWG accessions that carry a reduced-size *Sr39* alien fragment in a wheat background (Niu et al., 2011). These markers will increase the efficiency of incorporating *Sr* genes into cultivars that are widely adapted but susceptible to Ug99 and help for the development of new elite lines that are resistant to Ug99 and its derivatives.

Genetic mapping of *Sr* genes effective against Ug99

Pyramiding of several genes into one cultivar can be an alternative effective strategy to use resistance genes to enhance durability of wheat resistance to stem rust (Leonard and Szabo, 2005). Gene pyramiding using conventional method is difficult and time-consuming because it requires simultaneous tests of the same wheat breeding materials with several different rust races before making selection. Usually, it is not feasible for a regular breeding program to maintain all necessary rust races needed for this type of work (Wu, 2008). Therefore, marker-assisted selection (MAS) is a powerful alternative to facilitate new gene deployment and gene pyramiding for quick release of rust-resistant cultivars. Molecular markers are available for only few resistance genes such as *Sr2, Sr13, Sr22, Sr26, Sr35, Sr39, Sr40,* etc. (Table 1). However some of the markers have been used in MAS, but markers for some of the genes are not diagnostic for the genes (Haile et al., 2013b) and must be improved and markers for other genes are not available.

Validation of chromosome location of stem resistance genes that confer resistance for Ug99 and its derivatives through molecular mapping to identify closely linked markers for MAS was performed for *Sr22* (Khan et al., 2005), *Sr24* and *Sr26* (Mago et al., 2005), *Sr39* (Wu et al., 2009), *Sr35* (Zhang et al., 2010), *Sr13* (Admassu et al., 2011; Simons et al., 2011), *SrCad* (Hiebert et al., 2011), *Sr53* (Liu et al., 2011), *Sr42* (Ghazvini et al., 2012), *Sr28* (Rouse et al., 2012), etc. This will help the breeding programs to deploy these resistance genes in commercial wheat cultivars to prevent stem rust epidemics and to reduce the losses caused by the disease in future.

QUANTITATIVE TRAIT LOCI (QTL) STUDIES

QTL mapping studies can identify chromosomal regions with important traits and tightly linked markers that can then be used as an effective tool in marker- assisted selection (Collard et al., 2005). QTL mapping using high-throughput simple sequence repeat (SSR), single nucleotide polymorphism (SNP) or Diversity Arrays Technology (DArT) markers gives the opportunity for genome-wide mapping (Singh et al., 2013). QTL mapping has been utilized effectively to identify and map regions in the wheat genome that contain genes that confer resistance for Ug99 and other races of *Pgt*. Many consistent stem rust QTL conferring resistance to Ug99-complex races have been identified. Several additional newly discovered resistance loci are at various stages of development and validation (Pumphrey, 2012).

Ongoing characterizations of bi-parental and association mapping populations have indicated the presence of numerous other stem rust resistance loci, many likely contributing to Adult plant resistance (APR) (Pumphrey, 2012). Consistent QTL were identified using biparental QTL mapping and Association mapping studiers are given in Table 2. Many researchers have reported QTL regions which are significantly associated with resistance to stem rust races of *Pgt* including Ug99 at the seedling and adult plant stage in different germplasm (Pozniak et al., 2008; Kaur et al., 2009; Maccaferri et al., 2010b; Bhavani et al., 2011; Yu et al., 2011, 2012; Haile et al., 2012; Singh et al., 2013).

Some the QTL regions identified were co-localized with known *Sr* regions. Using the ‘Kristal’/’Sebatel’ RIL durum wheat population, nine consistent QTL regions that confer resistance for Ug99 were identified. The largest portion of resistance for Ug99 (R^2=34%) in this population is explained by the QTL identified on the short arm of chromosome 3B (*QSr.IPK-3B)* (Haile et al., 2012). This may be due to the presence of the adult plant resistance gene, *Sr2,* which maps in about the same region of chromosome 3BS. One of the flanking markers for this QTL (*Xgwm389*) is located in a distance of about 4.3 cM from one of the diagnostic microsatellite markers (*Xgwm533*) for *Sr2* (Spielmeyer et al., 2003). Haplotype analysis result (Haile et al., 2013b), based on expected fragment sizes of linked markers, and also confirmed the presence of *Sr2* in ‘Sebatel’.

