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Role of Wild Relatives in Imparting Disease Resistance to Wheat Rust

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ABSTRACT

Wheat is affected by various diseases, among them Rusts, Smuts and powdery mildews are of notable to mention. Leaf rust, stem rust and stripe rust are among the most important diseases of wheat and barley worldwide and are best controlled using genetic resistance. Wild related species have been considered until now much more as genitors of resistance to pests and diseases than as sources of diversity permitting deep modifications of architecture and physiology of the cultivated species. Rusts are the most important biotic constraints limiting wheat productivity worldwide. Deployment of cultivars with broad spectrum rust resistance is the only environmentally viable option to combat these diseases. Identification and introgression of novel sources of resistance is a continuous process to combat the ever evolving pathogens. The germplasm of non progenitor qwr4567890 Aegilops species with substantial amount of variability has been exploited to a limited extent. Diploid wheat has a very high level of resistance to leaf rust (Puccinia recondita f. sp. tritici). Various Aegilops species have been reported to possess resistance to several wheat diseases. Genes of leaf rust resistance have been transferred into wheat from T. monococcum and T. Boeoticum. A number of genes imparting resistance to various rusts have been tranfered to cultivated wheats from their wild relatives, Gene Sr25 from T. Elongatum, Gene Sr26 from T. Elongatum, gene Sr36 from T. Timopheevii etc. The Lr34/Yr18/Sr57/Pm38 gene is a globally important genetic resource for wheat resistance breeding against leaf rust and stripe rust. The gene Lr34 was first described as Lr T2 and later identified in several distinct groups of genetic material. A total of 67 leaf rust resistance genes (Lr) and 48 stripe rust resistance genes (Yr) have been catalogued so far. Several genes for resistance to leaf rust and stripe rust have been introgressed from Aegilops and Thinopyrum species to cultivated wheat. Lines with adult plant resistance, gene pyramiding and shuttle breeding have been practised to have resistance against various races of the rust pathogen.

Key words: *Rusts, Durable Resistance, APR, Genetic Mapping, MAS.*

INTRODUCTION

Wheat (*Triticum aestivum* L.), is the 2nd most important food crop of the country which contributes nearly 1/3rd of the total food grain production. It belongs to genus triticum and family graminae. Triticum is the only one of the 600 genera belonging to this great family, which itself comprises well over 5000 spp.

Wheat one of the key cereal crops, is grown on 222 million hectares worldwide and is a major source of calories and proteins globally. Wheat production has increased from 235 million tons in 1961 to an estimated 733 million tons in 2015[16]. The Green Revolution of 1960 and 1970s along with changes in policies, fertilizer use and advances in agronomy has stimulated wheat productivity over past decades. A highly cited example is the global success of two semi-dwarf wheat varieties "Sonalika and Kalyan Sona" in the 1960s which helped wheat production advance from deficit to surplus in South Asia. It is staple food of more than 1/3rd of world population grown on about 222mhac. Wheat, one of the most important staple food crops, is grown on about 222 million ha worldwide from the equator to latitudes of 60 N and 44 S and at altitudes ranging from sea level to more than 3000 m. Approximately 600 million tons of wheat is produced annually, roughly half of which is in developing countries[2]. The only limitation to production is humid and high-temperature areas in the tropics and high-latitude environments where fewer than 90 frost free days are available for crop growth. The world's largest producers of wheat are China, India, and the USA, producing annually 100, 70, and 64 million tons with productivities of 3.8, 2.6, and 2.9 t/ha, respectively[2]. Only 10% of total wheat produced is sold on the export market, the primary exporting countries are USA, Canada, Australia, and France, and developing countries consume most of the wheat sold on the export market[2].

Globally important fungal diseases of wheat, caused by biotrophs (obligate parasites), include the three rusts, powdery mildew and the bunts and smuts; whereas, those caused by hemibiotrophs (facultative parasites) include Septoria tritici leaf blotch, Septoria nodorum blotch, spot blotch, tan spot and Fusarium head blight (scab). The obligate parasites are highly specialized and significant variation exists in the pathogen population for virulence to specific resistance genes. Evolution of new virulence through migration, mutation, recombination of existing virulence genes and their selection has been more frequent in rust and powdery mildew fungi. Therefore, enhancement of the knowledge on the genetic basis of resistance and breeding resistant cultivars to these diseases has received larger attention. Among the most important diseases in wheat that significantly reduce wheat production are those caused by the rusts (leaf, stem, and stripe). The rusts of wheat are among the most important plant widespread pathogens that can be found in most areas of the world where wheat is grown. Wheat leaf rust is caused by *Puccinia triticina* Eriks, wheat stem rust by *Puccinia graminis* f. sp. *tritici*, and wheat stripe rust by *Puccinia striiformis* f. sp. *tritici*. Leaf rust occurs more regularly and in more world wide regions than stem rust or stripe rust of wheat. Yield losses in wheat from *P. triticina* infections are usually the result of decreased number of kernels per head and lower kernel weight and it may reach 40% in susceptible cultivars[36].

There are two ways in which CWRs have been defined. One is the gene pool (GP) concept proposed by Harlan and de Wet[26], where CWRs were classified into groups (GP-1–GP-3) based on the relative ease of gene exchange with cultivated crops. Gene exchange occurs relatively easily between primary (GP-1) and secondary GPs (GP-2) by crossing (and fertile hybrids can be produced), whereas gene transfer between primary and tertiary (GP-3) groups is usually difficult. Even though the CWRs that have been used in crop improvement mostly belong to GP-1[56] or GP-2 categories[17,65], there are some examples where useful alleles from distant wild relatives, such as GP-3 plants, have been successfully transferred for crop improvement[1,47]. The second concept for CWRs is that of the taxon group (TG), a system that is based on the ranking of the taxonomic hierarchy to crops[18,49]. A TG may include a wide range of wild species that may be evolutionarily closely or distantly related to crop species within the same genus. With this concept, CWRs were defined in a range from TG1 (same species as the crop) to TG4 (different species within the same genus as the crop)[93].

Crop wild relatives are widely distributed on all continents except for Antarctica, and many are located in Vavilov centers of diversity and adjacent regions[9,44,48]. The global distribution of CWRs suggests that there are ample resources to be explored for use in plant breeding. In fact, among the approximately 50,000–60,000 total crop and CWR species, it has been estimated that 10,739 species (or even more) have a direct value for food security[48]. Although the number of publications discussing the use of CWRs in breeding has increased over the years and the use of CWR for crop improvement has been gradually recognized[48], the exploration and utilization of the genetic diversity contained in wild relatives has lagged considerably. Over 70% of the total CWR species are in urgent need of collection and conservation in gene banks, and over 95% are insufficiently represented with respect to the full range of geographic and ecological variation in their native distributions[9].

Various efforts have been made to collect a large number of wild species for plant breeding as the importance of CWRs was recognized by the Russian botanist Nikolai Vavilov in the early 20th century. Several review papers have been written from different perspective to emphasize the importance of CWRs for crop improvement[8,11,18,25,48,56,58,59,62,85,92].

Historical account

The 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''[40]. 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.

