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MOLECULAR BREEDING FOR ENHANCING RESILIENCE AGAINST BIOTIC AND ABIOTIC STRESS IN MAJOR CEREALS

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SUMMARY

Molecular breeding includes marker-assisted selection, marker-assisted backcross breeding, along with other newer breeding approaches, such as marker-assisted recurrent selection and genomic selection. Marker-assisted selection is used to detect the presence or absence of genes in lines, cultivars, breeding populations and hence, accelerates the selection procedure in comparison to other conventional approaches. Researchers have identified and precisely mapped several genes through association with DNA markers. Genes linked to DNA markers include those governing resistance to biotic stresses and tolerance to abiotic stresses; for example in rice (*Oryza sativa* L.) for blast, bacterial blight, brown plant hopper, drought, submergence, salinity; in wheat (*Triticum aestivum* L.) for rusts, pre-harvest sprouting, and drought and heat tolerance; and in maize (*Zea mays* L.) for turcicum leaf blight, polysora rust, banded leaf sheath blight and drought tolerance. Incorporation of major genes or quantitative trait loci (QTL) into widely adapted cultivars has been achieved via marker-assisted backcross breeding. Marker-assisted pyramiding for 2 or more resistance genes provides opportunities for building resilience for serious diseases and insects. For complex traits such as drought, new strategies, such as marker-assisted recurrent selection and genomic selection are employed to increase precision and to reduce cost of phenotyping. Thus, molecular-breeding approaches offer ample opportunities for plant breeders to develop stress-resilient high-yielding cultivars. Furthermore, molecular and conventional breeding are not mutually exclusive; instead, they are complementary under most breeding schemes. This review highlights developments in molecular breeding relative to stress resilience in rice, wheat and maize.

Key words: Rice, wheat, maize, cold, molecular breeding, submergence, diseases, drought, heat, salinity

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INTRODUCTION

Plant breeding can be defined as a science and technology that has evolved gradually during the past 10,000 years. It started with collection and selection of wild plants by primitive man and encompassed during 1700-1800 hybridization, selection and evolution through natural selection. Subsequently, Mendelian and quantitative genetics, mutation, polyploidy (1900s), gene and molecular design-based science, i.e., gene cloning, direct gene transfer, marker-assisted selection (MAS), marker-assisted backcrossing (MABC), omics and

arrays, genomics-assisted breeding (2000s and beyond) became part of plant breeding. With the development of these modern molecular breeding tools, which will be discussed further in this review, plant breeding is becoming ever more precise, more efficient, easier and faster (Phillips ,2006). Traditional breeding approaches that rely on extensive phenotypic screening methods are effective but delay production of climate-resilient germplasm and also are not suitable for making rapid improvement in tolerance to multiple stresses. Hence, molecular breeding offers the opportunity to increase the speed and efficiency of plant breeding (Whitford *et al*., 2010). It lays the foundation for modern crop improvement in the 21st century (Moose and Mumm, 2008) and simultaneously helps to identify superior gene combinations, leading to significant disease resilience. The term molecular breeding is used collectively for several breeding strategies, such as MAS, MABC, marker-assisted recurrent selection (MARS) and genomic selection (Ribaut *et al*., 2010). Molecular breeding explains the application of molecular biotechnological strategies on the basis of genotypic assays used either to improve or to alter plant traits (Jiang, 2013). Marker-assisted selection means selection of alleles of interest precisely and MABC is the incorporation of one or more alleles from one genetic background into another background, across all gene pools. Marker-assisted recurrent selection is the identification of several regions in the genome that are involved in complex trait expression and selection of those regions to accumulate favorable alleles from best genotypes within a single population or across related populations (Ribaut *et al*., 2010). Genomic selection is selection on the basis of genome-wide molecular markers linked with the trait of interest (Bernardo and Yu, 2007). Molecular breeding strategies reduce the crop selection cycles by increasing genetic gain per cycle; hence accumulating favorable alleles at target loci quickly (Delannay *et al*., 2012). Among molecular breeding approaches, all these approaches are widely and successfully used except genomic selection, which is at the beginning stages in plants (Cooper *et al.,* 2006, Crosbie *et al.,* 2006; Eathington *et al.,* 2007). Molecular breeding approaches are most commonly used by the private sector and by some national and international institutions (Dwivedi *et al.,* 2007; Ragot and Lee 2007) as adoption of molecular breeding approaches is hindered because of lack of resources at various levels, i.e., lack of high throughput capacity, analysis tools, information systems and technically expert personnel (Delannay *et al*., 2012).

Major cereal crop i.e., rice, wheat and maize have been predominantly used as staple food around the world since time immemorial. Plant cultivar development and production are affected by several abiotic and biotic stresses all across the world (Wani *et al.,* 2013; Pathak *et al*., 2014). Molecular breeding has led to development of plants resilient to various biotic (Roswarne *et al.,* 2012, 2013, Yang *et al.,* 2013) and abiotic stresses (Gosal *et al.,* 2009). The potential applications of molecular breeding in crop plants for developing disease resilience have been well discussed by many (Babu *et al.,* 2004, Jena *et al.,* 2008; Collard and Mackill, 2008; Ibitoye and Akin-Idowu, 2010; Xu *et al.,* 2013). Identification and mapping of several genes and quantitative trait loci (QTL) associated with abiotic and biotic stress tolerance in major cereals have provided an abundance of DNA marker-trait associations (Collard and Mackill, 2008) and have assisted conventional breeders to develop stress-tolerant cultivars with precision and in less time duration. Thus, efforts of plant breeders, molecular biologists and scientists in meeting the food requirements on a sustainable basis for ever-increasing population are facilitated. This review discusses various molecular breeding strategies and successful examples from cereals.

