Available online at www.ijpab.com

DOI: http://dx.doi.org/10.18782/2320-7051.2880

ISSN: 2320 – 7051

Int. J. Pure App. Biosci. **5 (3):** 316-328 (2017)

Review Article

International Journal of Pure & Applied Bioscience

OPEN ACCESS

Stem Rust of Wheat- *A Basic Review*

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Received: 21.04.2017 | Revised: 30.04.2017 | Accepted: 1.05.2017

ABSTRACT

Throughout the history, stem rust has been considered a major threat to the wheat production. The three rust diseases of wheat namely stem, leaf and stripe rust are the most important biotic constraints to wheat production. Stem rust or black rust of wheat caused by the fungus Puccinia graminis Pers. f. sp. tritici Eriks. & E. Henn, is often the most damaging of the three wheat rust diseases due to the potential for complete crop loss. The spread of stem rust race Ug99 and variants are threat to worldwide wheat production and efforts are being made to identify and incorporate resistance. A primary source of concern at present is that Ug99 (TTKSK and its variants TTKST and TTTSK) has overcome major sources of stem rust resistance genes eg Sr31, Sr38 and other important gene complexes which confer resistance to stem rust. At present, among the 58 catalogued resistant genes against stem rust, only less than half of them are effective to Ug99[27] (McIntosh et al. 2014). There are a total of 26 stem rust resistant genes derived from common wheat, only three (Sr28, Sr29 and SrTmp) are resistant to Ug99, and the effects of these genes are moderate under heavy disease pressure. Among the catalogued genes conferring some level of resistance against Ug99, 32 genes were introduced into wheat from its wild relatives. Because of limited resistance in the wheat gene pool, the discovery of novel resistance in wild relatives and its transfer to wheat by chromosome engineering is an effective strategy of disease control.

Key words: *Stem Rust, UG-99, Sr-24, QTL Mapping, Durable Resistance, Shuttle Breeding.*

INTRODUCTION

Wheat, one of mankind's important staple foods, is grown on about 225 m ha worldwide. Stem rust is known for causing severe devastations periodically in all wheat- growing countries of the world. The fungus grows primarily on the leaf sheath or stem tissues of a wheat plant and can block the vascular system, leading to lodging, shriveled grains, and total crop loss during severe epidemic years. Pathogens generally display alternating sexual and asexual stages, thus harbouring complex life cycles that strongly impact their adaptive potential to both host and environmental selective pressures[25].

Cite this article: Sheikh, F.A., Dar, Z.A., Sofi, P.A., Lone, A.A. and Shiekh, N.A., Stem Rust of Wheat- *A Basic Review*, *Int. J. Pure App. Biosci.* **5(3):** 316-328 (2017). doi: http://dx.doi.org/10.18782/2320-7051.2880

Sexual reproduction allows the rapid production of advantageous gene combinations, while clonality enables the rapid amplification of strongly fitted individuals[6]. The most effective and environmentally sound method to control these diseases is through the deployment of resistant cultivars. Although a number of rust resistance genes have been identified in wheat[27], a major problem has been their short-lived effectiveness due to the fast emergence of virulent races of the pathogen that are capable of overcoming the resistance. For last several decades, epidemics of stem rust have been effectively controlled in most wheat growing regions because of the worldwide deployment of effective stem rust resistance genes in wheat varieties and removal of important alternate hosts, such as *Barberis vulgaris* L. from the proximity of wheat fields[17,39,40,43].

