Available online at www.ijpab.com

DOI: http://dx.doi.org/10.18782/2320-7051.4095

ISSN: 2320 – 7051

Int. J. Pure App. Biosci. **6 (1):** 407-417 (2018)

International Journal of Pure & Applied Bioscience

Review Article

OPEN ACCESS

Revealing of Brown Rust Resistance Genes by Molecular Marker in Wheat: A Review

Elangbam Premabati Devi[1*], Deepshikha[2], J. P. Jaiswal[2]

[1]Wheat Research Station, Vijapur, 382 870, S.D.A.U., Gujarat, India

[2]G. B. Pant University of Agriculture & Technology, Pantnagar, 263 145, Uttarakhand, India

*Corresponding Author E-mail: epremabati35@gmail.com

Received: 18.06.2017 | Revised: 29.07.2017 | Accepted: 5.08.2017

ABSTRACT

The main biotic constraint in sustaining and boosting wheat production is rusts caused by Puccinia species which are historic and devastating pathogens worldwide. Their ability to spread aerially over the continents, production of infectious pustules geometrically in trillions and evolution of new physiologic races makes the management strategies a very challenging task. Identification of pathotypes, anticipatory breeding, evaluation for rusts resistance and deployment of resistant cultivars is a time tested strategy to manage wheat rusts. However, the rust's pathogen being out smarted and new virulent pathotypes emerged which could overcome the novel rust resistance genes. But the most efficient and economic way for management of wheat rusts is utilization of resistant variety. Identification of resistance genes is essential for gene pyramiding, gene deployment and developing slow rusting wheat cultivars to manage wheat rusts. In this context, molecular markers linked to rust resistance genes assist in marker-assisted selection for validation of rust resistant genes in less time as compared to conventional breeding programme.

Key words: *Adult Plant Resistance, Gene deployment, Gene pyramiding, Marker Assisted Selection, Seedling Resistance*

INTRODUCTION

Brown/leaf rust of wheat, caused by *Puccinia triticina* Erisk. is most predominantly confined in northern wheat growing zone of India[4]. It is well distributed among the three wheat rusts and occurs in higher intensities as epidemics since the pathogen inoculums are prevalent in both North and South regions[29,47]. Epidemics of leaf rust had occurred in years of 1786, 1827, 1832, 1894, 1897, 1947, 1948, 1972 and 1973[55]. The Sonalika epidemic of leaf rust caused losses of 1mt which was occurred in Uttar Pradesh and a part of Bihar, India[29]. Maximum yield losses due to leaf rust were 30-40 per cent mostly due to reduction in 1000 grain weight[59]. The primary symptoms as orange to brown uredinia which are round to slightly elongate occurs on the leaf blades. Sometimes, leaf sheaths can also be infected in presence of favourable temperature range of 15 to 30^{0}C, under high inoculum densities along with the presence of susceptible cultivars.

Cite this article: Elangbam, P.D., Deepshikha and Jaiswal, J.P., Revealing of brown rust resistance genes by molecular marker in wheat: A review, *Int. J. Pure App. Biosci.* **6(1):** 407-417 (2018). doi: http://dx.doi.org/10.18782/2320-7051.4095

Environment has a significant influence on terminal disease reaction. The fungus can infect in dew periods of 3 hours or less at temperatures of 20°C, however, more infections occurred with longer dew periods. At cooler temperatures, longer dew periods are required but few if any infections occur where dew period temperatures are above 32°C or below 2°C[81]. In relation to stage of crop with disease development, severe epidemics and losses can occur when the flag leaf is infected before flowering stage resulting in reduced floret set and grain shrivelling[7].Since, it is an obligate parasite and heterocious, an alternate host i.e. *Thalictrum spp.* is requires for completion of its sexual life cycle on which fungus will overwinter. But there is no role of alternate host in the occurrence of leaf rust in entire wheat growing areas of India since the inoculum are continually present in Himalayas in north and some self sown crop along with wheat grown areas of Nilgiri hills in south where wheat are cultivated throughout the year that act as source of inoculum[47]. The germination process requires moisture and temperatures (15-20°C) and after 10-14 days of infection, fungus starts sporulation leading to symptoms development[74]. The pathogen has ability to disperse urediospores which is repeating spore through wind along with the production of infectious pustules geometrically in trillions. Moreover, evolution of new physiological races/pathotypes with time render earlier reported resistant variety to susceptible one which made the management strategies a very challenging task against rust.

Genetic resistance against leaf rust of wheat

Utilization of resistant cultivars is the most effective and economical method for reducing losses due to leaf rust. Development of new cultivars with improved genetic resistance helps to reduce production costs and risk of environmental pollution due to fungicide usage[11]. So, genetic manipulation of resistance genes has resulted in providing more stable form of resistance against rust[72]. It has been estimated that wheat genetic improvement has generated at least 27 times its value in benefits from leaf rust resistance breeding in spring wheat alone[45]. Two types of resistance has been characterized in rust pathosystems, which are qualitative (race-specific/vertical) and quantitative (race-nonspecific/horizontal) resistance[38,89]. Deployment of race-specific resistance gene has the capacity of providing effective complete protection[67]. In general, adult plant resistance (APR) confer a partial and slow rusting with durable resistance as compared to seedling resistance[69].