MOLECULAR BREEDING STRATEGIES

Marker assisted selection

The use of molecular markers for selection of plants carrying desirable genomic regions involved in the expression of a trait of interest governed by both major genes and QTL is referred to as marker-assisted selection (MAS) (Choudhary *et al.,* 2008). The term 'MAS' was first used by Beckmann and Soller (1986). Since

then, accelerated development and availability of molecular markers in plants have made MAS into a major molecular breeding strategy. Because of the general complexity of abiotic stress tolerance and the difficulty in phenotypic selection, MAS is considered an effective approach to improve tolerance. When a tightly linked marker which reliably predicts a trait phenotype is detected, it may be used for MAS. The MAS has several advantages over conventional phenotypic selection, i.e., it is quicker than phenotypic selection as desirable plants are selected at the seedling stage hence saving time, resources and efforts. With MAS, individual plants are selected based on their genotype. Prior to a breeding program and line/genotype development, DNA marker data allows certain applications i.e., assessment of genetic diversity, confirmation of hybrids, study of heterosis and identification of desirable genomic regions under selection (Collard and Mackill, 2008). Main important considerations of DNA markers in MAS include tightly linked marker (less than 5 centiMorgans (cM)), quantity and quality of DNA required in MAS, simplicity in marker assay procedure, cost effectiveness and highly polymorphic marker system (Collard and Mackill, 2008). Molecular marker systems have evolved during last decade (approximately 30 years) from hybridization based (1980s, restriction fragment length polymorphisms (RFLP)), PCR based markers (1990s i.e., random amplified polymorphic DNA (RAPD), and amplified fragment length polymorphism (AFLP), to present day markers of choice, e.g., simple sequence repeat (SSR) eand single nucleotide polymorphism (SNP). Discovery and introduction of efficient, high throughput and low-cost next generation sequencing (NGS) technologies have accelerated and revolutionized plant breeding. The NGS technologies are used for accelerating detection of genome-wide polymorphism (Mir and Varshney, 2013). These trends would accelerate the adoption of procedures, which require high density, genome-wide markers, such as genomic selection (Mir and Varshney, 2013).

Adoption and impact of MAS is still at early stages of DNA marker-technology development. For the success of MAS, the accuracy of QTL mapping is of utmost importance. Factors like population size, level of replication used to generate phenotypic data, sampling bias and large confidence intervals have important implications for MAS, since the basis for selecting markers is accurate determination of the effect and position of a QTL. Other issues involved in successful MAS include insufficient linkage between marker and desirable gene/QTL, QTL x environment interaction effects, limited marker polymorphism, poor phenotyping system, high cost, application gap between plant breeding institutes and research laboratories and knowledge gap among plant breeders, scientists, molecular biologists and other disciplines, and resource limitations at various levels (Collard and Mackill, 2008; Xu and Crouch, 2008; Ribaut, Vicente and Delannay 2010; Delannay *et al.* 2012). What leads to increased adoption of MAS in plant breeding programs are rapid genomics research growth, new high-throughput marker genotyping platforms, a large number of markers and parallel development of user-friendly software and databases for storing of marker data and QTL data, e.g., 'Gramene' (http://www.gramene.org/, 'GrainGenes' (http://wheat.pw.usda.gov/GG3/) in cereals and maize database (http://www.maizegdb.org/) (Collard and Mackill, 2008).

Marker-assisted backcross breeding (MABC)

Backcross is a most common breeding method used for incorporating one or several genes of interest into another variety. The recurrent parent used in backcrossing has a large number of desirable attributes but is deficient in only a few characteristics (Allard, 1999). Backcross breeding was popular in some crops during 1930-1960 (Stoskopf *et al*., 1993). Similarly, MABC aims to transfer one or more desirable genes/QTL from one genetic source (donor parent) into a superior, adapted, elite breeding line (which serves as a recurrent parent) to improve the targeted trait with the help of markers. Unlike traditional backcrossing, marker-assisted backcrossing is based on the marker alleles linked to gene(s)/QTL of interest instead of on phenotypic performance of target trait (Jiang, 2013). Marker-assisted backcrossing

is known to improve the efficiency of backcross breeding when the phenotype of the gene of interest cannot be easily ascertained. Then the backcross (BC) progeny possessing a marker allele from donor parent at a locus near or within the desirable gene can be selected with good probability of carrying the gene. Markers can be used to select BC progeny with less of donor parent genome outside the desirable region and markers can be used to select rare progeny that are a result of recombination near the desirable gene, thus minimizing linkage drag (Babu *et al.,* 2004).