‘Sebatel’ was bred at ICARDA through accumulating resistance genes from multiple crosses through field breeding for resistance to stem rust races in Syria, Lebanon and the Mediterranean region. This variety is tested in Syria and Ethiopia and showed a high level of resistance to *Pgt.* Therefore, this result confirmed the effectiveness of *Sr2* in controlling *Pgt* races of stem rust including Ug99. It has been reported that *Sr2* contributes to adult plant resistance through the interaction between *Sr2* and other unknown genes to form a '*Sr2* complex' (Singh et al., 2009; Yu et al., 2011). The effect of *Sr2* can be enhanced by adding race-specific *Sr* genes (Spielmeyer et al., 2003). So there might be other additional major or minor genes in addition to *Sr2* which account for the quantitative component of stem rust resistance in ‘Sebatel’. Additionally, the QTL region that is identified on the long arm of chromosome 7A (Haile et al., 2012) flanked by markers *Xbarc121* and *Xgwm984* may be due to the influence of stem rust resistance gene

Table 2. Consistent QTL regions identified by linkage mapping and association analysis for resistance to Ug99 and its derivatives in wheat.

Chromosome Region	Source	Citation	Remark
1A and 4B	'Sachem'	Singh et al., 2013	Biparental QTL mapping; Evaluated in Kenya.
1AL, 2AS, 3BS, 4BL, 5BL, 6AL, 7A, 7AL and 7BL	'Sebatel'	Haile et al., 2012	Biparental QTL mapping; Evaluated in Ethiopia.
1A, 2B, 3B, 4A, 5B, 6B, 7B and 7D	232 winter wheat lines of diverse origins	Yu et al., 2012	Genome-wide association; Evaluated in Kenya.
1B, 3B, 3D, 4B and 5A	'Pavon 76' and 'Avocet S'	Njau et al., 2012	Biparental QTL mapping; Evaluated in Kenya.
1B, 2B, 3B, 4A, 5B, 6A, 6B and 7D	276 elite spring wheat lines from CIMMYT	Yu et al., 2011	Association mapping; Evaluated in Kenya.
1A, 3BS, 5BL, 7A and 7DS	'Kingbird'	Bhavani et al., 2011	Biparental QTL mapping; Evaluated in Kenya.
2D, 3BS, 5BL and 7DS	'Kiribtati'	Bhavani et al., 2011	Biparental QTL mapping; Evaluated in Kenya.
2B, 3BS, 4A, 5BL and 6B	'Juchi'	Bhavani et al., 2011	Biparental QTL mapping; Evaluated at Kenya.
2B, 3BS, and 7B	'Huirivis#1'	Bhavani et al., 2011	Biparental QTL mapping; Evaluated in Kenya.
2B, 3BS and 5BL	'Muu'	Bhavani et al., 2011	Biparental QTL mapping; Evaluated in Kenya.
1BL, 3BS, 5A and 6B	'Pavon 76'	Bhavani et al., 2011	Biparental QTL mapping; Evaluated in Kenya.
6A and 6D	'Avocet S'	Prins et al., 2011	Biparental QTL mapping; Evaluated in Greenhouse.
2AS, 5BL and 7BL	187 durum wheat accessions	Maccaferri et al., 2010b	Association mapping; Evaluated in Ethiopia.
3BS, 5DL and 7A	'HD2009'	Kaur et al., 2009	Biparental QTL mapping; Tested in Australia.
1A, 1B, 2A, 3B, 4B, 5A, 5B, 6A, 7A and 7B	96 durum wheat cultivars and breeding lines of diverse origins	Pozniak et al., 2008	Association mapping; Evaluated in Kenya.

Sr22, since *Xbarc121* is one of the reported diagnostic markers for this gene (Olson et al., 2010). But so far there is no evidence that *Sr22* was transferred to durum wheat (Ravi Singh, personal communication).

Some QTL regions are either tightly linked or have pleiotropic effects on other resistance or end-used quality traits. For example, a QTL was identified on the long arm of chromosome 7B for resistance to Ug99 (Haile et al., 2012) and for leaf rust resistance by Maccaferri et al. (2010a), which may be caused by *Lr9* or *Lr14*. Several suggestive markers were also identified on chromosome 7BL that have found to be important for expression of yellow pigment by using association studies based on 183 durum wheat lines (Pozniak et al., 2012). It is known that many resistance genes appear in clusters which may consist of genes rendering resistance to different types of pathogens. Therefore, it is possible that such genomic region harbours a polygenic resistance gene cluster with specificities for at least two pathogens.