Currently 71 leaf rust resistance genes have been designated which are shown to be pathotype specific seedling and adult plant resistance. Identified leaf rust resistance genes of wheat consist of *Lr1, Lr2a, Lr2b, Lr2c, Lr3a, Lr3b, Lr3ka, Lr9, Lr10, Lr11, Lr12, Lr13, Lr14a, Lr14b, Lr14a, Lr15, Lr16, Lr17a, Lr17b, Lr18, Lr19, Lr20, Lr21, Lr22a, Lr22b, Lr23, Lr24, Lr25, Lr26, Lr27, Lr28, Lr29, Lr30, Lr31, Lr32, Lr33, Lr34, Lr35, Lr36, Lr37, Lr38, Lr39, Lr42, Lr44, Lr45, Lr46, Lr47, Lr48, Lr49, Lr50, Lr51, Lr52, Lr53, Lr54, Lr55, Lr56, Lr57, Lr58, Lr59, Lr60, Lr61, Lr62, Lr63, Lr64, Lr65, Lr66, Lr67, Lr68, Lr69, Lr70* and *Lr71*[49,50,51,52,53]. Most of the *Lr* genes conferred race-specific seedling resistance and are vulnerable to defeat by new virulent races. Greater durability of resistance could be achieved through combinations of race-specific genes or by using race-nonspecific resistance genes, such as *Lr34* and *Lr46*[35,36.] However, such genes provide low levels of resistance when deployed singly[90]. A third option is to combine both race-specific and race-nonspecific resistance. Thus, gene pyramiding plays a crucial role as a resistance breeding procedure where more than one gene is brought together to enhance the resistance life of an otherwise better performing variety against the pathogenic races. Accordingly, to prevent the rapid breakdown of seedling resistance genes, it is suggested that such genes should be used in combination with other resistant genes preferably with an APR gene[27,61]. However, the selection of genotypes carrying two or more genes using traditional host-parasite interaction is very time consuming in conventional breeding approach and often not possible due to lack of isolates

with specific virulence and difficulty of identifying one resistance gene in the presence of another gene. The traditional method of postulation of resistance genes is also extremely time and labour intensive[31]. Besides, 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[66]. Over the last 15 years many efficient markers for leaf rust resistance genes have been described. The molecular markers most closely linked to *Lr* genes are based on the PCR technique that can be applied easily in wheat breeding programmes[26]. Identification of molecular markers can facilitate gene pyramiding into one cultivar in less time and make it more cost effective. A marker assisted selection (MAS) scheme could allow breeders to efficiently select resistance gene without waiting for its phenotypic expression in plants. Indirect selection using DNA markers would be helpful in elucidating rarely occurring recombination between resistance genes, thus facilitating the combination of these closely-linked resistance genes into cultivars. Detail of applications of DNA molecular markers in validation of leaf rust resistance genes in wheat are summarized below along with types of resistance conferred against leaf rust.

Seedling Resistance

Seedling resistance genes are found to be monogenic with race specific and effective for the whole life cycle of the plant[32]. Race specific genes confer resistance to one or a few races of pathogen and also known as major gene. Although, incorporation of race-specific resistance genes may be challenging since it increases the risk of faster breakdown. Some examples of major genes effective against leaf rust include *Lr19*, *Lr26* and *Lr42* etc. Evaluation of 44 wheat cultivars for leaf rust resistance reported that 14 lines showed seedling resistance, while 30 lines showed seedling susceptibility to specific race 77-5. Besides, these 14 lines possessing seedling resistance against 77-5 also showed APR against pathotypes 77-5, 77-2 and 104-2 of leaf rust[74]. Similarly, results of study in resistance components at seedling stage and field resistance in some elite wheat lines showed that lines M-85-1, M-86-1 and C-85-10 had lower infection types, latent period and smaller pustules size and number. In general, 18 out of 62 lines were resistant at seedling and adult plant stages and 13 lines were susceptible at both stages. Lines C-85-15, C-86-7, C-86-9, M-85-11, M-86-6, M-86-5 and M-86-10 were susceptible at seedling stage and resistant at adult plant stage[87]. Moreover, *Lr15* has been shown to be present on wheat chromosome 2D and is reported to be a seedling resistance gene and is more effective when present with an APR gene[11]. But the importance of seedling resistance has major limitation since there were several reports of breakdown of these genes with the evolution of new virulent races of pathogen. So, we shall be focused on adult plant resistance which is a stable form of resistance with more durable and effective against several races of pathogen.

Adult Plant Resistance (APR)

Race non-specific resistance, is usually effective in the post-seedling growth stage, thus commonly referred to as adult plant resistance (APR). This resistance is generally quantitatively inherited by interacting additively with other non-specific resistance genes and shows moderate resistance. Johnson introduced the concept of durable resistance conditioned by race non-specific adult plant resistance genes in 1988[28]. This type of resistance is mainly associated with the minor genes which are also known as slow rusting genes. Varieties with high levels of durable resistance to multiple pathogens can be developed by combining multiple race non-specific resistance loci, especially to those which are known to confer resistance to multiple diseases[75]. Examples of these APR leaf rust resistance genes are *Lr34*, *Lr46* and *Lr67* etc. The breakdown of resistance genes like *Lr9* in 1999[56] and *Lr28* in 2008[5] has led to investigation of adult plant resistance. Wheat cultivars with slow rusting genes are often susceptible at the seedling stage but may be