The MABC is accomplished in 3 levels (Holland, 2004). In the first level, known as 'foreground selection', markers are used for screening the target gene or QTL (Hospital and Charcosset, 1997). Foreground selection is used for screening recessive alleles, which is time-consuming when conventional methods are used. Also selection is carried out at seedling stage, allowing selection of only those plants that carry the gene of interest and bypassing laborious procedures of phenotypic screening (Collard and Mackill, 2008). The second level of MABC, known as 'recombinant selection', involves selection of those backcross progenies that have had recombination events between the flanking markers and loci of interest. The size of introgression, i.e., the donor chromosome having the target locus, is reduced by this selection. In conventional backcross breeding, the chromosome segment from donor remains large even after many backcross generations (>10; Ribaut and Hoisington, 1998; Salina *et al.,* 2003). However, in MABC, with the help of flanking markers (e.g., < 5 cM on either side of target gene), this donor chromosome segment (linkage drag) is reduced (Hospital, 2005). Recombinant selection is performed usually by using 2 backcross generations (Frisch *et al*., 1999b; Collard and Mackill, 2008) because double recombination events on both sides of target locus are usually rare. Then the third level of MABC, known as background selection, involves selecting backcross progenies with the maximum of recurrent parent genomic region by utilizing genome-wide dense molecular markers (Hospital and Charcosset, 1997; Frisch *et al.,* 1999b). These genome-wide dense markers are not linked to target gene or QTL and hence selection is carried against the donor genomic segment (Collard and Mackill, 2008). Hence, background selection is very useful in accelerating the recovery of the recurrent parent's genetic complement, which otherwise takes much longer (6 or more backcross generations) via the conventional backcross method (Collard and Mackill, 2008). In MABC, recurrent parent genome is recovered in BC_2 or BC_3, BC_4 generation (Visscher *et al.,* 1996; Hospital and Charcosset 1997; Frisch *et al.,* 1999a, b).

Advantages of MAS (Collard and Mackill, 2008):

- allows selection for all kinds of traits at seedling stage only, thus it is faster and more accuratethan phenotypic selection.
- is not influenced by genotype x environment interaction. Hence, it can be performed in greenhouse and off-season nurseries.
- is carried out using co-dominant markers, i.e., SSR and SNP, which allow selection of homozygous or heterozygous individuals.
- The presence of multiple genes governing a particular trait can be un-ambiguously established.

Marker-assisted gene pyramiding (MAGP)

Assembling of more than 2 desirable genes from 2 or more donors into a single genotype or line for a specific trait is referred to as marker-assisted gene pyramiding, which enhances trait performance by combining 2 or more complementary genes and rectifies deficits by introgression of genes from donor sources and hence increases the durability of disease resistance (Collard and Mackill, 2008). With the advent of molecular breeding, further new approaches, such as genomic selection and MARS are developed for overcoming the limitations of MAS, MABC, particularly when multiple QTL control the expression of complex traits.

Marker-assisted recurrent selection (MARS)

Recurrent Selection is cyclical selection, evaluation and recombination in populations,

which aims to increase favorable allele frequency; and when markers are involved, it is called MARS, wherein genome dense markers linked with multiple favorable traits (gene/QTL) of interest from different sources are recognized and then selection is carried out based on genomic regions involved in complex trait expression so that best genotypes in a population are assembled (Ribaut *et al.,* 2010). It allows selection at genotypic level and intermating for first selection cycle during same crop season and hence improves efficiency and accelerates the conventional selection (Jiang *et al.,* 2007a). MARS allows phenotyping of F_2-derived generations (i.e., F_4 or F_5) and then genotyping of F_2 or F_3 (for estimating maker effect) followed by 2 to 3 cycles of recombination (Eathington *et al.,* 2007) established on the basis of presence or absence of marker alleles for minor QTL. Identification of QTL is done from a base population which is developed by crossing superior lines. Further, lines possessing best, superior and required alleles for major QTL are crossed to accumulate those alleles in one background. Derived lines from crossing are screened on phenotypic basis for selecting superior lines for varietal development. Multiple major and minor QTL are captured as a result of MARS as compared with MABC, thus harnessing more genetic gain (Bernardo and Charcosset 2006). Thus, MARS is a forward breeding procedure for accumulating several QTL governing abiotic and biotic tolerance in crops (Ribaut *et al.,* 2000; Ragot *et al.,* 2000; Crosbie *et al.,* 2006; Ribaut *et al.,* 2010).

Genomic selection

Concurrent selection of highly saturated genome-dense markers, some of which are expected to be in linkage disequilibrium with all genes in a genome is defined as genomic selection (Meuwissen, 2007). High throughput markers and novel statistical tools, along with highly efficient computing methods, are basic requirements for genomic selection. SNP markers and newer marker technologies have made genomic selection in plants feasible (Jiang 2013). Genotypic data made available from genome-wide dense markers are used to estimate complex traits, such as biotic resistance and abiotic tolerance, with much precision to allow selection on that estimation only. Selection of stress-resilient lines is established on the basis of values called genomic estimated breeding value (Nakaya and Isobe, 2012). The genomic estimated breeding values (GEBVs) are presumed values computed from novel statistical tools established on the basis of genome-dense highly saturated markers (Meuwissen *et al.,* 2001).

Prediction of the genetic merit of an individual is referred to as estimated breeding value (EBV). It is based on the concept that information on performance from offspring might more accurately indicate the real breeding value of an individual than using its own performance. EBVs are calculated on the basis of pedigree, performance of the individual (selection candidate) and progeny test results. Whereas genomic estimated breeding value (GEBV) is the prediction of the genetic merit of an individual based on its genome. GEBVs are estimated using the genomic relationship matrix (instead of the pedigree) in combination with the EBV or phenotypes of an individual. There is a wide variety of methods to estimate GEBVs that primarily differ in their assumptions about the genetic architecture of the trait of interest (Jonas and Koning, 2013). Statistical models, i.e., best linear unbiased prediction (BLUP), ridge and Bayes regression would help in prediction of genomic estimated breeding value in genomic selection (Nakaya and Isobe, 2012). Genotyping and phenotyping of individuals first takes place from training population and then data are subjected to statistical analyses. Then, genomic estimated breeding values are computed and selection of best individuals (validation population) is done to develop a breeding population. Figure 1 illustrates general concept of genomic selection. Also, the genomic estimated breeding values are calculated from marker effects rather than QTL effects (Goddard and Hayes, 2007).