However, stem rust has again become a major threat to the world wheat production with a new race of stem rust pathogen, Ug99, with virulence to a widely used resistance gene *Sr31*, was detected in Uganda in 1999[32], and was named TTKS based on the North American stem rust race nomenclature system[16,53]. Ug99 pathotypes defeat most of the race-specific resistance genes currently deployed worldwide and are considered to be the most virulent strain of stem rust to emerge in the last 50 years[49]. Ug99 is virulent to Sr31 (derived from chromosome 1RS of rye, *Secale cereale* L.), a gene widely deployed in winter and spring wheat varieties in China, Europe, India and USA, and Sr38 (derived from 2NS of *Aegilops ventricosa* Tausch), a gene deployed in some European, American and Australian cultivars[39,40,43]. Further concern has grown with the discovery of additional variants in the Ug99 lineage. Two new variants, TTKST and TTTSK, which were reported in 2006–2007 to be virulent to other widely deployed genes *Sr24* and *Sr36* (both were effective against race Ug99 or TTKSK)[16]. In addition, Ug99 has migrated from East Africa to Sudan and Yemen in 2006[16], and Iran in 2007[29]. Emergence and spread of these new races of stem rust pose an imminent threat to wheat production worldwide demand the rapid development of wheat cultivars with durable resistance to stem rust[24]. The proximity of Ug99 to highly vulnerable and vast wheat crops in the Indian subcontinent and China is concerning.

Breeding of genetic resistance is considered to be the most effective approach to prevent or slow the spread of stem rust caused by Ug99[40]. New sources of Ug99 resistance in alien wheat species have been reported[24,55,56] and a resistance gene from *Aegilops speltoides* Tausch has been transferred into wheat[9]. Stem rust at present provides a major challenge to the wheat breeders through out the globe. The ever evolving new races of the pathogen (as ug99, TTKSK etc) and their devastating nature make a think to the world breeding community to combat these threats, by means of use of efficient molecular techniques, use of alien novel genes and other breeding procedures to mitigate the potential threat. This chapter provides a general outlook about the stem rust, pathogen type and travels throughout the span of development of various stem rust resistance genes. At last this book chapter is prepared to make it very much clear that if the pathogen is not handled, it will create a disastrous situation in the world.

Historical account

Yield losses caused by the stem rust pathogens in the mid of 20th century reached 20-30% in Eastern and Central Europe and many other countries including Australia, China and India[23]. The yield losses caused by the most virulent stem rust race Ug99 emerged first in Uganda and after that in Kenya, Ethiopia, Yemen, in the Middle East and South Asia and losses were estimated to approximately USD 3 billions. Strong emphases to identify resistance to stem rust and to breed resistant wheat varieties were initially given in the USA, Canada, Australia, and Europe. Although the major epidemic of 1916 in the USA and Canada had already triggered extensive research on stem rust, efforts in the USA, Canada, and Australia were intensified further with subsequent epidemics in the following decades[38]. Although resistance present in some hexaploid wheat sources were used in breeding during early years, the most successful control of stem rust came when H. K. Hayes in the University of Minnesota and E. S. McFadden in South Dakota State University transferred the stem rust resistance from tetraploid sources ‘‘Iumillo’’ durum and ‘‘Yaroslav’’ emmer, respectively, into bread wheat that gave rise to hexaploid wheat varieties ‘‘Thatcher’’ and ‘‘Hope’’[21]. Although several race-specific genes are present in Hope and Thatcher, the most effective component of the resistance in these two varieties is due to adult plant resistance. Thatcher and Hope, Hope sib ‘‘H44–24a,’’ and other varieties derived from these parents such as ‘‘Selkirk’’ and ‘‘Chris’’ that combined resistance to stem rust from other sources including gene Sr6 found to be present in a plant selection by J. McMurachy in 1930. ‘‘Kenya 58’’ and other Kenyan varieties carrying the same gene Sr6 were also used extensively in Australia by I. A. Watson and in Mexico by N. E. Borlaug. Efforts to find a solution to the stem rust problems facilitated global collaboration amongst wheat scientists who shared, grew and evaluated wheat germplasm in the quest of finding different sources of resistance to stem rust. Resistant wheat materials developed at Njoro, Kenya through the support from Canadian scientists in 1960s and 1970s contributed substantially to international breeding efforts. Resistance from Hope and Chris formed the foundation of the high-yielding, semi-dwarf wheat varieties that led to ‘‘Green Revolution’’ in the 1970s[38].