moderately to highly resistant to all pathotypes at the adult plant stage[39]. Slow rusting is not affected by the types of pathotypes indicating its non race-specific nature of resistance[31]. Study conducted to determine the link between *Lr34* gene and leaf tip necrosis in two Thatcher near-isogenic lines reported that leaf tip necrosis could be used as a phenotypic marker for *Lr34*[70]. Confirmation of leaf rust resistance in thirty exotic wheat germplasm accessions at both seedling and adult stage reported that three accessions viz. EC 635627, EC 635721 and EC 664244 showed resistant at seedling stage while twenty nine accessions were characterized as resistant at adult plant stage with their low values of area under disease progress curve (AUDPC)[14]. Genetical studies to understand the inheritance of APR to leaf rust in Australian wheat cultivars reported that cultivars Cranbrook, Suneca and Harrier carry two APR genes for leaf rust. Cultivar Westphal 12A had three genes that conditioned resistance in seedling plants, and the gene *Lr34* which optimally expressed in adult plants. BH1146 was shown to have *Lr13* and *Lr34* APR genes[33,73]. The presence of APR gene *Lr46,* located on chromosome 1B, results in a longer latency period and lower infection levels than susceptible cultivars[86]. But the presence of this slow rusting gene *Lr46* does not provide sufficient resistance to protect yield levels, especially under high disease pressures. So, there should be a combination of different minor genes to impart adequate levels of resistance[77]. Results in identification of resistance genes in wheat cultivars, Alsen and Norm indicated that Alsen had seedling resistance genes *Lr2a, Lr10* and *Lr23*, with APR genes *Lr13* and *Lr34*. Norm carried seedling genes *Lr1, Lr10, Lr16* and *Lr23* along with adult plant genes *Lr13* and *Lr34*. They recommended the use of seedling resistance genes *Lr16* and *Lr23* in combination with the APR gene *Lr34* for enhancing resistance[57]. The presence of *Lr34* in a cultivar increases its general resistance to various races of pathogen[84]. This *Lr34* gene also plays an important role in improving tolerance to environmental stresses such as salinity[64]. Some of the SSR markers, particularly *Xgwm295, csLV34, Xwmc405* and *Xgwm44* for gene *Lr34,* showed good correlation with leaf rust resistance[54]. However, this non-specific resistance characteristic of *Lr34* makes it difficult to identify by traditional methods. So, the application of molecular markers may provide a more reliable tool to breeders to identify APR genes in segregating populations and their further incorporation into existing cultivars[53]. Thus, molecular markers can be used as selection tool and is important for the identification of loci carrying adult plant resistance genes for leaf rust to ensure their proper use in breeding for durable adult plant resistance.

Characterization of leaf rust resistance genes by molecular markers

Marker based breeding may revolutionize the process of cultivar development by eliminating the need for field trials and making it possible to select individuals lines with crossovers very near to a gene of interest, potentially removing linkage drag that frequently comes from the donor parent[88]. Moreover, identification of molecular markers for resistance genes can efficiently facilitate MAS and pyramiding of major genes in breeding programs into a valuable background in less time and make it more cost effective[1,68]. Similarly, gene deployment can be accelerated through MAS which aims at achieving durable resistance, in which farmers can grow cultivars with complementary sets of resistance genes with different race-specificities. Microsatellite (SSR) and Amplified fragment length polymorphism (AFLP) markers for *Lr3bg, Lr18, Lr40, Lr46* and *Lr50* genes had been developed[66]. Besides, some other markers viz. Cleaved Amplified Polymorphic Sequence (CAPS), Sequence Characterized Amplified Regions (SCAR) and Simple sequence repeats (SSR) markers also verified using *Triticum* spp. with different genetic background[8]. In earlier efforts, molecular markers linked to *Lr* genes such as *Lr3a*[30], *Lr12*[78], *Lr19*[19], *Lr22*[24], *Lr34*[6,15,41,42], *Lr39*[60], *Lr41*[83], *Lr48* and *Lr49*[3] have been identified. As *Lr15* gene shows effective resistance with APR gene *Lr34*, it