Earlier genomic selection studies were carried out in animals (Jannink *et al.,* Iwata 2010; Goddard and Hayes, 2007), but now it is gaining importance in plants also (Guo *et al.,* 2011; Heffner *et al.,* 2010, 2011; Bernardo 2010; Bernardo and Yu 2007; Lorenzana and Bernardo 2009; Zhong *et al.,* 2009; Wong and Bernardo

2008). Genomic selection in plants was first demonstrated for maize, *Arabidopsis thaliana* and barley by Lorenzana and Bernardo (2009). Studies have demonstrated that genomic selection provides greater accuracy as compared with studies based on pedigree information only (Jannink *et al.,* 2010).

Genomic selection experiments in oil palm (population size of 50) gave good results than as compared from phenotypic selection and MARS in terms of time and gain per unit cost (Wong and Bernardo, 2008). Genomic selection is recognized as a novel, valuable and powerful tool for plant breeding programs now for developing abiotic and biotic stress-resilience in plants. However, lack of knowledge of statistics and simulation studies for practical use of genomic selection in plant breeding programs has limited popularity of this approach (Nakaya and Isobe, 2012), also limited resources for public sector breeding has prevented use of GS because gentoyping costs are huge. Breeder-friendly and easily understandable software packages for genomic selection analysis and statistical formulae for estimation of genomic estimated breeding values need to be developed to facilitate and enhance application of genomic selection in plant breeding.

There are still some issues related to application of genomic selection when breeders must deal with thousands or more crosses or populations simultaneously (Jiang, 2013). Hence focus needs to be shifted towards additional applications of genomic selection; its usefulness needs to be demonstrated by practical and statistical ways instead of theoretical ways. Also cost effectiveness and precision of genomic selection need to be evaluated for it to be applied smoothly in practical plant breeding experiments (Heffner *et al.,* 2009).

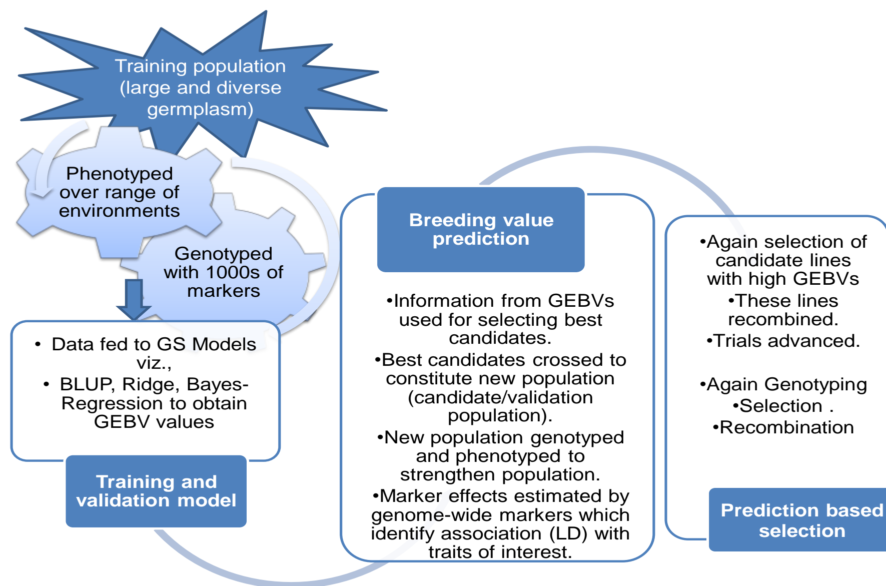

Figure 1. General concept of genomic selection (GS).

STRESS RESILIENCE IN CEREALS

Molecular breeding for biotic stresses in rice

Biotic stresses in rice, *i.e*., blast, bacterial blight and plant hopper result in huge production losses. Resistance genes to combat these stresses have been introgressed through MAS into susceptible cultivars (Jena and Mackill, 2008).