Some important spp. of wheat

S. No.	Species	Chromosome no.	Genome formula	Domestication
1.	*Triticum monococcum*	14	AA	Cultivated
2.	*Aegilopes speltoides*	14	BB	Wild
3.	*Triticum tauschii*	14	DD	Wild
4.	*Triticum turgidium*	28	AABB	Cultivated
5.	*Triticum timopheevi*	28	AAGG	Wild
6.	*Triticum aestivum*	42	AABBDD	Cultivated
7.	*Triticale*	42	AABBRR	Cultivated

Two species of Triticum are of commercial importance. The hexaploid spp. *T. aestivum* (bread wheat) and *T. turgidium* (principle wheat in commerce, the durum wheat). The wild tetraploid spp. *T. timopheevi* is the source of CMS. Triticale is a man made cereal in which the AABB genome of *T. tugidium* are combined with the RR genome of Rye. *T. timopheevi* differs from *T. turgidium* in having the AA genome combined with the GG genomes instead of BB genome. Intrinsic baking quality of *T. aestivum* are controlled by genes introduced through D genome. D genome is fully homologous with *T. tauschii,* its presumed progenitor.

Emergence of new rust races

The wide spread global popularity of the germplasm with 1B-1R translocation created monoculture situation. This lead to the evolution of some new devastating rust races resulting a serious threat to global wheat production. A race of *P. striiformis*, *Yr9* was 1st observed in East Africa in 1986 and subsequently migrated to North Africa and South Asia. Once it appeared in Yemen in 1991 it took just four years to reach wheat fields of south Asia[72]. On its way it caused major yield losses in Egypt, Syria, Turkey, Iran, Iraq, Afghanistan and Pakistan exceeding USD 1billion. Similarly, *Yr27* emergence and its movement following the same pathway posed major threat to wheat production in India and Pakistan, where mega cultivars PBW343 and Inqilab 91 were having *Yr27* gene based resistance. In 2005, the wheat crop in Nothern Pakistan was severely hit by this race of Yellow rust where most of the area was under Inqilab-91. Stem rust resistance in wheat cultivars with *Sr31* remained effective for more than 30 years.

Breeding for rust resistance

The semi dwarf and dwarf varieties developed at CIMMYT, Mexico in the early days of green revolution (Penjamo 62, Pitic 62, Lerma Rojo 64, Sanora 64 and Siete Cerros etc.) had been responsible for yield break through in India, Pakistan, Turkey, Afghanistan and many other parts of the world. The life time of most of these Mexican varieties was short as appearance of new stem rust race has terminated their useful life time, however, there were some exceptions also. The variety Lerma Rojo 64 had life time of eleven year, while others like Yaqui 50, Champingo 52 and Champingo 53 retained their resistance until they were displaced from commercial cultivation by new high yielding varieties[4]. The long life of these varieties is attributable to their genetic background. They had combination of Hope and Thacher type and Kenya type resistance. During the period 1965-85, the CMMYT breeding programme has incorporated diversity of genes. Most of the material distributed during this period contains *Sr2* and two to four additional genes for stem rust resistant. These additional genes include *Sr5, Sr6, Sr7a, Sr7b, Sr8a, Sr9b, Sr9d, Sr9e, Sr9g, Sr10, Sr11, Sr12, Sr17, Sr24, Sr26, Sr30, Sr31, Sr36*[37]. The parallel strategy was also adopted by many national programs.

The importance of *Lr13* gene for leaf rust (*Puccinia triticina*) resistance was recognized in the early 1970's when it was transferred along with other genes in to many wheat varieties. Some varieties containing *Lr13* in combination with other genes developed in Mexico, India and Pakistan. The gene, *Lr13* itself does not provide desired level of resistance but when present in combination with other genes it provides a degree of resistance of high probability of being durable. The mode of action of *Lr13* complex in CIMMYT program is non specific type of resistance. Its presence in combination with *Lr34* in some members of Bluebird series gave them long life.

Breeding for durable rust resistance

Accumulating minor genes for attaining desired level of resistance in a variety is a challenging task[76] as it requires identification of parents with minor genes, crossing them in specific schemes following back cross or top cross approach, maintaining desirable population size and selection of desirable genotypes from segregating populations. The crossing schemes and selection strategies used for breeding major gene based resistance are not suitable for breeding minor gene

resistance. The modified pedigree method used for breeding major gene based resistance can not give any progress for minor gene based resistance. Singh *et al*[74]., compared different crossing and selection schemes for working out their efficiency in terms of genetic gains and cost efficiency. The influence of type of cross and selection scheme was minimal on main grain yield. They found that selection of parents was the most important feature in breeding for achieving desirable results. They also reported that mean rust severity of top cross progenies was less as compared to simple cross because two parents contributed resistance factors to the top cross progenies. Non selected bulk method was found to be least effective and selected bulk method as the most attractive schemes in terms of genetic gain and cost efficiency. An example of breeding for minor gene based resistance is the development of wheat stock resistant to leaf and yellow rust at CIMMYT.

Since early days of breeding for minor genes, plants and lines with infection intensity of 20-30% and compatible infection type were targetted. This led to the development of wheat varieties Nacozari F-76, Pavon F-76 and several others[76] which were released not only in Mexico but also in Ethiopia, Bangladesh, Pakistan and other countries. Pavon was released in 16 countries with different names. This material provided the foundation for breeding for minor gene resistance. In Pakistan the varieties Uqab 2000 , Bhakkar-02 and Seher-06 have this type of resistance. Bhakkar-02 has dominated the mega wheat cultivar Inqilab-91 since 2005 after Inqilab-91 was hit by yellow rust epidemic and Seher-06 is gaining popularity now, due to its higher yield and better resistance to leaf and yellow rusts. The variety, Uqab 2000 proved the best option for the rain fed northern Pakistan after severe epidemic of yellow rust in 2005.

The interest of Triticum and aegilops genepool for the improvement of rusts:-

A number of genes imparting resistance to various rusts have been tranfered to cultivated wheats from their wild relatives. Gene Sr25 from T. Elongatum[74], Gene Sr26 from T.

Elongatum[52], gene Sr36 from T. Timopheevii[34] etc. The Lr34/Yr18/Sr57/Pm38 gene is a globally important genetic resource for wheat resistance breeding against leaf rust and stripe rust. The gene Lr34 was first described as LrT2 and later identified in several distinct groups of genetic material[39,41]. A total of 67 leaf rust resistance genes (Lr) and 48 stripe rust resistance genes (Yr) have been catalogued so far[50,51]. Several genes for resistance to leaf rust and stripe rust have been introgressed from Aegilops and Thinopyrum species to cultivated wheat: for example Ae. umbellulata (Lr9); Ae. ventricosa (Lr37, Yr17); Th. intermedium (Lr38); Ae. speltoides (Lr28, Lr35, Lr36, Lr51 and Lr66); Ae. tauschii (Lr21, Lr22a, Lr32, Lr39, Lr40, Lr41 and Yr28); Ae. geniculata (Lr57 Yr40); Ae. triuncialis (Lr58); Ae. longissima and T. dicoc- coides (Lr53, Yr15, Yr35, Yr36)[50,51] and commercially exploited. Lines with adult plant resistance, gene pyramiding and shuttle breeding have been practised to have resistance against various races of the rust pathogen.