would be desirable to stack these effective resistance genes. At present, *Xgwm4562* and *Xgwm102* markers are used for gene pyramiding of *Lr15* and *Lr34* in wheat cultivars[6,41,42]. The mapping of sixteen *Lr* resistance genes using restriction fragments length polymorphism (RFLP) markers has suggested that cultivars Frontana with *Lr34* gene had operative durable rust resistance[12] and also soft red winter wheat having *Lr34* in combination with seedling resistant *Lr2a*, *Lr9*, *Lr26* were highly resistant, whereas, in combination with *Lr10*, *Lr11*, *Lr18* were moderately to low resistant[37]. Another characteristic of *Lr34* resistance is that it is genetically tightly linked with *Yr18* gene, which confers adult plant resistance to leaf and yellow rust[49,70,71]. This gene also co-segregates with leaf tip necrosis (*Ltn1*), powdery mildew resistance (*Pm38*), Barley yellow dwarf virus (*Bydv1*) genes[11,44,70,71,80]. Pyramiding of rust resistance can be a better approach as the cultivars with single resistance genes have been successfully attacked by emergence of new virulent pathotypes[48]. Marker assisted study on 107 double haploid wheat lines by using 400 SSR primers suggested that *Xgwm295.1* is the closest known SSR marker for *Lr34* and alleles of *Xgwm295.1* can be used for detection of *Lr34* in different cultivars[82]. The molecular characterization of the *Lr34* by wheat expressed sequence tags (wESTs) identified a genomic interval predicted to span *Lr34* on chromosome 7DS. While, conversion of the RFLP to a co-dominant sequence tagged site (*csLV34*) revealed a bi-allelic locus, where a variant size of 79 bp insertion in an intron sequence was associated with lines or cultivars that lacked *Lr34.* Genetic linkage between *csLV34* and *Lr34* was estimated at 0.4 cM[41,42]. STS marker based tracking of slow rusting of *Lr34* gene in Indian wheat genotypes and some advance breeding lines has confirmed their slow rusting nature with lower AUDPC values (less than 200) in *Lr34* positive lines. Lines falling in the range of 101-200 for AUDPC truly represent the slow rusters so these lines infer long lasting field resistance and must be preferred while breeding[58]. The utility of *csLV34* marker in postulating for occurrence of *Lr34* across a wide range of wheat germplasm was confirmed in wheat breeding by the result of strong association between *Lr34* and *csLV34b* allele[34]. Identification of microsatellites linked to *Lr47* gene in isogenic lines with and without *Lr47* developed from 10 cultivars/breeding lines as well as 10 microsatellites previously mapped in 7AS chromosome revealed that microsatellite marker *Xgwm60* was co-segregated completely linked to *Lr47*[42]. Resistance genes *Lr10*, *Lr26* and *Lr37* in 27 winter wheat cultivars tested by molecular markers resulted that gene *Lr37* was determined in 11 cultivars, gene *Lr10* in 10 cultivars and gene *Lr26* in 4 cultivars[20]. Another *Lr19*, an exotic gene conditioning resistance with hypersensitive response, was considered likely to be a member of the major nucleotide binding site (NBS) leucine rich repeat (LRR) R gene family[16].Incorporation of *Lr* genes *viz. Lr9*, *Lr24*, *Lr25*, *Lr29*, *Lr35* and *Lr37* into winter wheat varieties by application of MAS in wheat breeding were currently effective in Hungary which were identified using STS, SCAR and RAPD markers closely linked to them[85]. Another report also confirmed that eleven different *Lr* genes: *Lr1*, *Lr3a*, *Lr3ka*, *Lr9*, *Lr10*, *Lr16*, *Lr17*, *Lr19*, *Lr24*, *Lr26* and *Lr41* were postulated in the tested material and also suggested that combinations including seedling resistance genes like *Lr16*, *Lr47*, *Lr19*, *Lr41*, *Lr21*, *Lr25* and *Lr29* with APR genes like *Lr34*, *Lr42* and *Lr46* which will probably provide durable resistance[43]. PCR-based molecular markers analysis using SCS123 marker linked to *Lr19* gene in different bread wheat cultivars detected 737 bp in 48 genotypes while fragment of 688 bp was detected in 53 genotypes using the SCS253 marker. So, the results obtained using both markers indicated that the *Lr19* gene is present on 7D chromosomes[25].Besides, *Lr42* gene confer resistance at both seedling and adult plant stages and remains effective against all the races of leaf rust reported till date. Thus, lines containing *Lr42* have been used as a parent in

some breeding programs with success[2]. Previous work located *Lr42* on chromosome 1DS[10] and found that *Lr42* also played a significant role in increasing wheat yield and kernel size[46]. Report also suggested that adult plants carrying *Lr46* gene have longer latency period since the plants with this gene show higher rate of fungal colonies abortion without any chlorotic or necrotic effects and also decrease the colony size suggesting that the resistance conferred by *Lr46* gene is not of hypersensitive type[46]. The microsatellite locus *Xwmc44* has located 5.6-cM proximal to the putative QTL for *Lr46*[82]. Later, leaf tip necrosis has been reported to be highly correlated with the presence of *Lr46*[62]. The molecular and phenotypic diagnostics for *Lr24* gene in genotype HW 5207 suited for cultivation in Central India was validated by applying SCAR marker *SCS1302* at 607 bp fragment[79]. Moreover, *Lr24* gene is linked with *Sr24* gene which is apparently effective against all races of stem rust that paved the way for MAS of rust resistance genes[31]. Thus, MAS offers the opportunity to select desirable lines on the basis of genotype rather than phenotype, especially in the case of combining different genes in a single genotype and it is a powerful alternative to facilitate new gene deployment and gene pyramiding for quick release of rust resistant cultivars in wheat resistance breeding programme.

Introgression of leaf rust resistance gene from Aegilops and alien species into wheat

The germplasm of wild relatives and progenitor species of cultivated wheat comprise an excellent source of disease resistance that can be exploited for wheat improvement[13]. 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[9,17,18,40,63]. Numerous wheat-*Aegilops* addition, substitution and translocation lines have been developed to dissect and introgress many agronomically useful traits into the wheat gene pool. Several genes for resistance to leaf rust have been introgressed from *Aegilops* and *Thinopyrum* species to cultivated wheat: e.g. *Aegilops umbellulata* (*Lr9*); *Thinopyrum ponticum* (*Lr19*, *Lr24* and *Lr29*); *Ae. ventricosa* (*Lr37*); *Th. intermedium* (*Lr38*); *Ae. speltoides* (*Lr28*, *Lr35*, *Lr36*, *Lr51* and *Lr66*); *Ae. tauschii* (*Lr21*, *Lr22a*, *Lr32*, *Lr39*, *Lr40*, *Lr41*); *Ae. geniculata* (*Lr57*); *Ae. triuncialis* (*Lr58*); *Ae. longissima* and *T. dicoccoides* (*Lr53*)[49,52,53]. *Aegilops* species with C, U and M genomes have been identified as very good sources of resistance to leaf rust[76]. Resistance gene *Lr47* was derived from short arm of chromosome 7S of *Triticum speltoides* and translocated onto short arm of chromosome 7A of wheat[23]. Similarly, *Lr37* gene has been introgressed into wheat from short arm of chromosome 2N of *Triticum ventricosum*[21]. Another gene *Lr51* has been transferred from *Triticum speltoides* to common wheat[22]. In another study of Random amplified polymorphic DNA (RAPD) based molecular markers developed for alien rust resistance genes has incorporated in wheat from *T. speltoides* (*Lr47*, *Lr51)* and *T. ventricosum* (*Lr37*)[65].