Blast resistance

Rice blast disease is a major biotic stress worldwide. Several DNA markers corresponding to major race-specific blast-resistance genes have been identified (Fjellstrom *et al.,* 2004). Major gene resistance can be risky as evolution of new races of the pathogen breaks down the major gene resistance; thus, focus is given to partial resistance (Wisser *et al.,* 2005; Wu *et al.,* 2004). Considerable number of blast-resistance major genes have been identified and mapped. InDel and polymerase chain reaction (PCR) specific marker sets for several resistance genes are accessible for blast resistance molecular breeding (Hayashi *et al.,* 2006). Marker-assisted pyramiding (MAP) of resistance genes *Pi2* (using STMS marker, RM208) and *Pi9* (using STMS marker, AP5930) from donors C101A51 $^{\text{Pi-2}}$ and *O. minuta* $^{P\text{-}9}$ in rice varieties 'Kalinga III' and 'Vandana' in Central Rice Research Institute (CRRI) Cuttack has been achieved to reduce susceptibility to blast. Likewise, pyramiding of genes *Pi1* (using STMS marker, RM224), *Pi2* (using STMS marker, RM208) and *Pi4 (Pita)* (using STMS marker, RM247) in cultivar 'CO39' in University of Agricultural Sciences, Bangalore using donors LAC23$^{Pi\text{-}1}$, 5173$^{Pi\text{-}2}$ and Pai-kan-tao$^{Pi\text{-}4}$ resulted in new improved CO39$^{Pi\text{-}1+P\text{-}2+P\ \ 4}$ (Hittalmani *et al.*, 2000). The MABC has been successfully utilized in transferring blast-resistance genes *Pi-Kh* (using STMS marker, RM206) and *Piz-5* (using STMS marker, AP5930) into the parental lines, i.e., Pusa 6B and PRR 78 of the popular superfine grain aromatic rice hybrid Pusa RH10. A simultaneous but stepwise transfer method was adopted for transferring the resistance genes *Pi-kh* (using STMS marker, RM206) and *Piz 5* (using STMS marker, AP5930) from the donor Tetep and C101A51, respectively. The improved versions of Pusa 6B and PRR 78 with 2 blast-resistance genes *Pi-kh* and *Piz-5* each were achieved via MABC at the Division of Genetics, IARI, New Delhi (Prabhu *et al.,* 2009). The MABC was employed by Singh *et al.* (2012) to incorporate blast resistance into a popular high-yielding aromatic rice hybrid, Pusa RH10 and its parents Pusa6B and PRR78 Blast-resistance genes, i.e., *Piz-5* (using STMS marker, AP5930) and *Pi54* (using STMS marker, RM206), from the donor lines C101A51 and Tetep were introgressed into PRR78 to develop Pusa1602 (PRR78 + *Piz5*) and Pusa1603 (PRR78 + *Pi54*) with linked molecular markers, AP5930 and RM206, respectively.

Bacterial leaf blight resistance

Significant number of bacterial leaf blight (BLB) resistance genes have been identified using molecular markers, some of which have been cloned (*Xa27, Xa26, Xa21*, *xa13, xa5*, *Xa1*) (Jena and Mackill, 2008). Availability of numerous DNA markers linked with resistance genes enables incorporation and pyramiding of these genes into elite susceptible rice cultivars. Marker-assisted pyramidying has enabled development of *indica* rice cultivars incorporated with BB-resistance genes, i.e., *Xa4* and *Xa21* (Jena and Mackill 2008). Using MAS, resistance genes, *xa5*, *xa13* and *Xa21*, have been pyramided into PR-106 (an *indica* rice cultivar) (Singh *et al.,* 2001). Similarly, in the Philippines, combinations of *Xa4, xa5* and *Xa21* were pyramided into 2 rice cultivars (NSICRc142 and NSICRc154). Also same gene combination has been pyramided into another susceptible cultivar IR64 using MAS (Toenniessen *et al.,* 2003). At Punjab Agricultural University (PAU) efforts were made for transferring blast-resistance genes, i.e., *xa5* + *xa13* + *Xa21*, into a popular rice cultivar PR-106 (Singh *et al.,* 2001). Other examples include pyramiding of *xa13* and *Xa21* into Pusa Basmati 1 ('PB1') from IRBB55, using flanking Sequence Tagged Sites (STS) markers, RG136 and pTA248 (Joseph *et al.,* 2004). Improved Pusa Basmati-1 ('IPB-1') was developed from Pusa Basmati-1 via MABC (Gopalakrishnan *et al.,* 2008). Also, this same gene combination (*xa5, xa13* and *Xa21*) was incorporated into

BPT5204 (Samba Mahsuri) and improved Samba Mahsuri was developed and released in India (Sundaram *et al.,* 2008). Improvement of parental lines of a most popular aromatic rice hybrid, Pusa RH10, i.e., Pusa 6B and PRR 78, via MABC was achieved by incorporating resistance against bacterial blight by genes *xa13* and *Xa21* (Basavaraj *et al.,* 2010) from donor improved Pusa Basmati-1 and by incorporating *Pi-kh* and *Piz-5* against blast (Singh *et al.,* 2012) from donors Tetep and C101A51. Production of basmati rice is mostly affected by BB, blast and sheath blight (ShB). Therefore, MABC was utilized to develop biotic stress-resilient basmati rice by using blast-resistance gene *Pi54* and ShB resistance QTL, qSBR11-1 (from 'Tetep' used as donor parent) and BB resistance genes *xa13* and *Xa21* (from 'Improved Pusa Basmati 1', used as recurrent parent) (Singh *et al.,* 2012).

Brown plant hopper resistance

A significant number of genes have been identified for brown plant hopper (BPH) resistance. Land races, *indica* cultivars and several wild species, i.e., *Oryza. minuta, O. australiensis* and *O. officinalis*, usually serve as sources of resistance against brown plant hopper (Jena *et al.,* 2006; Rahman *et al.,* 2009). Fine-mapped genes, such as *Bph21, bph20, Bph19, Bph18, Bph15, Bph14, Bph9, bph3, Bph2* and *Bph1*, have been utilized in BPH resistance MAS programs (Rahman *et al.,* 2009; Zhang 2007; Jena *et al.,* 2006; Chen *et al.,* 2006; Sharma *et al.,* 2003, 2004). In tropical *indica* and temperate *japonica* rice cultivars, genes *Bph18 and Bph1*, *bph2* have been incorporated via MAS for brown plant hopper resistance (Jena *et al.,* 2006). *Bph1* and *bph2* provide resistance to the evolved Japanese biotypes of BPH (Sharma *et al.,* 2004). Also, enhanced resistance was provided by *Bph18* to new Korean biotypes (Jena *et al.,* 2006). *Bph18* gene derived from *O. australiensis* was incorporated into an elite but highly susceptible japonica cultivar, Junambyeo via MABC (Suh *et al.,* 2011).