Pathogen and Epidemiology

Macrocyclic, heteroecious, Stem rust appears as elongated blister like pustules (uredinia), most frequently on the leaf sheaths of the plant besides the true stem leaves, tissues, glumes and awns. Pustules are mostly on lower side but sporulation on upper side. On the leaf sheath and glumes pustules rupture the epidermis and give a ragged appearance. Primary infection by means of uredospores of wheat while as secondary infection by means of aeciospores of barbery. Urediniospores are rather resistant to atmospheric conditions if their moisture content is moderate (20-30%). The minimum, optimum and maximum temperature for uredinospore germination are 2°, 15-24° and 30° C, and for sporulation 5°, 30° and 40° C[34]. Stakman[48] showed various races of stem rust pathogen. More recently concerns over non- accidental release of plant pathogens as a form of “agricultural bio-terrorism” have arisen with wheat stem rust considered one pathogen of concern[13].

The disease causing wheat rust fungi are spread in the form of clonally produced dikaryotic urediniospores, which can be dispersed by wind for thousands of kilometers from initial infection sites across different continents and oceans. Epidemics of wheat rusts can occur on a continental scale due to the widespread dispersal of urediniospores[35]. Wheat rust fungi are highly specific obligate parasites. Their avirulent genes interact with resistance genes in wheat in a gene-for-gene manner. Rust populations can be characterized by distribution of races and the frequencies of virulence against specific rust resistance genes on a defined set of wheat differential hosts. The avirulence genes that are present reflect only a small proportion of the total genetic variation found in rust populations, but this variation is subject to intense selection by the resistance genes in commonly grown wheat cultivars. Selectively neutral markers such as isozymes or more recently developed molecular markers, such as random amplified polymorphic DNA (RAPD), simple sequence repeat (SSR) and amplified fragment length polymorphism (AFLP) can also be used to characterize and compare rust populations. As the wheat rust fungi are spread easily within and between continents, it is essential to document the genetic changes in rust populations over large geographic areas in order to facilitate the development of rational strategies or durable resistance[38].

Shuttle Breeding

In the absence of molecular markers for adult plant resistance genes and the absence of Ug99 race in Mexico, a shuttle breeding scheme between two Mexican sites and Njoro, Kenya was initiated in 2006 to transfer adult plant resistance identified in semi dwarf CIMMYT wheat germplasm to a range of important wheat germplasm. Two crop seasons per year in Mexico and Kenya will accelerate the breeding. The ‘‘single-backcross, selected-bulk’’ breeding approach[46] 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. In the single-backcross approach, we crossed resistance sources with the adapted high-yielding wheat varieties and then a single backcross was made with the recurrent parent to obtain about 400 BC1 seeds. BC1 plants were then selected for desired agronomic features and resistance to leaf and stripe rusts, and harvested as bulk. F2 plants derived from BC1, simple and three-way crosses with desired agronomic features and resistance to leaf and stripe rusts were selected for agronomic traits and resistance to other diseases at CIMMYT research stations in Ciudad Obregon in northwestern Mexico or Toluca in the highlands near Mexico City and harvested as bulk. If F2 populations were grown in Ciudad Obregon, where quarantine disease ‘‘Karnal bunt’’ is known to occur, the F3 populations are grown at Toluca for another round of selection[38].

About 1000 seeds of each of the F3 and F4 populations obtained from harvesting materials at Toluca were grown densely in Njoro, Kenya for selection under high stem rust pressure during the off-season. After removing tall plants, the remaining populations were bulk harvested and about thousand plump grains selected to grow F4 and F5 populations during the main season in Kenya under high disease pressure. Because stem rust affects grain filling, we expect that plants with insufficient resistance will have shriveled grains. About 400 plump seeds harvested from the selected plants were sent back to Mexico for final selection as individual plants in the F5 and F6 generations at Ciudad Obregon. Individual plant selections will also be made in Kenya. This is the current status as of the 2007–2008 crop season. Selected plants in Ciudad Obregon with good characteristics were grown as small plots in Toluca and El Batan field sites in Mexico and selected lines will be grown in Kenya for stem rust screening. Selected plants in Kenya with good grain characteristics will be grown in F6 as hill plots or short rows in Kenya as well as small plots in Mexico for final selection. Finally, the resistant F6 plots will be harvested for conducting yield trials in the following crop season in Ciudad Obregon and simultaneously evaluated for stem rust resistance in Kenya. The single-backcross, selected-bulk scheme is also being applied to transfer resistance from old, tall Kenyan cultivars into adapted semi dwarf wheats[38].