CONCLUSION

Molecular markers act as an efficient means for identification of leaf rust resistance genes in wheat breeding programs. The knowledge gained so far has suggests that markers flanking *Lr* genes can be used simply and effectively in marker-assisted backcross programme for providing durable resistance. So, the most important aims should be focusing on incorporation of durable and diverse resistance, characterization of additive genes and identification of a closely linked molecular marker which will progress the design of selection process in wheat breeding programs. Although, there is a need for better understanding of dynamics of pathotypes population over time and space, preliminary idea for designing breeding strategies at the regional level, scientific awareness of deploying available resistance sources for improving the status of wheat resistance breeding against leaf rust.

REFERENCES

1. Babu, R., Nair, S. K., Prasanna, B. M. and Gupta, H. S. Integrating marker-assisted selection in crop breeding prospects and challenges. *Curr. Sci*.**87:** 607-619 (2004).
2. Bacon, R. K., Kelly, J. T., Milus, E. A. and Parsons, C. E. Registration of soft wheat germplasm AR93005 resistant to leaf rust. *Crop Sci*.**46:** 1398-1399 (2006).
3. Bansal, U. K., Hayden, M. J., Venkata, B. P., Khanna, R., Saini, R. G. and Bariana, H. S. Genetic mapping of adult plant leaf rust resistance genes *Lr48* and *Lr49* in common wheat. *Theor. Appl. Genet.***117:** 307-312 (2008).
4. Bhardwaj, S. C., Prashar, M., Kumar, S. and Datta, D. Virulence and diversity of *Puccinia triticina* on wheat in India during 2002-04. *Indian J. Agr. Sci*.**76:** 302-306 (2006).
5. Bhardwaj, S. C., Prashar, M., Kumar, S., Jain, S. K. and Datta, D. Adult plant resistance gene in some Indian wheat genotypes and postulation of leaf rust resistance genes. *Indian Phytopath.* **63(2):** 174-180 (2010).
6. Bossolini, E., Krattinger, S. G. and Keller, B. Developments of simple sequence repeat markers specific for the *Lr34* resistance region of wheat using sequence information from rice and *Aegilops tauschii*. *Theor. Appl. Genet*.**113:** 1049-1062 (2006).
7. Chester, K. S. The nature and prevention of the cereal rusts as exemplified in the leaf rust of wheat. In *Chronica botanica*. Walthan, MA, USA. 269 pp (1946).
8. Chelkowski, J. Molecular markers for leaf rust resistance genes in wheat. *J. Appl. Genet.* **42(2):** 117-122 (2001).
9. 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. Resourc. Crop Evol*.**55:** 849-859 (2008).
10. Cox, T. S., Raupp, W. J. and Gill, B. S. Leaf rust-resistance genes *Lr41*, *Lr42* and *Lr43* transferred from *Triticum tauschii* to common wheat. *Crop Sci.* **34:** 339-343 (1994).
11. Dholakia, B. B., Khan, R. R., Bansal, U. K., Rajwade, A. V., Chavan, S., Saini, R. G., Hosmani, P., Reddy, D. M. R., Gupta, V. S. and Lagu, M. D. Molecular mapping of leaf rust resistance gene *Lr15* in hexaploid wheat. *Mol. Breed*. **31:** 743-747 (2013).
12. Dyck, P. L., Samborski, D. J. and Anderson, A. G. Inheritance of adult plant resistance derived from the common wheat varieties Exchange and Frontana. *Can. J. Geneti. Cytol*. **8:** 665-671 (1966).
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. Elangbam, P. D., Deepshikha. and Kumari, B. Confirmation of resistance in wheat germplasms against brown/leaf rust through Seedling Resistance Test (SRT) and Adult Plant Reaction (APR). *Indian Phytopath*o. **68(4):** 386-389 (2015).
15. Elangbam, P. D., Deepshikha., Kumari, B., Tewari, R. and Jaiswal, J. P. Screening and molecular characterization for durable rust resistance in wheat germplasm resources. *Env. Ecol*. **35**(1A):253-257 (2017).
16. Gennaro, A., Robert, K. M. D. and Ceoloni, C. A candidate for *Lr19*, an exotic gene conditioning leaf rust resistance in wheat. *Funct. Integr. Genomics*. **9:** 325-334 (2009).
17. Gill, B. S., Browder, L. E., Hatchett, J. H., Harvey, T. L., Martin, T. J., Raupp, W. J. 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).
18. Gill, B. S., Sharma, H. C., Raupp, W. J., Browder, L. E., Hatchett, J. H., Harvey, T. L. Evaluation of *Aegilops* species for resistance to wheat powdery mildew,

wheat leaf rust, Hessian fly and greenbug. *Plant Breed*. **69:** 314-316 (1985).