Diploid *Triticum* species

Diploid wheat pool comprises three species, *T. urartu*, *T. boeoticum* and *T. monococcum* ("cultivated einkorn"). *T. monococcum* which is widely distributed throughout the Near East, Transcaucasia, the Mediterranean region and the Balkans, was one of the first cereals cultivated for food. Today, einkorn cultivation is limited to small regions of South Europe and India. Diploid wheats have a very high level of resistance to leaf rust (*Puccinia recondita* f. sp. *tritici*)[33]. Various Aegilops species have been reported to possess resistance to several wheat diseases[42]. Genes of leaf rust resistance have been transferred into wheat from *T. monococcum* and *T. boeoticum* by Hussien *et al*[32]. Resistance to stem rust (*Puccinia graminis* f. sp. *tritici*) was also found in these two species by Soshnikova[78] and a resistance gene (SrTm) transferred from *T. monococcum* to wheat by Valkoun *et al*[84]. AABB amphiploids derived from crosses of diploid *Triticum* with *T. durum* and resistant to stripe rust can be used to transfer resistance to durum

wheat. *T. monococcum* is considered by Mihova[53] as the most useful diploid *Triticum* to improve stripe rust (*Puccinia striiformis* West.) resistance. Major gene for powdery mildew resistance was transferred from *T. boeoticum* to bread wheat by Shi *et al*[70]. Sources of resistance to the M-PAV strain of BYDV was identified in the three diploid wheat species[24]. Resistance to root rot (*Fusarium roseum* plus *Cochliobolus sativus*) was found to be closely associated with A genome[90].

Tetraploid *Triticum* species:-
AB genome.

The tetraploid wheat group is composed by ten species, carrying either AB or AG genome and growing in a wider range of environments than diploids. Cultivated emmer (*T. dicoccum*) was the predominant cultivated wheat during Neolithic Age. During Bronze Age the naked tetraploid wheats slowly displaced emmer wheat which however remains an important crop in Ethiopia and Yemen. *T. dicoccoides* has been recognised as a valuable source of powdery mildew resistance and leaf rust resistance by El-Morshidy *et al*[15]. Leaf rust resistance has been transferred into wheat by Dyck[14]. Yr15, a gene for resistance to stripe rust, was described in *T. dicoccoides* by Gerechter-Amitai *et al*[21]. Molecular markers linked to the Yr15 gene were further identified by Sun *et al*[80]. *T. dicoccum* is considered as resistant to powdery mildew[71] and also constitutes a valuable source of resistance to leaf and stem rusts[38]. Among AB species, T. dicoccum was found to have the lowest natural susceptibility to the Russian Wheat Aphid (*Diuraphis noxia*)[46,64]. Some lines with resistance to Septoria were also identified within AB Triticum[91]. T. carthlicum was found to have also resistance to leaf and stripe rusts[12]. T. polonicum is considered by Mishra et al[54]., as the best AB species for increasing yield as it had the highest yielding ability, number of grains per spike and tillering ability.

AG genome

T. timopheevi and T. araraticum species are known as valuable sources of resistance to the main fungal diseases[7,81] respectively. T.

araraticum was found to be resistant to root-rot[90]. Transfer of rusts and mildew resistance from timopheevi into wheat was performed by Sawhney and Goel[66]. Successful transfers from araraticum have concerned leaf rust[5,6] and powdery mildew[89,].

Sr2/Yr30 Gene

The gene, *Sr2* was transferred to hexaploid wheat from tetraploid emmer wheat cultivar Yaroslav in 1920. It is present on chromosome 3BS and is also reported to be associated with *Lr27*[73]. It is completely linked with pseudo black chaff (Pbc), which is used as morphological marker for identification of lines carrying this gene. The genotypes with Pbc show varying level of stem rust infection. The maximum severity level of 60-70% has been noted as compared to 100% severity of susceptible check in disease screening nurseries in Kenya. When present alone it does not provide sufficient level of resistance but in combination with other genes desirable level of resistance can be achieved. Much information is not available about the interaction of *Sr2* and other genes in *Sr2* complex. The adequate resistance level can be achieved by accumulating 4-5 minor genes. *Sr2* was detected in several highly resistant old, tall Kenyan cultivars like Kenya plume and semidwarf CIMMYT, cultivars Pavon F 76, Parula, Kingbird, Dollarbird etc. These cultivars show maximum disease severity of 10-15% with moderately resistant reactions. The gene *Sr2* is tightly linked with *Yr30* or has pleotropic effects[75]. A microsatellite(S*SR*) marker *gwm533* is tightly linked and associated with the presence of this gene, which can be used to facilitate selection of this difficult to score gene[79].

Trigenomic chromosomes by recombination of *Thinopyrum intermedium* and *Th. ponticum* translocations in wheat.

Recombination between *Th. intermedium* (TC5) and *Th. ponticum* (T4m) translocated fragments, both on distal positions on chromosome arm 7DL of wheat, was achieved by bringing them together in a homozygous *ph1b* mutant background. IdentiWcation of trigenomic recombinant chromosomes was

facilitated by the use of molecular markers. The presence of leaf rust and BYDV resistance could be determined on the same individuals by sequential leaf rust and virus bioassays. Recombinants carrying both leaf rust (*Lr19*) and BYDV (*Bdv2*) resistances were found. Since the source of *Lr19* employed in this work was already mutated to reduce the unwanted yellow pigment in the Xour, we have not yet attempted to analyze the recombinants for Xour color. Preliminary testing for the presence of *Sr25* suggests that some of the recombinants do carry this gene; however, the wheat backgrounds employed in this work carry other stem rust resistance genes which mask the eVect of *Sr25*. Further analyses on testcross progenies will be required to assign the presence of *Sr25* to particular recombinant translocations unambiguously[57].

Marker–Assisted Selection (MAS) and resistance gene isolation as tool for improving the resistance to leaf and stem rust resistance in wheat.

Pyramiding of several genes into one cultivar can be an effective strategy to use resistance genes to enhance durability of wheat resistance to leaf and stem rust[45]. Durable resistance may be achieved by combination of several genes encoding partial resistance. Gene pyramiding through conventional methods is difficult and time consuming because it requires simultaneous tests of the same wheat breeding materials with several different rust races before a selection is made. Usually, it is not feasible for a regular breeding program to maintain all necessary rust races needed for this type of work. Therefore, MAS is a powerful alternative to facilitate new gene deployment and gene pyramiding for quick release of rust-resistant cultivars. Molecular markers such as STS or SCAR and CAPS are available for leaf rust resistance genes Lr1, Lr9, Lr10, Lr 19, Lr21, Lr24, Lr 25, Lr28, Lr29, Lr34, Lr35, Lr37, Lr39, Lr47 and Lr51. Enzymatic marker (endopeptidase, Ep-D1c) for Lr19 has also been developed[86]. Microsatellite (SSR) and AFLP markers for some Lr genes such as Lr3bg, Lr18, Lr40,

Lr46 and Lr50 have been developed by Purnhauser *et al*[61]. Molecular markers are available also for stem resistance genes such as *Sr2*, Sr 9a, *Sr22*, *Sr24*, *Sr26*, *Sr31*, *Sr36* and *Sr39*[82] . Some of the 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. At the present time, the research of stem rust in wheat has focused on identifying more resistance genes to control Ug99. According to the Farm and Ranch Guide report, currently 50% of winter wheat and 70 to 80% of spring wheat used in the USA are susceptible to Ug99. Moreover, 75-80% of the breeding materials are susceptible to Ug99 and most stem rust resistance genes deployed in breeding programs have been overcome by this new fungus.