Molecular breeding for abiotic stresses in rice

Abiotic stresses, i.e., drought, submergence, cold stress and unproductive soils affect rice production and productivity. Traditional landraces of rice are potential sources of genes for tolerance to these stresses, but the transfer of genes from these useful sources is hindered by the complex nature of these traits (Jena and Mackill, 2008). However, QTLs responsible for tolerance to abiotic stresses discussed below have already been identified, thus allowing molecular breeding approaches for introgression into stress-susceptible rice varieties (Collard and Mackill, 2008; Steele *et al.,* 2006).

Drought tolerance

Molecular breeding approaches can accelerate breeding for drought tolerance in plants as it is a complex trait. At IRRI, Moroberekan and IR20 crosses were made during 1984 to identify lines with thick and deeper root system. Shashidhar *et al.* (2001) reported 2 flanking markers, i.e., OPBH14 and RM201, to be linked with long roots in rice. An upland rice variety, released as PY 84 (Birsa Vikas Dhan 111) in Jharkhand (Shashidhar *et al.,* 2012), was bred using MABC by selecting for root QTL on chromosome 9 (using SSR markers RM242 – RM201) for increased root length under drought conditions. This variety was bred using MAS in combination with participatory or client-oriented breeding. This variety is drought tolerant, early maturing, high yielding and possesses good grain quality (Shashidhar *et al.,* 2012). Also MABC and MAGP were used to incorporate QTL for root length and root thickness into Kalinga III (*indica*) for drought tolerance using Azucena (*japonica*) Philippines as donor parent (Steele *et al.,* 2006). Flanking markers, RM242 and RM201, detected target segment on chromosome 9, which increased root length under drought stress (Steele *et al.,* 2006). Plentiful QTLs for drought tolerance have been identified and markers are used to map and tag them for developing drought-resilience (Venuprasad *et al.,* 2002). A QTL related to spikelet fertility under stress conditions was identified on chromosome 9 (Yue *et al.,* 2006; Li *et al.,* 2005; Courtois *et al.,* 2000). 'Lemont' (*japonica*) when used as a donor parent in MABC provided drought tolerance to Teqing'

(*indica*) (Xu *et al.,* 2005). A QTL (*DTY12.1*) was identified by Bernier *et al.* (2007) on chromosome number 12 in Vandana/Way Rarem population. This QTL explained 51% of genetic variance and was mapped to 2.7 Mb using flanking SSR markers RM28048 and RM28166. Bernier *et al.* (2009) reported consistent effects of this QTL in target locations. Ghimire *et al.* (2012) reported a major-effect QTL, *qDTY1.1*, for grain yield under drought on chromosome 1 between markers RM431 and RM12091 in both populations (Dhagaddeshi × Swarna and Dhagaddeshi × IR64 populations). Several QTL have been reported, i.e, *qDTY1.1* in Nagina22/Swarna and Nagina22/IR64 (Vikram *et al.,* 2011) and *qDTY6.1* in Apo/IR72 and Vandana/IR72 (Venuprasad *et al.,* 2011).

Submergence tolerance

In coastal areas, rice productivity is affected by submergence conditions caused by poor drainage and heavy rains. Mackill *et al.* (1996) reported that 15 M ha of area under rice in South Asia and South East Asia were submerged, resulting in losses of one billion US dollars. Rice varieties are easily adversely affected when submerged during early and vegetative stages; high mortality occurs within 5 to 7 days. Thus, introducing submergence-tolerant varieties for stabilizing rice productivity in rainfed areas is the utmost priority (Mackill *et al.,* 1996). *Sub1* QTL has been identified for submergence tolerance and fine mapped on rice chromosome number 9 in FR13A, a submergence-tolerant cultivar. This QTL accounts for 70% of phenotypic variation under stress conditions (Xu *et al.,* 2000). The *Sub1* gene is associated with the "ethylene response factors" gene family identified as *Sub1 A*, *B* and *C.* Varieties with *Sub1* have less carbohydrate reduction and high fermentation of alcohol, thus providing sufficient energy for plant processes under submergence (Singh *et al.,* 2011). *Sub1* has been incorporated into "mega varieties" like Samba Mahsuri, IR64, Thadokkam 1 (TDK1), CR1009, BR11 and Swarna in India and Bangladesh via MABC for submergence tolerance (Xu *et al.,* 2006; Neeraja *et al.,* 2007, Septiningsih *et al.,* 2009; Singh *et al.,* 2009).

Cold tolerance

Breeding for tolerance to low temperatures in rice during both vegetative and reproductive stages is an important breeding objective in temperate and highlands of subtropical and tropical areas (Jena and Mackill, 2008). Rice yields are affected by male sterility induced by cold stress. The booting stage in rice is most sensitive to low temperatures, causing degeneration of the young microspores and increasing in tapetal cell size (Saito *et al.,* 2010). Several QTL for cold tolerance have been mapped in a population developed from M202 (*japonica*) and IR50 (*indica*) (Andaya and Mackill, 2003c). The QTL were mapped on chromosomes 11, 7 and 1 from Koshihikari (cold-tolerant *japonica*) and Akihikari (sensitive *japonica*) (Takeuchi *et al.,* 2001). Also QTL for cold tolerance were mapped on chromosomes 11, 10, 5, 4 and 1 in near-isogenic line (NIL) population between a cold-tolerant *japonica*, Kunming x iaobaigu and a cold-sensitive *japonica*, Towada (Zeng *et al.,* 2009; Xu *et al.,* 2008. Significant QTL have been identified using different populations in different crosses (Andaya and Mackill, 2003b; Andaya and Mackill 2003a; Andaya and Tai 2006; Andaya and Tai 2007; Han *et al.,* 2004; Lou *et al.,* 2007), which lead to tolerance and hence are utilized in developing tolerant cultivars via molecular breeding approaches. Saito *et al.* (2010) mapped QTL *Ctb1* to a 17-kb region containing 2 genes encoding an F-box protein expressed in young panicles and a serine/threonine (ser/thr) protein kinase expressed in leaves and young panicles cloned from a cold-tolerant variety, Norin-PL8 and then incorporated into a cold-sensitive variety, Hokkai241 and a line named BT4-74-8.