Combining resistance genes in wheat breeding to facilitate the development of more durable resistances is a well-known procedure in wheat breeding (Lagudah, 2011). The markers that are closely linked with these reported QTL could be used for MAS for resistance to race Ug99 (TTKSK) and its variants. Therefore, it could be a good strategy to pyramid three or four QTL during development of wheat varieties in order to obtain durable resistance. Therefore, the results reported from QTL studies by different authors offer important perspectives for the transfer of stem rust resistance to new varieties by MAS, as three or more loci from resistant sources particularly if the source is a variety with good yield performance and high grain quality. Such sources could be used as donor variety to transfer stem rust resistance to new and productive genotypes by MAS without the risk of introducing undesired traits together with the resistance gene(s).

Even if many QTL were identified in crop species during the last two decades, relatively only few are used practically in breeding programs (Bernardo, 2008). Genotype–environment interactions and/or epistasis are the reasons making difficult practical application of marker-assisted selection for quantitative traits (Pozniak et al., 2012). Epistatic interactions are more difficult to study, requiring segregating populations of uniform lines; nevertheless, they have to be studied to obtain a complete picture of the genetic control of the trait and to control MAS failure (Asins, 2002).

POTENTIAL OF MOLECULAR MARKERS FOR VARIETY DEVELOPMENT

To facilitate breeding for durable resistance to stem rust, molecular markers are useful tools for the development of resistant cultivars and, especially, for pyramiding of resistance genes for several diseases (Anderson, 2003). It is possible to predict the presence of a specific resistance gene using linked molecular markers without the need for disease evaluation (Yu et al., 2010). This aids indirectly the transfer of several resistance genes into adapted materials to pyramid several genes in one variety.

Markers linked to resistance genes *Sr2, Sr13, Sr22, Sr25, Sr26, Sr28, Sr32, Sr35, Sr39, Sr40, Sr47, Sr52, SrCad* and *SrWeb* have been reported (Spielmeyer et al., 2003; Hayden et al., 2004; Khan et al., 2005; Mago et al., 2005, 2009, 2011; Dundas et al., 2007; McNeil et al., 2008; Wu et al., 2009; Yu et al., 2009; Hiebert et al., 2010, 2011; Liu et al., 2010; Niu et al., 2011; Periyannan et al., 2011; Qi et al., 2011; Simons et al., 2011; Klindworth et al., 2012; Rouse et al., 2012; http://maswheat.ucdavis.edu/). Some of these markers have been used in MAS, but markers for some of the genes are not diagnostic for the genes and must be improved and markers for other genes are not available (Todorovska et al., 2009). Many of the introgressed genes are also associated with undesirable effects on agronomic traits (McIntosh et al., 1995).

Although several markers were reported as tightly linked to target resistance genes in a specific population in previous studies, they were not diagnostic when in different backgrounds. For example, markers *CFA2019* for *Sr2*; CFA*2123* for *Sr22*; and *GWM480, CFA217, BF485004, BE405552, CFA2193* and *BE423242* for *Sr35* showed a similar haplotypes with the reference lines in Ug99 susceptible varieties and landraces (Haile et al., 2013b) and markers *3B042G11*, *3B028F08,* and *STM559TGAG* for *Sr2*; CFA*2123* for *Sr22*; *STM773* for *Sr32*; *RWG29* for *Sr39*; and WMC*344, WMC477, GWM319,* and *WMC661* for *Sr40* gave false positives in different accessions without target resistance genes (Bernardo et al., 2012) Therefore these markers are not recommended for detecting the presence of target resistance genes and MAS. This may be due to a reason that most of these markers were identified using a specific bi-parental mapping population, and levels of polymorphism for these markers may vary with parents and genetic distances between markers and the resistance genes are also different among the genes (Bernardo et al., 2012). Thus it is useful to use phenotypic selection together with MAS to improve response to selection and thereby to increase rates of genetic progress (William et al., 2007).