Microsatellite marker closely linked to resistance gene Sr40 have been also obtained[87]. To date three genes for leaf rust resistance in wheat Lr1, Lr10 and Lr 21[30] have been isolated, cloned and sequenced. They all have sequences that encode nucleotide binding site (NBS) leucine-rich repeat (LRR) regions, which are characteristic of disease resistance genes in plants. Molecular description of these genes in wheat provides a unique biological system to study the molecular mechanisms of wheat-pathogen interaction and transduction as well as the resistance gene function, evolution and diversity. This will allow further manipulation of wheat resistance genes to increase the resistance durability by genetic transformation of wheat.

Development of Molecular Markers for Leaf Rust Resistance Genes Incorporated from Alien Species into Common Wheat

Presently wheat breeders and geneticists are extracting rust resistant genes from wild relatives of wheat and utilizing them for wheat improvement. A leaf rust resistance gene *Lr47* was derived from short arm of chromosome 7S of *Triticum Speltoides* and translocated onto short arm of chromosome 7A of wheat[29]. Similarly a rust resistant gene *Lr37* has been introgreessed into common wheat from short arm of chromosome 2N of *Triticum*

ventricosum[27]. Another leaf rust resistance gene *Lr51* has been transferred from *Triticum speltoides* to common wheat[28]. In another study RAPD based molecular markers were developed for alien rust resistance genes incorporated in wheat from *T. speltoides* (*Lr47, Lr51)* and *T. ventricosum* (*Lr37*)[69].

Introgression of a leaf rust resistance gene from *Aegilops caudata*to bread wheat.

The germplasm of wild relatives and progenitor species of cultivated wheat comprise an excellent reservoir of useful traits, including disease resistance that can be exploited for wheat improvement[13,35]. A number of leaf rust resistance genes have been introgressed from the wild relatives to the wheat cultivars through interspecific hybridization. Various *Aegilops* species have been reported to possess resistance to several wheat diseases[10,22,23,42,43,67]. Numerous wheat-*Aegilops* addition, substitution and translocation lines have been developed to dissect and introgress many agronomically useful traits into the wheat gene pool[19]. Several genes for resistance to leaf rust and stripe rust have been introgressed from *Aegilops* and *Thinopyrum* species to cultivated wheat: for example *Ae. umbellulata* (*Lr9*); *Thinopyrum ponticum* (*Lr19, Lr24* and *Lr29*); *Ae. Ventricosa* (*Lr37, Yr17*); *Th. intermedium* (*Lr38*); *Ae. speltoides* (*Lr28, Lr35, Lr36, Lr51* and *Lr66*); *Ae. tauschii* (*Lr21, Lr22a, Lr32, Lr39, Lr40, Lr41* and *Yr28*); *Ae. geniculata* (*Lr57, Yr40*); *Ae. triuncialis* (*Lr58*); *Ae. longissima* and *T. dicoccoides* (*Lr53, Yr15, Yr35, Yr36*)[50,51] and commercially exploited. *Aegilops* species with C, U, and M genomes have been identified as very good sources of resistance to leaf rust and stripe rust[72,83]. *Ae. caudata*, a diploid non progenitor species of wheat with CC genome carries resistance genes against several wheat diseases, especially rust and powdery mildew in addition to genes for high protein and lysine[20,60]. This article describes introgression of a leaf rust resistance gene from a rust resistant accession of *Ae. Caudate* L. acc. pau#3556 into bread wheat and molecular mapping of the leaf rust resistance gene[63].

Introgression, inheritance and molecular mapping of a leaf rust resistance gene of *Ae. caudata* (CC) acc. pau3556 in cultivated wheat were undertaken. An F2 population derived from the cross of *Triticum aestivum* cv.WL711 – *Ae. caudata* introgression line T291-2 with wheat cultivar PBW343 segregated for a single dominant leaf rust resistance gene at the seedling and adult plant stages. Progeny testing in F3 confirmed the introgression of a single gene for leaf rust resistance. Bulked segregant analysis using polymorphic D-genome-specific SSR markers and the cosegregation of the 5DS anchored markers (*Xcfd18*, *Xcfd78*, *Xfd81* and *Xcfd189*) with the rust resistance in the F2 population mapped the leaf rust resistance gene (*LrAC*) on the short arm of wheat chromosome 5D. Genetic complementation and the linked molecular markers revealed that *LrAC* is a novel homoeoallele of an orthologue *Lr57* already introgressed from the 5M chromosome of *Ae. geniculata* on 5DS of wheat[64].

Characterization of Yr54 and other genes associated with adult plant resistance to yellow rust and leaf rust in common wheat Quaiu 3.

Quaiu 3, a common wheat line developed at the International Maize and Wheat Improvement Center (CIMMYT), is immune to YR in Mexico despite seedling susceptibility to predominant races. Quaiu 3 also shows immunity to LR in field trials and is known to possess the race-specific gene Lr42. A mapping population of 182 recombinant inbred lines (RILs) was developed by crossing Quaiu 3 with susceptible Avocet- YrA and phenotyped with LR and YR in field trials for 2 years in Mexico. Quantitative trait loci (QTL) associated with YR and LR resistance in the RILs were identified using Diversity Arrays Technology and simple sequence repeat markers. A large-effect QTL on the long arm of chromosome 2Dexplained 49–54 % of the phenotypic variation in Quaiu 3 and was designated as Yr54. Two additional loci on 1BL and 3BS explained 8–17 % of the phenotypic variation for YR and coincided

with previously characterized adult plant resistance (APR) genes Lr46/Yr29 and Sr2/Yr30, respectively. QTL on 1DS and 1BL corresponding to Lr42 and Lr46/Yr29, respectively, contributed 60–71 % of the variation for LR resistance. A locus on 3D associated with APR to both diseases explained up to 7 % of the phenotypic variance. Additional Avocet- Yr A-derived minor QTL were also detected for YR on chromosomes 1A, 3D, 4A, and 6A. Yr54 is a newly characterized APR gene which can be combined with other genes by using closely linked molecular markers[3].

Genetic mapping of a putative *Thinopyrum intermedium*‑derived stripe rust resistance gene on wheat chromosome 1B.

Rust resistance was transferred from *Thinopyrum intermedium* to common wheat, and the resulting introgression line (L693) exhibited all-stage resistance to the widely virulent and predominant Chinese pathotypes CYR32 and CYR33 and to the new virulent pathotype V26. There was no cytological evidence that L693 had alien chromosomal segments from *Th. intermedium*. Genetic analysis of stripe rust resistance was performed by crossing L693 with the susceptible line L661. F1, F2, and F2:3 populations from reciprocal crosses showed that resistance was controlled by a single dominant gene. A total 479 F2:3 lines and 781 pairs of genomic simple sequence repeat (SSR) primers were employed to determine the chromosomal location of the resistance gene. The gene was linked to six publicly available and three recently developed wheat genomic SSR markers. The linked markers were localized to wheat chromosome 1B using Chinese Spring nulli -tetrasomic lines, and the resistance gene was localized to chromosome 1B based on SSR and wheat genomic information. A high-density genetic map was also produced. The pedigree, molecular marker data, and resistance response indicated that the stripe rust resistance gene in L693 is a novel gene, which was temporarily designated *YrL693*. The SSR markers that co-segregate with this gene (*Xbarc187- 1B*, *Xbarc187-1B-1*,

Xgwm18-1B, and *Xgwm11-1B*) have potential application in marker-assisted breeding of wheat, and *YrL693* will be useful for broadening the genetic basis of stripe rust resistance in wheat[31].