Salinity tolerance

Rice cultivars are sensitive to saline environments; although some *indica* rice types, such as Kala-rata, Nona Bokra and Pokkali, can withstand salinity (Yeo *et al.,* 1990). Salinity tolerance again is a complex trait, which involves many processes, such as sodium discharge from roots, movement of sodium between shoots and roots and assimilation of

sodium in vacuoles and older tissues (Thomson *et al.,* 2007). There are numerous genes conferring tolerance to salinity, but *Saltol* QTL associated with the Na-K ratio under salinity stress (low Na^+ to K^+ ratio; high K^+ and low Na^+ adsorptions) is considered a major QTL for salinity tolerance at the seedling stage. *Saltol* is fine-mapped on short arm of chromosome 1 by use of flanking markers RM23 and RM140 from 80 recombinant inbred lines (RILs) developed from a cross between IR29 (sensitive) and Pokkali (tolerant). *Saltol* explained 64 to 80% of the phenotypic variance (Bonilla *et al.,* 2002). It has also been detected in other varieties (Takehisa *et al.,* 2004). Another QTL, *SKC1* coding HKT-type transporters, controls K^+ homoeostatis under stress in tolerant varieties (Ren *et al.,* 2005) and can be used for breeding salinity-tolerant cultivars. Thomson *et al.* (2010) analyzed 100 SSR markers in 140 IR29/Pokkali RILs, which confirmed the location of the *Saltol* QTL on chromosome 1 and identified additional QTL associated with tolerance, providing an opportunity for MABC to improve salinity tolerance of popular varieties, followed by marker-assisted gene pyramiding for areas with high salt stress.

Tolerance to adverse soils

Quantitative trait loci for phosphorous, aluminum and iron deficiency and toxicity have been identified (Wissuwa *et al.,* 2002; Nguyen *et al.,* 2003; Mackill 2006). A major QTL *Phosphorus uptake 1* (*Pup1*; derived from Kasalath) associated with phosphorous (P) uptake in deficient environments is mapped on chromosome 12 (Wissuwa *et al.,* 1998). *Pup1* was placed in a 3-cM interval flanked by RFLP markers S14025 and S13126, which is within 1 cM of the position identified in the original QTL mapping experiment (Wissuwa *et al.,* 2002). Kasalath was identified during an experiment consisting of 30 diverse rice genotypes in Japan in a phosphorous-deficient soil. A major gene *OsPSTOL1* (*Phosphorus starvation tolerance 1*) in this QTL enhances root growth. *OsPSTOL1* encodes protein kinase [functional ser/thr], which resembles receptors, such as kinases (Gamuyao *et al.,* 2012). *Pup1* enhances *P* uptake (Wissuwa *et al.,* 2002) and increases yield (up to 4% higher grain weight plant^{-1}) (Chin *et al.,* 2010). Kasalath and NILC443 have been used in breeding programs as donors for varieties, such as Batur, Dodokan and Situ Bagendit. NIL14-4 was used as the donor in crosses with IR64 and IR74 populations (Chin *et al.,* 2011).

Molecular breeding for biotic stresses in wheat

Stem rust (*Puccinia graminis* Pers f. sp. *tritici* Eriks and Henn.), leaf rust (*Puccinia triticina*) and stripe rust (*Puccinia striiformis* West) are among major wheat diseases causing economic crises and resulting in significant yield losses all over the world (Sawhney 1994).

Stem rust resistance in wheat

Stem rust of wheat caused by *Puccinia graminis* f. sp. *tritici* has been brought under control primarily by growing resistant varieties. The eradication of alternate hosts of stem rust pathogen also contributed to the control, especially in North America, by reducing early infections on wheat crop. Detection of Ug99 virulent race (Pretorius *et al.,* 2000) with its further evolution and spread beyond eastern Africa poses new risks to production of wheat worldwide. Ug99 race, termed as TTKSK using North American nomenclature (Jin *et al.,* 2007), possesses virulence to many known resistance genes used in breeding programs worldwide (Singh *et al.,* 2008). In addition, Ug99 also possesses virulence to 2 additional important resistance genes, *Sr31* and *Sr38*, transferred to wheat from rye (*Secale cereale*) and *Triticum ventricosa*, respectively. Winter wheat varieties possessing the wheat-rye translocation 1BL.1RS carrying the resistance gene *Sr31*, such as Kavkaz and Aurora, have been utilized in the development of Veery lines, which had significantly superior yield potential, wide adaptation and possessed tolerance to rust and powdery mildew conferred by resistance genes *Lr26*, *Yr9*, *Sr31* and *Pm8* located on the translocation (McIntosh *et al.,* 1995). These CIMMYT-derived and many other 1BL.1RS-carrying varieties spread so fast that by the

1990s stem rust seemed to have been wiped out. By 2005, Ug99 was well established in Ethiopia and Kenya (Wanyera *et al.,* 2006) and was identified in 2006 in Yemen and Sudan (Jin *et al.,* 2008).