Ug99: evolution, distribution and migration. Race Ug99, that emerged in Uganda in 1998 and was identified in 1999[32], is the only known race of *P. graminis tritici* that has virulence gene Sr31 known to be located in the translocation 1BL.1RS in rye *(Secale cereale)* (Fig 1). It was designated as TTKS by Wanyera *et al*[53]., using the North American nomenclature system[34] and more recently as TTKSK after a fifth set of differentials was added to further expand the characterization[16]. The most striking feature of race Ug99 is that it not only carries virulence to gene Sr31 but also this unique virulence is present together with virulence to most of the genes of wheat origin, and virulence to gene Sr38 introduced into wheat from *Triticum ventricosum* that is present in several European and Australian cultivars and a small portion of new CIMMYT germplasm. US wheat cultivar Chris, not known to carry Sr2, however possesses several seedling resistance genes including Sr7a[44] displayed adequate level of resistance to Ug99 in Kenya. Preliminary studies of inheritance of seedling resistance to Ug99 in Chris indicated that Ug99 resistance in Chris is controlled by two complementary recessive genes[14], and the same seedling resistance is present in AC Barrie (a Canadian spring wheat cultivar), Thatcher, and Bonza 65 (a CIMMYT-derived cultivar). Singh and McIntosh[44] indicated the possibility that the adult plant resistance to Sr7a-avirulent Australian races may involve interaction of the moderately effective gene Sr7a and other unknown adult plant resistance genes. Seedling tests indicated that Ug99 is virulent on the Sr7a-tester line[18] although Chris did show seedling resistance. Singh and McIntosh[44] indicated that resistance conferred by Sr7a is difficult to evaluate both in seedlings and adult plants when the gene is present alone. Therefore, at this stage we cannot determine the role Sr7a may have played in resistance of ‘‘Chris’’ observed in Kenya. Recently, a popular wheat cultivar, Robin, sustained severe damage in some farmers’ fields by stem rust in the 2014 crop season in Kenya. Robin became popular because of high yield potential and resistance to previously known Ug99 races. The resistance was conferred by stem rust gene *SrTmp*, which was effective to the previous races of the Ug99 race group[11].

As described by Singh *et al*[39]., Ug99 was first identified in Uganda in 1998, although there is some evidence indicating that the race may have been present in Kenya since 1993, and had spread to most of the wheat growing areas of Kenya and Ethiopia by 2003. In 2005, Ethiopian reports confirmed its presence in at least six dispersed locations. The East African highlands are a known ‘‘hot-spot’’ for the evolution and survival of new rust races[36]. In early 2006 (February/March), stem rust—tentatively caused by the Ug99 race—was reported from a site near New Halfa in eastern Sudan. Later the same year (October/November), reports were obtained from at least two sites in western Yemen. The observed expansion into new areas is in-line with previous predictions on the likely movement of Ug99[12] and fits the stepwise dispersal model following prevailing winds as outlined by Singh *et al*[39].

Crossing of the Red Sea into Yemen by Ug99 is regarded as being particularly significant, as the pattern of regional airflows, combined with historical recorded migration of Yr9-virulent stripe rust race[46], both support the potential for onward movement from Yemen into significant wheat production areas of the Middle East and West-South Asia. More detailed analysis of further potential onward movements were undertaken using the HYSPLIT (HYbrid Single-Particle Lagrangian Integrated Trajectory) airborne particle trajectory model developed by NOAA. Draxler and Rolph[7], supports the hypothesis that Yemen could be a staging post for onward movement into the Middle East and Asia. Air-borne particle trajectories, derived from the HYSPLIT model, originating from the confirmed Ug99 site of Al Kedan, Yemen (trajectories represent weekly 72-h movements for the period 1st December 2006 to 28th February 2007), confirmed Ug99 site Al Kedan in Yemen as a source. Similar results were obtained from an identical analysis covering the period 1st December 2005 to 28th February 2006, supporting the notion that the possibility of onward movements from sites in Yemen in the direction of key wheat areas occurs on a regular basis[38].