Disease Resistance

Diseases, caused by both fungi and fungi-like pathogens pose a major threat to wheat production. Evolution of new virulence through migration, mutation, selection, and recombination of virulence genes occurs in all pathogens, but has been more frequent in those causing rust and powdery mildew. One of the strategies to mitigate the threat from diseases is to identify and utilize diverse sources of durable resistance. Resistance genes can be characterized as race specific and race non-specific, this classification dates back to 1962 when Vander Plank proposed the first theoretical concepts of disease resistance. Race specific genes confer resistance to one or a few races of a pathogen and are known to be based on 'gene for gene' interaction. Also known as 'major genes, 'they usually have large phenotypic effects, but may not confer complete resistance. Although incorporation of race-specific resistance genes may be promising, it increases the risk of faster breakdown. Some examples of major genes for rust resistance include *Lr19*, *Lr26,* and *Lr42* effective against leaf rust, *Yr5*, *Yr10*, and *Yr15* against yellow rust and *Sr22*, *Sr26*, and *Sr35* against stem rust. Race non- specific resistance, is usually effective in the post-seedling growth stage, thus commonly referred to as adult plant resistance (APR). Race-non specific resistance is generally quantitatively inherited and ranges from moderate resistance/moderate susceptibility to nearly complete resistance and interact additively with other non- specific resistance genes. Varieties with high levels of durable resistance to multiple pathogen can be developed by combining multiple race non-specific resistance loci, especially to those which are known to confer resistance to multiple diseases[77]. Examples of these pleiotropic resistance genes are *Lr34*, *Lr46*, and *Lr67* which provide resistance to leaf, yellow and

stem rust and powdery mildew. Because race non-specific resistance can provide broader and robust resistance to fight pathogen evolution it has been recommended for the high risk areas, for instance in East African highlands where wheat cultivation and pathogen evolution is continuous[77].

Though most rust resistance genes originated from hexaploid wheat, there are also many genes that originated from the wild relatives and other genera such as *Aegilops*, *Dasypyrum*, *Thinopyrum,* and *Secale*. As early as 1920 and 1930s, introgression of stem rust resistance from *T. turgidum* sub sp. durum and *T. dicoccum* sub sp. Dicoccum Schrankex Schubler into bread wheat was reported. Both race-specific and non-specific genes have been identified from diverse genetic sources. For instance, *Lr9* from *Aegilops umbellulata* Zhuk, *Yr5* from *Triticum spelta* L., *Yr28* from *A. tauschii*, *Sr9e* from tetraploids and *Sr35* from *Triticum monococcum* L. are race-specific genes. Examples of race non- specific genes /APR include *Lr22a* from *A. tauschii*, *Yr36* from *Triticum diccocoides* (Korn. Ex Asch. And Graebn) Schweinf, *Yr48* from synthetic hexaploid wheat PI610750 and *Yr52, 56, 57,* and *62* from land races. Introgressions are also associated with multiple disease resistance as well, such as *Pm8/Sr31/Lr26/Yr9* from rye, *Sr36/Pm6* from *Triticum timopheevi* (Zhuk.) Zhuk., Pch1and *Sr38/Lr37/Lr17* from *Aegilops ventricosa* Tausch, and *Lr19/Sr25*, *Sr24/Lr24,* and *Sr26* from *A. elongatum* (Host) P. Beauy[68,88]. Some genes introgressed from wild relatives have been associated with negative linkage drag and therefore have not been widely deployed inbreeding: examples include *Sr32* and *Sr37* identified in *A. speltoides* and *T. timopheevi* respectively. Other temporarily designated genes that are common in high yielding wheat germplasm offer additional possibilities for combining resistance genes combinations[55].

REFERENCES

1. Abedinia, M., Henry, R.J., Blakeney, A.B., and Lewin, L.G., Accessing genes in the tertiary gene pool of rice by direct introduction of total DNA from *Zizania palustris* (Wild rice). *Plant Molecular Biology Reporter*, **18:** 133–138 (2000).

2. Aquino, P., Carrion, F., and Calvo, R., Selected wheat statistics. In ''CIMMYT 2000–2001 World Wheat Overview and Outlook: Developing No-Till Packages for Small Scale Farmers'' (J. Ekboir, ed.), pp. **52–62.** CIMMYT, Mexico, D.F. (2002).

3. Basnet B.R., Singh R.P., Ibrahim A.M.H., Herrera-Foessel S.A., Huerta-Espino, J., Lan, C., and Rudd, J.C., Characterization of Yr54 and other genes associated with adult plant resistance to yellow rust and leaf rust in common wheat Quaiu 3. Mol Breeding., **33:** 385–399. (2014),

4. Borlauge, N.E., Wheat breeding and its impact on world food supply In: 3rd Inter Wheat Genet Symp, Canberra, Australia, pp 1-36. (1968).

5. Brown-Guedira, G.L., Cox, T.S., Gill, B.S. and Sears, R.G., Registration of KS96WGRC35 and KS96WGRC36 leaf rust-resistant hard red winter wheat germplasm. *Crop Science*, **39:** 595 (1999a).

6. Brown-Guedira, G.L., Cox, T.S., Gill, B.S., Sears, R.G. and Leath, S., Registration of KS96WGRC37 powdery mildew-resistant hard white winter wheat germplasm. *Crop Science*, **39:** 596 (1999b).

7. Brown-Guedira, G.L., Gill, B.S., Bockus, W.W., Cox, T.S., Hatchett, J.H., Leath, S., Peterson, C.J., Thomas, J.B. and Zwer, P.K., Evaluation of a collection of wild *timopheevi* wheat for resistance to disease and arthropod pests. *Plant disease*, **80:** 928-933 (1996).

8. Brozynska, M., Furtado, A. and Henry, R.J., Genomics of crop wild relatives: Expanding the gene pool for crop improvement. *Plant Biotechnology Journal*, *14*, 1070–1085 (2015).

9. Castaneda-Alvarez, N.P., Khoury, C.K., Achicanoy, H.A., Bernau, V., Dempewolf, H., Eastwood, R. J. and Toll, J., Global conservation priorities for crop wild relatives. *Nature Plants*, **2:** 16022 (2016).

10. Chhuneja, P., Kaur, S., Goel, R.K., Aghaee-Sarbarzeh, M., Prashar, M. and Dhaliwal, H.S., Transfer of leaf rust and stripe rust resistance from *Aegilops umbellulata* Zhuk. to bread wheat (*Triticum aestivum* L.). *Genet. Res. Crop Evol.* **55:** 849–859 (2008).