19. Gupta, S. K., Charpe, A., Prabhu, K. V. and Haque, Q. M. R. Identification and validation of molecular markers linked to the leaf rust resistance gene *Lr19* in wheat. *Theor. Appl. Genet.* **113:** 1027-1036 (2006).
20. Hanzalova, A., Sumikova, T. and Bartos, P. Determination of leaf rust resistance genes *Lr10*, *Lr26* and *Lr37* by molecular markers in wheat cultivars registered in the Czech Republic. *Czech J. Genet. Plant Breed.* **45:** 79-84 (2009).
21. 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).
22. 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 near-isogenic lines. *Crop Sci*. **45:** 728-734 (2005).
23. 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).
24. Hiebert,C., Thomas, J., Somers, D., Mccallum, B. and Fox, S. Microsatellite mapping of adult-plant leaf rust resistance gene *Lr22* in wheat. *Theor. Appl. Genet.* **115:** 877-884 (2007).
25. Huseynova, I. M. F., Guliyeva, B., Rustamova, S. M. and Aliyev, J. A. PCR-based molecular markers linked to the leaf rust resistance gene *Lr19* in different bread wheat cultivars. *Adv. Biol. Chem.* **3:** 153-158 (2013).
26. Imbaby, I. A., Mahmoud, M. A., Hassan, M. E. M. and Abd-El-Aziz, A. R. M. Identification of leaf rust resistance genes in selected Egyptian wheat cultivars by molecular markers. *Scientific World J*.1-7 (2014).
27. Jiang, J., Friebe, B. and Gill, B. S. Recent advances in alien gene transfer in wheat. *Euphytica*. **73:** 199-212 (1994).
28. Johnson, R. Durable resistance to yellow rust in wheat and its implications in plant breeding. In: Simmonds, N.W. and Rajaram, S. Eds. *Breeding strategies for resistance to the rusts of wheat*, Mexico, DF, CIM-MYT, pp. 63-75 (1988).
29. Joshi, L. M. An analysis of Brown rust epidemics of 1971-1972-1973. *Indian Phytopath*. **28:** 138 (1975).
30. Khan, M. A., Hussain, M. and Mujahid, H. Wheat leaf rust (*Puccinia recondita*) occurrence and shifts in its virulence in Punjab and N.W.F.P. *Pak. J. Phytopathol.* **14:** 1-6 (2005).
31. Knott, D. R., The Wheat Rust-Breeding for Resistance. Monographs on Theoretical and Applied Genetics, **12:** Springer, Berlin, Germany (1989).
32. Kolmer, J. A. Genetics of resistance to wheat leaf rust. *Annu. Rev. Phytopathol*. **34:** 435-455 (1996).
33. Kolmer, J. A. and Liu, J. Q. Inheritance of leaf rust resistance in the wheat cultivars AC Majestic, AC Splendor and AC Karma. *Can. J. Plant Patho*. **24:** 327-331 (2002).
34. Kolmer, J. A., Singh, R. P., Garvin, D. F., Viccars, L., William, H. M., Huerta-Espino, J., Ogbonnaya, F. C., Orford. H. R. S., Bariana, H. S. and Lagudah, E. S. Analysis of the *Lr34/Yr18* rust resistance region in wheat germplasm. *Crop Sci*. **48:** 1841-1852 (2008).
35. Kolmer, J. A., Chen, X. and Y. Jin. Diseases which challenge global wheat production the wheat rusts. In: B.F. Carver, editor, Wheat: Science and trade. Wiley-Blackwell, Ames, I A (2008a).
36. Kolmer, J. A., Long, D. L. and M. E. Hughes. Physiological specialization of *Puccinia triticina* on wheat in the United States in 2006. *Plant Dis*. **92:** 1241-1246 (2008b).
37. Kolmer, J. A. Postulation of leaf rust resistant genes in selected soft red winter wheat. *Crop Sci.* **43:** 1266-1274 (2009).