Even though seedling tests indicate that Sr23, another gene whose expression is difficult to evaluate in seedlings and adult plants when present alone, may be ineffective against Ug99, adequate resistance in ‘‘Selkirk’’ may involve interactions of moderately effective genes Sr2 and Sr23 (linked to leaf rust resistance gene Lr16) and perhaps additional unknown adult plant resistance genes. These observations, although they still require validation through genetic analyses, indicate that complex resistance to stem rust present in some tall cultivars developed in the 1960s and 1970s continue to remain effective[38].

Race non-specific stem rust resistance

Two classes of genes are used for breeding rust resistant wheat. The first class, called R (for resistance) genes, are pathogen race specific in their action, effective at all plant growth stages and probably mostly encode immune receptors of the nucleotide binding leucine rich repeat (NB-LRR) class. The second class is called adult plant resistance genes (APR) because resistance is usually functional only in adult plants, and, in contrast to most R genes, the levels of resistance conferred by single APR genes are only partial and allow considerable disease development. Some but not all APR genes provide resistance to all isolates of a rust pathogen species and a sub-class of these provides resistance to several fungal pathogen species[8].

Closeto 60 stem rust resistance genes, derived directly from wheat or introgressed from related species, have been cataloged. Of these only *Sr2* has been characterized as an APR with a slow rusting phenotype[10,51]. *Sr2* was originally introgressed from cultivated emmer (*T. dicoccum*) over 80 years ago by McFadden[26] in developing the bread wheat lines Hope and H-44. Durable stem rust resistance in some older wheat genotypes was attributed to *Sr2* along with unknown minor genes with additive effects[38]. As part of the ongoing evaluation of wheat cultivars at field sites in Kenya it is evident that genotypes combining *Sr2* and other seedling resistance genes exhibit enhanced levels of adult plant resistance relative to the effects attributed to the seedling resistance genes alone[31]. These evaluations managed by CIMMYT in Kenya and elsewhere, enabled identification of wheat cultivars carrying APR genes additional to *Sr2*[31,38]. *Sr2* shows parallels with *Lr34* and *Lr46*, in that it is associated with multi-pathogen resistance. Tight linkage between *Sr2*, the leaf rust resistance gene *Lr27*, and partial APR to stripe rust (*Yr30*) and powdery mildew were observed[44,45]. Wheat plants with inactivated *Lr27* alleles from mutagenesis appear to have lost *Sr2* possibly indicating pleiotrophism[47]. In addition to the plant morphological phenotypes of leaf tip necrosis associated with *Lr34* and *Lr46*, an associated *Sr2* plant morphology with dark pigmentation or necrotic region on the peduncle and glumes often referred to as pseudo black chaff has remained inseparable from *Sr2* resistance in high resolution mapping[22] (Kota *et al*. 2006). Another stem rust APR gene from a durum wheat cultivar, Glossy Huguenot, (designated *SrGH*) was characterised using Australian stem rust isolates[10]. *SrGH* was considered to differ from *Sr2* due to its dominant inheritance pattern in contrast to the recessiveness of *Sr2*, the pattern of pustule distribution on the stems and absence of the pseudo black chaff trait. Recent tests conducted in Kenya showed *SrGH* to be effective against Ug99, providing further incentive to continue ongoing characterization of *SrGH* in terms of gene location and transfer to bread wheat. Mutational studies on Glossy Huguenot have so far failed to recover susceptible plants. In combining the observations from the mutational analysis and ongoing mapping studies it is not certain if a single gene is responsible for all the stem rust APR in Glosssy Huguenot.