11. Colmer, T.D., Flowers, T.J., and Munns, R., Use of wild relatives to improve salt tolerance in wheat. *Journal of Experimental Botany*, **57:** 1059–1078 (2006).

12. Dekaprelevitch, L.L. and Naskidashvili, P.P., *Triticum persicum* v. *stramineum*, genetic source ofresistance to yellow and brown rust [Georgian]. *Soobsccheniya Akademii Nauk Gruzinskoi Ssr.*, **82:** 689-691 (1976).

13. Dyck, P.L., Kerber, E.R. and Marters, J.W., Transfer of a gene for stem rust resistance from *Aegilops caudata* to common wheat. *Can. J. Plant Sci.*, **70:** 931–934 (1990).

14. Dyck, P.L., The transfer of leaf rust resistance from *Triticum turgidum* ssp. *dicoccoides* to hexaploid wheat. *Canadian Journal of Plant Science*b., **671-673** (1994).

15. El-Morshidy, M.A., Moseman, J.G., Nevo, E., Gerechter-Amitai, Z.K. and Zohary, D., *Triticumdicoccoides* as a source of resistance to powdery mildew and leaf rust diseases *Agronomy Abstracts*: 62 (1983).

16. FAO. (Food and Agriculture Organization of the United Nations). (2001, 2009, 2010). ''Food Outlook.''FAO, Rome, Italy. (2010).

17. Fetch, T., Johnston, P.A., and Pickering, R., Chromosomal location and inheritance of stem rust resistance transferred from *Hordeum bulbosum* into cultivated barley (*H. vulgare*). *Phytopathology*, **99:** 339–343 (2009).

18. Ford-Lloyd, B.V., Schmidt, M., Armstrong, S.J., Barazani, O., Engels, J., Hadas, R. and Maxted, N., Crop wild relatives-undervalued, underutilized and under threat? *BioScience*, **61:** 559–565 (2011).

19. Friebe, B., Qi, L.L., Nasuda, A., Zhang, P., Tuleen, N.A. and Gill, B.S., Development of a complete set of *Triticum aestivum– Aegilops speltoides* chromosome addition lines. *Theor. Appl. Genet.* **101:** 51–58 (2000).

20. Friebe, B., Schubert, V., Bluthner, W.D. and Hammer, K., C-banding pattern and polymorphism of *Aegilops caudata* and chromosomal constitutions of the amphiploid *T. aestivum–Ae. caudata* and six derived chromosome additional lines. *Theor. Appl. Genet.* **83:** 589–596 (1992).

21. Gerechter-Amitai, Z.K., Silfhout, C.H. van, Grama, A. and Kleitman, E., Y15 – A new gene for resistance to *Puccinia striiformis* in *Triticum dicoccoides* sel. G-25. *Euphytica*, **43:** 187-190 (1989).

22. Gill, B.S., Browder, L.E., Hatchett, J.H., Harvey, T.L., Martin, T.J., Raupp, W.J. *et al.*, Disease and insect resistance in wild wheats. In *Proceedings of the 6th International Wheat Genetics Symposium* (ed. S. Sakamoto), pp. 785–792. Faculty of Agriculture, Kyoto University, Japan (1983).

23. Gill, B.S., Sharma, H.C., Raupp, W.J., Browder, L.E., Hatchett, J.H., Harvey, T. L. *et al.*, Evaluation of *Aegilops* species forresistance to wheat powdery mildew, wheat leaf rust, Hessian fly and greenbug. *Plant Breeding*, **69:** 314–316 (1985).

24. Goletti, T., Lio, N., Pace, C. di, Osler, R., Porceddu, E. and Scarascia Mugnozza, G.T., Comparison of techniques for diagnosing barley yellow dwarf virus (BYDV) in *Triticeae* for identification of sources of genetic resistance [Italian]. *Revista di Agricoltura Subtropicale e Tropicale*, **84:** 367-375 (1990).

25. Hajjar, R. and Hodgkin, T., The use of wild relatives in crop improvement: A survey of developments over the last 20 years. *Euphytica*, **156:** 1–13 (2007).

26. Harlan, J.R., and de Wet, J.M.J., Toward a rational classification of cultivated plants. *Taxon*, **20:** 509–517 (1971).

27. Helguera, M., Khan, I.A., Kolmer, J., Lijavetzki, D., Zhong-qi, L. and

Dubcovsky, J.D., PCR assays for the *Lr37-Yr17-Sr38* cluster of rust resistance genes and their use to develop isogenic hard red spring wheat lines. Crop Sci., 43: 1839-1847 (2003).

28. Helguera, M., Vanzetti, L., Soria, M., Khan, I.A., Kolmer, J. and Dubcovsky, J.D., Markers for *triticum speltoides* leaf rust resistance gene *Lr51* and their use to develop nearisogenic lines. *Crop Sci.*, **45:** 728-734 (2005).

29. Heulgara, M., Khan, I.A. and Dubcovsky, J.D., Development of PCR marker for wheat leaf rust resistance gene *Lr47. Theor. Appl. Genet.*, **100:** 1137-1143 (2000).

30. Huang, L., Brooks, S.A., Li, W., Fellers, J.P., Trick, H.N. and Gill, B.S., *Genetics*, **164:** 655-664 (2003).

31. Huang, Q., Li, X., Chen, W.Q., Xiang, Z.P., Zhong, S.F., Chang, Z.J., Zhang, M., Zhang, H.Y., Tan, F.Q., Ren, Z.L. and Luo, P.G., *Theor Appl Genet.*, **127:** 843–853 (2014) .

32. Hussien, T., Bowden, R.L., Gill, B.S., Cox, T.S. and Marshall, D.S., Performance of four new rustresistance genes transferred to common wheat from *Aegilops tauschii* and *Triticum monococcum.Plant disease*, **81:** 582-586 (1997).

33. Jacobs, A.S., Pretorius, Z.A., Kloppers, F.J. and Cox, T.S., Mechanisms associated with wheat leaf rust resistance derived from *Triticum monococcum. Phytopathology*, **86:** 588-595 (1996).

34. Jin, Y., Pretoriou, Z.A. and Singh, R.P., New virulence with in race TTKS(Ug99) of the stem rust pathogen and effective resistant genes. *Phytopathology*, **97:** S137(Abstract). (2007).

35. Khush, G.S. and Brar, D.S., Overcoming the barriers in hybridization. In *Distant hybridisation of crop plants* (ed. G. Kallo and J. B. Chawdhury), pp. 47–61. Springer, Berlin, Germany (1992).

36. Knott, D.R., The wheat rust – breeding for resistance. In: Monographs on Theoretical and Applied Genetics, **12**, Springer-Verlag, Berlin. (1989).

37. Knott, D.R., Using polygenic resistance to breed for stem rust resistance in wheat. In: Breeding strategies for resistance to the rusts of wheat. Simmonds NW, Rajaram S (eds). CIMMYT, Mexico, pp 39-47 (1988).

38. Knott, D.R. and Zang, H.T., Leaf rust resistance in durum wheat and its relatives. In: *WheatGenetic Resources: Meeting Diverse Needs*, Srivastava, J.P. and Damania, A.B. (eds). John Wiley and Sons, Chichester, UK, pp. 311-316. (1990).