Even though, new resistance genes were transferred to wheat from cultivated emmer and other wild relatives, the pathogen has demonstrated an ability to adapt to different resistance genes by gaining virulence. Therefore, deployment of single new resistance genes is unlikely to be durable. A more effective method to combat Ug99 races would be to pyramid several new resistance genes into each new adapted variety (Mago et al., 2011b; Bernardo et al., 2012). Using molecular markers it is also possible to pyramid 2-3 genes to achieve durable resistance. Pyramiding of *Sr24, Sr26*, *Sr31,* and *SrR* has been reported by (Mago et al., 2011b), and of *Sr22, Sr26,* and *Sr35 to* confer resistance to Ug99 and other important races (Singh et al., 2011). Markers for these genes could then aid selecting APR, pyramiding *R*-genes, and in combining APR genes with *R*-genes (Yu et al., 2011). For example, varieties have been released in Egypt, Afghanistan, and Pakistan whose resistance is based on single race-specific gene *Sr25* and slow rusting resistance gene *Sr2* (Singh et al., 2011).

An increased research focus on APR in recent years has enhanced the characterization of APR genes and identification of tightly linked molecular markers. These advances will further aid their utilization and the exploration of new genetic diversity in landraces and related species. For example, the availability of landraces that showed moderate resistance to *Pgt* race of Ug99 (Haile et al., 2013a) showed the availability of potential germplasm (Ethiopian tetraploid wheat landraces) for breeding to stem rust resistance. The presence of *Sr2* in some of the landraces (Haile et al., 2013b), also strengthen this fact and showed that Ethiopian cultivated tetraploid wheat accessions are still good sources of stem rust resistance. New selection tools, such as genomic selection, can also be employed to pyramid multiple small effect APR genes (Singh 2012).

CONCLUSIONS

Due to the current state of world affairs with the initiation of the Borlaug Global Rust Initiative (BGRI), there are ongoing research activities to combat the potential threat that stem rust race Ug99 poses to a large percentage of world wheat germplasm. Identification of novel sources of stem rust and Ug99 resistance in rye, goat grasses, perennial wheat grasses, and other wild species; and combined classical cytogenetics with molecular marker techniques to develop bread and durum wheat lines carrying resistance genes derived from wild relatives of wheat that are free of “linkage drag” is one of the objectives of this initiative in collaboration with International and National investigators (Pumphrey, 2012). This is because these unwanted segments of chromosome that can be inherited from wild species along with rust resistance genes hinder commercial breeding efforts.

With low numbers of reported resistant varieties with resistance to Ug99, markers closely linked to QTL/genes conferring resistance for stem rust could aid in combating local and global threats from Ug99 and any new virulent rust races. Race specific resistance is the dominantly utilised source of resistance to develop wheat varieties resistant to *Pgt* races of stem rust. Combinations of APR and/or major genes should be a more attractive, farmer- and environment-friendly rust control strategy. Currently, most wheat improvement programs particularly of CIMMYT shifted to non-race-specific durable resistance. A large proportion of high-yielding spring bread wheat germplasm developed and distributed worldwide by CIMMYT has high to adequate APR to all three rusts, including the *Pgt* Ug99 group (Singh, 2012).

Breeding for resistance to rust diseases particularly for stem rust is a current issue of wheat growing areas of the world due to the emergence of race Ug99 (TTKSK). Deployment of wheat varieties with adequate to high levels of resistance is advantageous to farmers and seed agencies as well as breeding programs. Successful breeding relies on the identification of new resistance sources via QTL or gene mapping and incorporation of these resistance sources into breeding lines to release new resistant varieties. Additionally, development of molecular markers linked to *Sr* genes is one of the focus areas of current research. These markers will increase the efficiency of incorporating *Sr* genes into cultivars that are widely adapted but susceptible to Ug99 and help for the development of new elite lines that are resistant to Ug99 and its derivatives. Furthermore, it is required to exploit the potential genetic resources.

Abbreviations: APR, Adult plant resistance; **BGRI,** Borlaug Global Rust Initiative; **CIMMYT,** International Maize and Wheat Improvement Center; **DRRW,** durable rust resistance in wheat; **ICARDA,** International Center for Agricultural Research in the Dry Areas; ***Pgt,*** *Puccinia graminis* f. sp. *tritici;* **MAS,** marker- assisted selection; **QTL,** quantitative trait loci; ***Sr,*** stem rust resistance.

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