Semi-dwarf wheat and stem rust

The semi-dwarf wheat varieties were developed by Dr. N. E. Borlaug in Mexico during early 1960s under the program sponsored by the Mexican Government and the Rockefeller Foundation. These varities were also resistant to stem rust and early maturing as compared to tall varieties. The two semi dwarf ‘‘Green Revolution’’ mega-varieties, ‘‘Sonalika’’ and ‘‘Siete Cerros,’’ continued to have moderate levels of resistance to race Ug99 even today; however, they were mostly replaced as they succumbed to leaf and yellow rusts and better varieties became available. These semidwarf varieties significantly reduced stem rust incidence in many areas, which is often attributed to a combination of resistance and early maturity that avoided stem rust inoculum buildup[36]. The tall variety ‘‘Yaqui 50,’’ released in Mexico during the 1950s, and other Sr2-carrying semidwarf varieties released since then had stabilized the stem rust situation in Mexico and possibly in many other countries where modern semidwarf wheats were adopted. Changes in stem rust races have not been observed in Mexico for almost 40 years and natural infections are nonexistent. Successful transfers and utilization of alien resistance genes Sr24 and Sr26 from *Agropyron elongatum (Thinopyrum ponticum),* Sr31 located in the1BL.1RS translocation from ‘‘Pektus’’ rye and an undesignated gene on 1AL.1RS translocation from ‘‘Insave’’ rye, Sr36 from *T. timopheevi* and more recently Sr38 from T. ventricosum further reduced stem rust incidence in various countries around the world in 1970s and 1980s.

The use of 1BL.1RS translocation was initially associated with increased grain yields and resistance to all three rusts and powdery mildew as it carried resistance genes for all these diseases on the same translocation. Large-scale deployment of Sr31 surprisingly did not result in its breakdown until the detection of race Ug99 in Uganda. CIMMYT scientists continued to select for stem rust resistance in Mexico using artificial inoculation with six *P. graminis tritici* races of historical importance. New stem rust races have rarely occurred since the ‘‘Green Revolution’’ in Mexico[37]. Moreover, a majority of wheat lines selected in Mexico remained resistant at international sites either due to absence of disease, inadequate disease pressure, or presence of races that lacked necessary virulence for the resistance genes contained in CIMMYT wheat germplasm. Frequency of 1BL.1RS translocation went up to 70% at one stage in CIMMYT’s spring wheat germplasm but has declined to about 30% in more recent advanced lines. Such alien chromosome segments on the one hand are very useful for controlling multiple diseases, but on the other hand could lead to ‘‘vertifolia’’ or a masking effect[52] resulting in decrease in frequency or even loss of other useful genes, especially minor types, in breeding materials. Jin and Singh[17] compared seedling reactions of US wheat cultivars and germplasm with highly virulent races present in the USA and race Ug99. Several wheat lines, especially spring wheat that were highly resistant to US races and did not carry the1BL.1RS translocation, were also found to be susceptible to Ug99. This further supports the hypothesis that race Ug99 carries a unique combination of virulence to known and unknown resistance genes present in wheat germplasm. The major susceptibility is due to the specific nature of avirulence /virulence combination that Ug99 possesses, which had led to the susceptibility of many wheat materials irrespective of where they were developed[38].

Reducing the area planted to susceptible cultivars in ‘‘Primary Risk Areas’’ of East Africa, Arabian Peninsula, North Africa, Middle East and West-South Asia is the best strategy if major losses are to be avoided. The ‘‘Global Rust Initiative’’ launched in 2005, is using the following strategies to reduce the possibilities of major epidemics:(1) monitoring the spread of race Ug99 beyond eastern Africa for early warning and potential chemical interventions,(2) screening of released varieties and germplasm for resistance, (3) distributing sources of resistance worldwide for either direct use as varieties or for breeding, and (4) breeding to incorporate diverse resistance genes and adult plant resistance into high-yielding adapted varieties and new germplasm. The best long-term strategy to mitigate the threat from Ug99 is to identify resistant sources among existing materials, or develop resistant wheat varieties that can adapt to the prevalent environments in countries under high risk, and release them after proper testing while simultaneously multiplying the seed. An aggressive strategy to promote these resistant varieties in farmers’ fields is the only viable option as resource-poor as well as commercial farmers in most of Africa, Middle East and Asia cannot afford chemical control or may not be able to apply chemicals in the event of large-scale epidemics due to their unavailability for timely application. A reduction in disease pressure in East Africa and Yemen will likely reduce chances of migration beyond these areas to other primary risk areas; however, it is unlikely that further range expansion of Ug99 can be stopped at this stage. Reduction of susceptible varieties throughout the primary risk area should reduce wind dispersal of spores from these areas to ‘‘Secondary Risk Areas.’’ For a long-term control, we like to discuss strategies that are already implemented or can be applied to identify, develop, and deploy varieties with race-specific resistance genes or with adult plant resistance[38].