39. Kolmer, J.A., Singh, R.P., Gravin, D.F., Vicaars, L., William, H.M., Huerta-Espino, J., Ogbonnayya, F.C., Raman, H., Orford, S., Bariana, H.S. and Lagudha, E.S., Analysis of Lr34/*Yr*18 rust resistance region in wheat germplasm. *Crop Sci.*, **48:** 1841-1852 (2008).

40. Kolmer, J.A., Early research on the genetics of Puccinia graminis stem rust resistance in wheat in Canada and the United States. In ''Stem Rust of Wheat: From Ancient Enemy to Modern Foe'' (P. D. Peterson, ed.), pp. 51–82. APS Press, St. Paul, MN (2001).

41. Krattinger, S.G., Lagudah, E.S., Spilmeyer, W., Singh, R.P., Huerta-Espinno, J., McFadden, H., Bossolini, E., Selter, L.L. and Keller, B., A putative ABC transporter confers durable resistance to multiple fungal pathogen in wheat. *Science*, **323:** 1360-1363 (2009).

42. Kuraparthy, V., Chhuneja, P., Dhaliwal, H.S., Kaur, S., Bowden, R.L. and Gill, B. S., Characterization and mapping of cryptic alien introgression from *Aegilops geniculata* with new leaf rust and stripe rust resistance genes *Lr57* and *Yr40* in wheat. *Theor. Appl. Genet.*, **114:** 1379–1389 (2007a).

43. Kuraparthy, V., Sood, S., Chhuneja, P., Dhaliwal, H.S., Kaur, S., Bowden, R.L. and Gill, B.S., A cryptic wheat-*Aegilops triuncialis* translocation with leaf rust

resistance gene *Lr58. Crop Sci.*, **47:** 1995–2003 (2007b).

44. Larson, G., Piperno, D.R., Allaby, R.G., Purugganan, M.D., Andersson, L., Arroyo-Kalin, M. and Fuller, D.Q., Current perspectives and the future of domestication studies. *Proceedings of the National Academy of Sciences of the United States of America*, **111:** 6139–6146 (2014).

45. Leonard, K.J. and Szabo, L.J., *Mol. Plant Pathol.*, **6:** 99-111 (2005).

46. Liu, Y.L., Zhang, R.Z. and Mannuti, M., Evaluation of natural tolerance and resistance of wheat varieties to *Diuraphis noxia* [Chinese]. *Plant Protection*, **22:** 23-24 (1996).

47. Marais, G.F., Pretorius, Z.A., Marais, A.S. and Wellings, C.R., Transfer of rust resistance genes from *Triticum* species to common wheat. *South African Journal of Plant and Soil*, **20:** 193–198 (2003).

48. Maxted, N. and Kell, S.P., *Establishment of a global network for the in situ conservation of crop wild relatives: Status and needs*. Rome, Italy: Food and Agriculture Organization of the United Nations Commission on Genetic Resources for Food and Agriculture. (2009).

49. Maxted, N., Ford-Lloyd, B.V., Jury, S., Kell, S. and Scholten, M., Towards a definition of a crop wild relative. *Biodiversity and Conservation*, **15:** 2673–2685 (2006).

50. McIntosh, R.A., Yamazaki, Y., Dubcovsky, J., Rogers, W.J., Morris, C.F. and Somers, D.J. *et al*., Catalogue of gene symbols for wheat. Proceedings of the 11th International Wheat Genetics Symposium. Brisbane, Australia. (2008).

51. McIntosh, R.A., Yamazaki, Y., Rogers, W.J., Morris, C.F. and Devos, K.M., Catalogue of gene symbols for wheat (http://www.shigen.nig.ac.jp/wheat/komug i/genes/download.jsp). (2010).

52. McIntosh, R.A., The role of specific genes in breeding for durable stem rust resistance in wheat and triticale. In ''Breeding Strategies for Resistance to the Rust of Wheat'' (N. W. Simmonds and S. Rajaram, eds.), pp. 1–9. CIMMYT, Mexico, D.F. (1988).

53. Mihova, S., Sources of resistance to yellow rust (*Puccinia striiformis* West.) in the genus *Triticum*[Bulgarian]. *Rasteniev'Dni Nauki*, **25:** 3-8 (1988).

54. Mishra, P.C., Kurmwanshi, S.M. and Soni, S.N., xEvaluation of *Triticum* species under wheatimprovement programme. *Journal of Soils and Crops*, **6:** 200-201 (1988).

55. Mondal, S., Jessica, E., Rutkoski, Velu, G., Singh, P.K., Leonardo, A., Crespo-Herrera, Guzmán. C., Bhavani, S., Lan, C., He, X. and Ravi, P. Singh, Harnessing Diversity in Wheat to Enhance Grain Yield, Climate Resilience, Disease and Insect Pest Resistance and Nutrition Through Conventional and Modern Breeding Approaches. Frontiers in Plant Science | www.frontiersin.org. published: 06 July 2016 doi: 10.3389/fpls.2016.00991 (2016).

56. Munns, R., James, R.A., Xu, B., Athman, A., Conn, S.J., Jordans, C., Gilliham, M., Wheat grain yield on saline soils is improved by an ancestral Na+ transporter gene. *Nature Biotechnology*, **30:** 360–364 (2012).

57. Navarrete, L., Ayala, Bariana, H.S., Singh, R.P., Gibson, J.M., Mechanicos, A. A., Larkin, P.J., Trigenomic chromosomes by recombination of *Thinopyrum intermedium* and *Th. ponticum* translocations in wheat. Theor Appl Genet. **116:** 63–75 (2007).

58. Nevo, E. and Chen, G. X., Drought and salt tolerances in wild relatives for wheat and barley improvement. *Plant Cell and Environment*, **33:** 670–685 (2010).

59. Porth, T., Beaver, J.S., Debouck, D.G., Jackson, S.A., Kelly, J.D. and Dempewolf, H., Use of wild relatives and closely related species to adapt common bean to climate change. *Agronomy*, **3:** 433–461 (2013).

60. Potz, H., Schubert, V., Houben, A., Schubert, I. and Weber W.E., Aneuploids as a key for new molecular cloning strategies: development of DNA markers by microdissection using *Triticum aestivum– Aegilops markgraffi* chromosome addition line B. *Euphytica.*, **89:** 41–47 (1996).

61. Purnhauser, L., Gyulai, G., Csosz, M., Heszky, L. and Mesterhazy, A., *Acta Phytopathol. Entomol. Hung.*, **35(1-4):** 31-36 (2000).

62. Redden, R., Yadav, S.S., Maxted, N., Dulloo, M.E., Guarino, L. and Smith, P., *Crop wild relatives and climate change*. Hoboken, NJ: John Wiley & Sons Inc. (2015).

63. Riar, A.K., Kaur, S., Dhaliwal, H.S., Singh, K. and Chhuneja, P., Introgression of a leaf rust resistance gene from *Aegilops caudate* to bread wheat. *J. Genet.*, **91:** 155–161 (2012).

64. Robinson, J. and Skovmand, B., Evaluation of emmer wheat and other *Triticeae* for resistance to Russian wheat aphid. *Genetic Resources and Crop Evolution*, **39:** 159-163 (1992).