38. Kumar, S. Studies on brown and yellow rust resistance of some Indian wheat cultivars. Ph.D. Thesis, G. B. Pant University of Agriculture and Technology, Pantnagar (2013).
39. Kumar, S., Awasthi, R. P. and Kumar, J. Adult plant resistance in some Indian wheat cultivars and postulation of yellow rust resistance genes. *Indian Phytopath*. **67:** 134-137 (2015).
40. 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. *Theoretical Theor. Appl. Genet.* **114:** 1379-1389 (2007).
41. Lagudah, E. S., McFadden, H., Singh, R. P., Huerta-Espino, J., Bariana, H. S. and Spielmeyer, W. Molecular genetic characterization of the *Lr34/Yr18* slow rusting resistance gene region in wheat. *Theor. Appl. Genet*. **114:** 21-30 (2006).
42. Lagudah, E. S., Krattinger, S. G., Herrera-Foessel, S., Singh, R. P., Huerta-Espino, J., Spielmeyer, W., Brown-Guedira, G., Selter, L. L. and Keller, B. Gene-specific markers for the wheat gene *Lr34/Yr18/Pm38* which confers resistance to multiple fungal pathogens. *Theor. Appl. Genet*. **119:** 889-898 (2009).
43. Leonardo, S. V., Campos, P., Demichelis, M., Lombardo, L. A., Aurelia, R. P., Vaschetto, L. M., Bainotti, T. and Helguera, M. Identification of leaf rust resistance genes in selected Argentinean bread wheat cultivars by gene postulation and molecular markers. *Electron. J. Biotechnol*. **14(3):** 1-17 (2011).
44. Liang, S. S., Savenaga, K., He, Z. H., Wang, Z. L., Liu, H. Y., Wang, D. S., Singh, R. P., Sourdille, P. and Xia, Y. C. Quantitative trait loci mapping for adult plant resistance to powdery mildew in bread wheat. *Phytopatho.* **96:** 784-789 (2006).
45. Marasas, C. N., Smale, M. and Singh, R. P. The economic impact in developing countries of leaf rust resistance breeding in CIMMYT related spring wheat. Economic program paper, 04-01, CIMMYT, Mexico DF, Mexico (2004).
46. Martinez, F., Nicks, R. E., Singh, R. P. and Rubiales, D. Characterization of *Lr*46, a gene conferring partial resistance to wheat leaf rust. *Hereditas.* **135:** 111-114 (2001).
47. Mehta, K. C. Further Studies on Cereal Rusts in India. Imperial Council Agric. Res. New Delhi Sci. Monogr. **18:** 165pp (1952).
48. Messmer, M., Seyfarth, R., Keller, M., Schachermayr, G. M., Winzeler, M., Zanetti, S., Feuillet, C. and Keller, B. Genetic analysis of durable leaf rust resistance in winter wheat. *Theor. Appl. Genet.* **100:** 419-431 (2000).
49. McIntosh, R. A., Wellings, C.R. and Park, R.F. Wheat Rusts: An Atlas of Resistance Genes. *Australia: CSIRO*. 200 (1995).
50. McIntosh, R. A., Dudcovsky, J., Rogers, W. J., Morris, C., Applels, R. and Xia, X. C. Catalouge of gene symbols foe wheat: Supplement. In the 11th International Wheat Genetics Symposium held in Brisbane, Australia. Grain gene websites (2009).
51. McIntosh, R. A., Dudcovsky, J., Rogers, W. J., Morris, C., Applels, R. and Xia, X. C. Catalouge of gene symbols. *KOMUGI Integrated Wheat Science Database*.http://www.shigen.nig (2010).
52. McIntosh, R. A., Dudcovsky, J., Rogers, W. J., Morris, C., Applels, R. and Xia, X. C. 2011. Catalouge of gene symbols. *KOMUGI Integrated Wheat Science Database*.http://www.shigen.nig
53. McIntosh, R. A., Dudcovsky, J., Rogers, W. J., Morris, C., Applels, R and Xia, X. C. Catalouge of gene symbols. *KOMUGI Integrated Wheat Science Database*.http://www.shigen.nig (2012).
54. Muhammad, H. Identification of genes contributing to adult plant leaf rust resistance in winter wheat in Oklahoma. Ph. D. Thesis, Oklahoma State University, pp.72 (2006).

55. Nagaranjan, S. and Joshi, L. M. A historical account of wheat rust epidemics in India and their significance. *Cereal rust Bulletin*. **2:** 29-33 (1975).
56. Nayar, S. K, Bhardwaj, S. C. and Prashar, M. Slow rusting in wheat. *Annu. Rev. Phytopathol*. **2:** 271-286 (2003).
57. Oelke, L. M. and Kolmer, J. A. Genetics of leaf rust resistance in the spring wheat cultivars Alsen and Norm. *Phytopatho*. **95:** 773-778 (2005).
58. Priyamvada, R.T., Saharan, M. S., Chatrath, R., Siwach, P. and Mishra, B. STS marker based tracking of slow rusting of *Lr 34* gene in Indian wheat genotypes. *Indian J. Biotechnol*. **8:** 207-213 (2008).
59. Rao, M. V. Progress Report of All India Coordinated Wheat & Barley Improvement Project. Directorate of Wheat Research, Karnal, India, pp.104 (1989).
60. Raupp, W. J., Singh, S., Brown-Guedira, G. L. and Gill, B. S. Cytogenetic and molecular mapping of the leaf rust resistance gene *Lr*39 in wheat. *Theor. Appl. Genet***. 102**:347-352 (2001).
61. Roelfs, A. P., Singh, R. P. and Saari, E. E. Rust diseases of wheat: Concepts and methods of disease management. CIMMYT, Mexico, D. F. CIMMYT. P 81 (1992).
62. Rosenwarne, G., Singh, R. P., William, W. and Huerta-Espino, J. Identification of phenotypic and molecular markers associated with slow rusting resistance gene *Lr46*. *In Proc: 11th Int. Cereal Rusts and Powdery Mildew Conference*. Abstract 1.36 (2010).
63. 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).
64. Seyed, T. D. Phenotypic and molecular characterization of wheat leaf rust resistance gene *Lr34* in Iranian wheat cultivars and advanced lines. *Am. J. Plant Sci*. **4:** 1821-1833 (2013).
65. 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 J. Agric. Sci*. **3 (1):** 55-57 (2011).
66. Sheikh, F. A., Wani, S, H., Aziz, M. A. and Razvi, S. M. Role of Wild Relatives in Imparting Disease Resistance to Wheat Rust. *Inter J. Pure App. Biosci*. **5**(1):645-659 (2017).
67. Shah, S. J. A., Muhammad, I. and Hussain, S. Phenotypic and molecular characterization of wheat for slow rusting resistance against *Puccinia striiformis* Westend. f. sp. *tritici. J. Phytopath.***158:** 393-402 (2010).
68. Sharp, P. J., Johnston, S., Brown, G., McIntosh, R. A., Pallotta, M., Carter, M., Bariana, H. S., Khartkar, S., Lagudah, E.S., Singh, R. P., Khairallah, M., Potter, R. and Jones, M. G. K. Validation of molecular markers for wheat breeding. *Aus. J. Agric. Sci*. **52:** 1357-1366 (2001).
69. Singh, A., Pallavi, J. K., Gupta, P. and Prabhu, K. V. Identification of microsatellite markers linked to leaf rust adult plant resistance (APR) gene *Lr48* in wheat. *Plant Breed*. **130:** 31-34 (2011).
70. Singh, R. P. Genetic association between gene *Lr34* for leaf rust resistance and leaf tip necrosis in bread wheat. *Crop Sci*. **32:** 874-878 (1992a).
71. Singh, R. P. Genetic association of leaf rust resistance gene *Lr34* with adult plant resistance to stripe rust in bread wheat. *Phytopatho*. **82:** 835-838 (1992b).
72. Singh, R. P. and Dubin, H. J. Sustainable Control of Wheat Diseases in Mexico. Memorias de 1er Simposio Internacional de Trigo, 7-9 April 1997, cd Obregon, Sanora, Mexico, CIMMYT (1997).
73. Singh, R. P., Huerto-Espino, J. and William, M. H. Slow rusting gene based resistance to leaf and yellow rusts in wheat genetics and breeding at CIMMYT. In: Proc 10th Assembly of the Wheat Breeding Society of Australia Inc., Mildura, Australia, 16-21 September, 2001. Australia: Wheat Breeding Society of Australia Inc pp103-108 (2001).