Prevalence of Sr24 and its breakdown

A high frequency of the highly resistant wheat materials from South America, Australia, USA, and CIMMYT identified from 2005 to 2006 screening with Ug99 in Kenya possess Sr24 indicating it as an important resistance gene especially due to its presence in adapted genetic backgrounds. Sr24 is located on the *Thinopyrum elongatum* translocation on chromosome 3DL together with leaf rust resistance gene Lr24. There are three distinct Sr24 carrying translocations: the original one linked to a gene for red grain color, the shorter segment with white grain and a third segment where a very small segment has been re translocated onto chromosome 1BS. In all three segments both Sr24 and Lr24 are present together. Detection of race TTKST with Sr24 virulence in Ug99 lineage during 2006 in low frequency[15] resulted in rapid buildup to cause an epidemic on Sr24 carrying variety Kenya Mwamba in 2007, which occupied about 30% of the Kenyan wheat area. Three Sr24- based resistant varieties, ‘‘ETBW19,’’ ‘‘ETBW21,’’ and ‘‘ETBW22’’ were multiplied under the emergency program in Ethiopia during the 2006 and 2007 to obtain several tons of seed. However, these varieties are now susceptible to the Sr24-virulent race TTKST present in Kenya indicating their genetic vulnerability if they occupy significant areas of rust-prone areas in Ethiopia in coming years[38].

QTL Mapping

Quantitative trait locus (QTL) mapping is a useful strategy to determine genetic regions controlling stem rust resistance. In addition to genomic regions for Sr2/Yr30 (3B), Sr57/Lr34/Yr18/Pm38 (7D), QTL for APR to stem rust were reported on chromosomes 1A, 2B, 2D, 4A, 4B, 5A, 5B, 6B, and 7A[4]. A QTL mapping study identified a Thatcher APR stem rust resistance QTL on chromosome arm 2BL[21]. In a RIL population derived from HD2009/WL711, QTL for stem rust resistance were identified on chromosomes 3B, 5DL, and 7A. In addition, QTL were also identified on chromosomes 1D, 2B, 4B, 5B, and 7D. In a QTL study involving a RIL population derived from Arina/ Forno, QTL were mapped on chromosome 5B and 7D along with minor QTL on chromosome 1AS and 7BL[1]. Recently, various studies have investigated the relevance of epistatic interactions of genes/ QTL for stem rust in durum, spring wheat[57], and winter wheat[57].

Durable Resistance-Concept

The problem of newly emerged races of pathogens has led to the adoption of alternative forms of resistance by the breeders that are more durable such as slow rusting or partial resistance[41]. It has been indicated that durable rust resistance is more likely to be of adult plant type rather than seedling type and is not associated with the genes conferring hypersensitive reaction[2]. Durable rust resistance is a mechanism conferring resistance to a cultivar for long period of time during its widespread cultivation in a favorable environment for a disease[19]. This type of resistance is mainly associated with the minor genes which are also known as slow rusting genes. The concept of slow rusting in wheat was proposed by Caldwell[5], similar to partial resistance to late blight of potato put forth by Niederhauser *et al*[30]. Various workers have stressed the need to recognize and exploit longer-lasting resistance. A general concept of a durable resistance (a race non-specific) resistance source for a cereal rusts is as

- It may be controlled by more than a single gene.
- It is more likely to operate at the adult-plant stage rather than at both the juvenile and adult stage.
- It confers non-hypersensitive response to infection.