65. Saintenac, C., Zhang, W.J., Salcedo, A., Rouse, M.N., Trick, H.N., Akhunov, E., and Dubcovsky, J., Identification of wheat gene *Sr35* that confers resistance to Ug99 stem rust race group. *Science*, **341:** 783–786 (2013).

66. Sawhney, R.N. and Goel, L.B., Stem rust resistance in accessions of *Triticum timopheevi* and three *Triticum aestivum* lines with resistance from *timopheevi*. *Wheat Information Service*, **50:** 56-58 (1979).

67. Schneider, A., Molnar, I. and Molnar Lang, M., Utilisation of *Aegilops* (goatgrass) species to widen the genetic diversity of cultivated wheat. *Euphytica* **163:** 1–19 (2008).

68. Sears, E.R., The transfer of leaf rust resistance from Aegilops umbellulata to wheat. *Brookhaven Symp. Biol.*, **9:** 1–21 (1956).

69. Shabnam, N., Ahmad, H., Sahib, G.A., Ghafoor, S. and Khan, I.A., Development of Molecular Markers for Leaf Rust Resistance Genes Incorporated from Alien Species into Common Wheat. *Asian Journal of Agricultural Sciences*, **3(1):** 55-57 (2011).

70. Shi, A.N., Leath, S. and Murphy, J.P., A major gene for powdery mildew resistance transferred to common wheat from wild einkorn wheat. *Phytopathology*, **88:** 144-147 (1998).

71. Simeone, R., Sciancalepore, A. and Simonetti, M.C., Identification of powdery mildew resistance genes in tetraploid wheats. *Ewac Newsletter*, pp. **110-113** (1998).

72. Singh, R.P. and Huerta-Espino, J., Global monitoring of wheat rusts and assessment of genetic diversity and vulnerability of popular cultivars. Research Highlight of CIMMYT wheat program: 1999-2000. CIMMYT, Mexico. (2000).

73. Singh, R.P. and McIntosh, R.A., Complementary genes for resistance to *Puccinnia recondita tritici* in *Triticun aestivum L.* Genetics and linkage studies. *Can J Genet and Cytol.*, **26:** 723-735 (1984).

74. Singh, R.P., Mujeeb-Kazi, A. and Huerta-Espino, J., *Lr46*: a gene conferring slow rusting resistance to leaf rust in wheat. *Phytopathology*, **88(9):** 890-894 (1998).

75. Singh, R.P., Nelson, J.C. and Sorrells, M.E., Mapping *Yr28* and other genes for resistance to stripe rust in wheat. *Crop Sci.*, **40:** 1148-1155 (2000b).

76. Singh, R.P. and Trethewan, R., Breeding spring wheat for irrigated and rainfed production systems of the developing world. In: Breeding major food staples: Kang MS and Priyadarshan PM (ed) Blackwell Pub Ltd, UK, pp 109-140 (2007).

77. Singh, R.P., Hodson, D.P., Huerta-Espino, J., Jin, Y., Njau, P., Wanyera, R., Herrera-Foessel, S.A. and Ward, R.W., Will stem rust destroy the world's wheat crop? *Adv Agron.*, **98:** 271–309 (2008).

78. Soshnikova, E.A., Promising species of *Triticum* for the production of donors of resistance to stemrust of wheat [Russian]. *Nauchno-tekhnicheskii Byulleten'Vsesoyuznogo Ordena Lenina i Ordena Druzhby Narodov Nauchno-issledovatel'skogo Instituta Rastenievodstva Imeni N.I. Vavilova*, **197:** 4-5 (1990).

79. Spilmeyer, W., Sharp, P.J. and Lagudah, E.S., Identification and validation of markers linked to broad spectrum stem rust resistance gene *Sr2* in wheat (*Triticum aestivum L.*). *Crop Sci.*, **43:** 333-336 (2003).

80. Sun, G.L., Fahima, T., Korol, A.B., Turpeinen, T., Grama, A., Ronin, Y.I. and Nevo, E., Identification of molecular markers linked to the Yr15 stripe rust disease resistance gene originated in wild emmer wheat, *Triticum dicoccoides*. *Theor. and Applied Genet.*, **95:** 622-628 (1997).

81. Tomerlin, J.R., El-Morshidy, M.A., Moseman, J.G., Baenziger, P.S. and Kimber, G., Resistance to *Erysiphe graminis* f. sp. *tritici*, *Puccinia recondita* f. sp. *tritici* and *Septoria nodorum* in wild *Triticeae* species. *Plant disease*, **68:** 10-13 (1984).

82. Tsilo, T.J., Jin, Y. and Anderson, J.A., *Crop Sci.*, **48:** 253-261 (2008).

83. Valkoun, J., Hammer, K., Kucerova, D. and Bartos, P., Disease resistance in the genus *Aegilops* L.—stem rust, leaf rust, stripe rust, and powdery mildew. *Kulturpflanzen* **33:** 133–153 (1985).

84. Valkoun,, J., Kucerova, D. and Bartos, P., Transfer of a new gene for stem rust resistance from *T. monococcum* L. to hexaploid wheat, *T. aestivum* L. *Sbornik Uvtiz, Genetika a Sletchteni*, **25:** 209-214 (1989).

85. Warschefsky, E., Penmetsa, R.V., Cook, D.R. and von Wettberg, E.J.B., Back to the wilds: Tapping evolutionary adaptations for resilient crops through systematic hybridization with crop wild relatives. *American Journal of Botany*, **101:** 1791–1800 (2014).

86. Winzeler, M., Winzeler, H. and Keller, B., Plant Breeding, **114:** 24-28 (1995).

87. Wu, Molecular mapping of stem rust resistance genes in wheat. A MS Thesis, B. S. Kansas State University (2003).

88. Wulf, B. and Moscou, M., Strategies for transferring resistance into wheat: from wide crosses to GM cassettes. *Front Plant Sci.*, **5:** 1–11. doi:10.3389/fpls.2014.00692. (2014).

89. Xiang, Q.J., Sheng, B.Q., Duan, X.Y. and Zhou, Y.L., The analysis of effective wheat powderymildew resistance genes of some breeding lines [Chinese]. *Acta, Agronomica Sinica*, **22:** 741-744 (1996).

90. Yamaleev, A.M., Dolotovskii, I.M. and Noikonov, V.I., Relationship between resistance of wheat root rots and genome composition [Russian]. *Doklady Vsesoyuznoi Ordena Lenina i Ordena* (1989).

91. Yu, B.S. and Sun, G.R., Preliminary study of several spring wheat varieties for resistance to*Septoria* diseases [Chinese]. *Crop Genetic Resources*, **1:** 27-29 (1995).

92. Zamir, D., Improving plant breeding with exotic genetic libraries. *Nature Reviews Genetics*, **2:** 983–989 (2001).

93. Zhang, H., Mittal, N., Leamy, L.J., Barazani, O. and Song, B.H., Back into the wild—Apply untapped genetic diversity of wild relatives for crop improvement *Evolutionary Applications*, **10:** 5–24 (2016).

94. Zhang, X., Zhong, S.B. and Yao, J.X., Cytological and powdery mildew resistance analyses of common wheat x *Triticum araraticum* hybrids and their progenies [Chinese]. *Jiangsu Journal of Agricultural Sciences*, **13:** 185-187 (1997).