74. Singh, R. P., Huerta-Espino, J., Pfeiffer, W. and Igueroa-Lopez, P. Occurrence and impact of a new leaf rust race on durum wheat in Northwestern Mexico from 2001 to 2003. *Plant Dis*. **88:** 703-708 (2004).
75. 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).
76. 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.Singh, R. P. and Rajaram, S. 1991. Resistance to *Puccinia recondita* f. sp. *tritici* in 50 Mexican bread wheat cultivars. *Crop Sci.* **31:** 1472-1479 (2000).
77. Singh, R. P., Mujeeb-Kazi, A. and Huerta-Espino, J. *Lr46*: A gene conferring slow rusting resistance to leaf rust in wheat in. *Phytopatho*. **88:** 890-894 (1998).
78. Singh, S. and Bowden, R. L. Molecular mapping of adult-plant race-specific leaf rust resistance gene *Lr12* in bread wheat. *Mol. Breed.* **28:** 137-142 (2011).
79. Sivasamy, M., Kumar, J., Jayprakash, P., Vikas, V. K., Nisha, R., Peter, J. and Vinod. Molecular and phenotypic diagnostics applied to verify the presence of rust resistance genes *Lr24*, *Yr15*, and *Sr2* in a high-yielding bread wheat genotype suited for cultivation in Central India. *Annual Wheat Newsletter*. **58:** 81-85 (2010).
80. Spielmeyer, W., McIntosh, R. A., Kolmer, J. and Lagudah, E. S. Powdery mildew resistance and *Lr34/Yr18* genes for durable resistance to leaf and stripe rust, co-segregate at a locus on the short arm of chromosome 7D of wheat. *Theor. Appl. Genet***. 111:** 731-735 (2005).
81. Stubbs, R. W., Prescott, J. M., Saari, E. E. and Dubin, H. J. Cereal disease methodology manual, p. 46. Mexico, DF, CIMMYT (1986).
82. Suenaga, K., Singh, R. P. and William, H. M. Microsatellite markers for genes *Lr*34/*Yr*18 and other quantitative trait Loci for leaf rust and stripe rust resistance in bread wheat. *Phytopatho*. **93:** 881-890 (2003).
83. Sun, X., Bai, G., Carver, B. F. and Bowden, R. Molecular markers for wheat leaf rust resistance gene *Lr41*. *Mol. Breed.* **23:** 311-321 (2009).
84. Urbanovich, Y., Malyshev, S. V., Dolmatovich, T. V. and Kartel, N. A. Identification of leaf rust resistance genes in wheat (*Triticum aestivum* L.) cultivars using molecular markers. *Russ. J. Genet.* **42(5):** 546-554 (2006).
85. Vida, G., Gal, M., Uhrin, A., Veisz, O., Syed, N. H., Flavell, A. J., Wang, Z. L. and Bedo, Z. Molecular markers for the identification of resistance genes and marker-assisted selection in breeding wheat for leaf rust resistance. *Euphytica.* **170:** 67-76 (2009).
86. William, M., Singh, R. P., Huerta-Espino, J., Ortiz Islas, S. and Hoisington, D. Molecular marker mapping of leaf rust resistance gene *Lr46* and its association with stripe rust resistance gene *Yr29* in wheat. *Phytopatho.* **93:** 153-159 (2003).
87. Zarandi, F., Afshari, F. and Rezaei, S. Study of resistance components at seedling stage and field resistance to leaf rust in some elite wheat lines. *Seed and Plant Improvement J*. **25:** 569-584 (2009).
88. Zeven, A. C., Knott, D. R. and Johnson, R. S. Investigation of linkage drag in near isogenic lines of wheat by testing for seedling reaction to races of stem rust and yellow rust. *Euphytica*. **32:** 319-327 (1983).
89. Zhang, H. and Knott, D. R. Inheritance of adult plant resistance to leaf rust in six durum wheat cultivars. *Crop Sci.* **33:** 694-97 (1993).
90. Zhang, J. X., Singh, R. P., Kolmer, J. A., Huerta-Espino, J., Jin, Y. and Anderson, J. A. Genetics of leaf rust resistance in brambling wheat. *Plant Dis*. **92:** 1111-1118 (2008).