Example of durable resistance include resistance to stem rust transferred from tetraploid emmer to bread wheat Hope and H-44[10], resistance to leaf rust in the South American wheat cultivar Frontana and related sources[33].

Durable resistance- its genetic base

The durable resistance is based on additive effect of partial resistant minor genes, usually polygenic in nature and active in adult plant stage. Genetic studies conducted at CIMMYT, Mexico has shown that at least 10-12 different genes are involved in group of CIMMYT germplasm and by accumulating 4-5 minor genes resistance level near to immunity can be achieved. However, 2-3 genes in a line provide moderate level of resistance[42]. Most of these genes are undesignated only the genes *Lr34*/ *Yr18*, *Lr46*/*Yr29* and *Sr2*/*Yr30* have been given names and designated to specific chromosomes. Each pair of these genes is tightly linked or pleiotropic. The varieties possessing minor gene based resistance show almost same level of resistance over space and time. For example, Lyalpur-73 which was among major varieties of Pakistan in 1970, s still shows very good level of resistance in screening nurseries. Whereas, the varieties having major gene based race specific resistance did not have long life and collapsed usually after 4-5 years. Varieties having durable type of resistance show almost same level of reaction against different races and their resistance remained effective in different climatic conditions. William *et al*[54]., identified 6 independent loci, contributing to adult plant resistance (APR) or slow rusting contributing to two rusts in a population derived from cross of Avocet S and Pavon. The putative loci identified on chromosomes 1BL, 4BL and 6AL influenced resistance to both stripe and yellow rust. The loci on chromosome 3BS and 6BL had significant effect on stripe rust. The locus on the distal region of chromosome 1BL with highly significant effects had also detected in other mapping populations[2,50]. The distortion associated with chromosome 4B linkage map has also been observed in some other research reports[50]. Even Morocco and Avocet S have some genetic factors that contain some slow rusting resistance which results in significant delay in becoming completely susceptible[54].

Preparedness and breeding for stem rust resistance in India

Although the stem rust prone area in India is less than 25 % of the total area, the possible implications of entry of Ug99 race into the country or independent mutation for Sr*31* cannot be ignored[3]. In a study on diversity for stem rust resistance in Indian wheat, commendable diversity was observed[3]. Seven different types of resistance to stem rust were observed in wheat lines evaluated during 2000–2001. Further we have preparedness to combat Ug99 threat. Indian wheat researchers lead by Rust Laboratory, Shimla (Regional Station, ICAR-IIWBR) have already initiated activities in association with CIMMYT and BGRI to identify and develop suitable resistant cultivars for rapid deployment in its different wheat zones. So far more than 947 lines have been screened against Ug99 type of races in Kenya and Ethiopia. During summer (off-season) crop of 2005, a set of 19 Indian wheat varieties and 3 genetic stocks were screened under natural outbreak of Ug99 at Njoro, Kenya. Wheat variety HW 1085, developed by IARI Regional station, Wellington for South Hill zone and three genetic stocks, i.e. FLW 2 (PBW 343 + Sr 24), FLW 6 (HP 1633 + Sr 24) and FLW 8 (HI 1077 + Sr 25), developed at IIWBR, Regional Station, Shimla, India, were found resistant against Ug99 race under natural conditions in Kenya. Three genetic stocks carrying *Sr26*, *Sr32*, and *Sr43* were tested at Kenya during 2013-14 against Ug99 pathotypes and were found effective (personal communication). Scientists at IIWBR regional station Shimla are also searching novel genes for rust resistance in wheat material and identified potential new source for resistance against stem and leaf rust[20].

Index Keywords	
APR	Adult Plant Resistance
QTL	Quantitative Trait Loci
CIMMYT	International Centre For Maize And Wheat Improvement
ICARDA	International Centre For Agricultural Research In Dryland Areas.
IARI	Indian Agriculture Research Institute
HYSPLIT	Hybrid Single Particle Lagrangian Integrated Trajectory
BaYMV	Barley Yellow Mosaic Virus
Ug99	Uganda 99
BGRI.	Borlaug Global Rust Initiative.
SrGH	Stem Rust Glossy Haguenot

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