Genomic selection has been very well reviewed in wheat for durable stem rust resistance (Rutkoski *et al.,* 2011). Genomic selection has also been reported to improve quantitative adult plant resistance (APR) in a set of CIMMYT germplasm towards stem rust (*Puccinia graminis* f. sp. *tritici*). Prediction model, i.e., genomic-best linear unbiased prediction (G-BLUP), incorporated markers linked to main APR loci and the *Sr2* region was found to play main role in APR (Rutkoski *et al.,* 2014). Markers linked to moderate-effect gene loci, such as *Sr2*, could be predictive alone or modeled as fixed effects in combination with genome-wide markers, leading to better predictions to develop resilient varieties (Rutkoski *et al.,* 2014). Also, Ornella *et al.* (2012) used genomic selection to accumulate favorable alleles of slow-rusting genes from 5 wheat populations (PBW343/Juchi, PBW343/Pavon76, PBW343/Muu, PBW343/Kingbird and PBW343/K-Nyangumi) by using 1400 Diversity Arrays Technology markers for assessing all parents and populations. Genomic selection was carried out using Bayesian least absolute shrinkage and selection operator (LASSO), ridge regression and support vector regression with linear or radial basis function kernel models to make better predictions for stem rust (*Puccinia graminis*) and yellow rust (*Puccinia striiformis*) resistant cultivars. Ornella *et al.* (2012) reported that prediction ability for yellow rust was lower than for stem rust, probably due to differences in infection conditions of both diseases. For within population and environment, the correlation between predicted and observed values (Pearson's correlation) was greater than 0.50 in 90% of the evaluation, whereas for yellow rust, the correlation ranged from 0.06 to 0.63. The LASSO and ridge regression models have similar prediction ability, with a slight superiority of the LASSO, indicating the additive nature of rust resistance.

Also, from Kristal/Sebatel durum wheat mapping population (RILs), 9 consistent QTL regions conferring resistance to Ug99 were identified (Haile and Roder, 2013). The greatest portion of resistance for Ug99 in the population was explained by a QTL (R^2 = 34%) identified on short arm of chromosome 3B (QSr.IPK-3B) (Haile *et al.,* 2012) due to the presence of the adult plant resistance gene, *Sr2* mapped in same region of 3BS chromosome. From haplotype analysis based on expected fragment sizes of linked markers, the presence of *Sr2* in 'Sebatel' (Haile *et al.,* 2013b) was confirmed. 'Sebatel' variety was resistant to stem rust races in Syria, Lebanon and the Mediterranean region; it was developed at ICARDA (International Center for Agricultural Research in the Dry Areas) by accumulating resistance genes from multiple crosses and showed a high level of resistance. Hence, *Sr2* contributes to adult plant resistance through the interaction between *Sr2* and unknown genes to form a '*Sr2* complex' (Singh *et al.,* 2009; Yu *et al.,* 2011). Additionally, the QTL region identified on the long arm of chromosome 7A (Haile *et al.,* 2012) flanked by Xbarc121 and Xgwm984 markers may be associated with the stem rust resistance gene *Sr22*, since Xbarc121 is among the reported diagnostic markers for this gene (Olson *et al.,* 2010). Additional races belonging to Ug99 lineage have been found in East Africa, Zimbabwe and South Africa (Pretorius *et al.,* 2010) and 7 races are now known (Hodson 2010). Therefore, breeding for rust resilience is the utmost priority for wheat breeders. Durable stem rust resistance has been made possible by deployment of *Sr2* gene complex linked with morphological marker pseudo-black chaff (PBC) along with other minor genes. *Sr2* was detected in CIMMYT-derived semi-dwarf wheats, e.g., Kritati, Kingbird, Pavon 76 and Parula (Njau *et al.,* 2010). The *Sr2* gene is tightly linked to the powdery mildew resistance and to leaf rust resistance gene *Lr27* (Mago *et al.,* 2011). By incorporating diverse resistance sources via MABC and by using co-segregating markers (Prins *et al.,* 2001; Mago *et al.,* 2005), selection is accelerated so that rust susceptibility of cultivars and germplasm is reduced.

Leaf rust resistance

Various genes for leaf rust resistance have been incorporated into *Triticum aestivum* from several wild species, such as *Aegilops ventricosa* (*Lr 37), A. speltoides* (*Lr 28, Lr 35, Lr 36, Lr 47), A. umbellulata* (*Lr 9)*, *A. squarrosa* (*Lr 21, Lr 22, Lr 32, Lr 39, Lr 40, Lr 41, Lr 42, Lr 43) and Agropyron elongatum (Lr 19, Lr 24, Lr 29)* (Prabhu *et al.,* 2009). A number of *Lr* resistance genes, i.e., *Lr 48, Lr 28, Lr 24, Lr 19* and *Lr* 9 are mapped and tagged on different wheat chromosomes with different markers viz., *Lr9* with SCAR marker SCS5 on chromosome $6B^L$, *Lr*19 with SSR markers (Xgwm437, Xgwm421, Xgwm37) on chromosome $7D^L$, Lr24 with SCAR marker SCS1302 on chromosome $3D^L$, *Lr*28 with SCAR marker SCS421 on chromosome $4A^L$ and *Lr*48 with RAPD marker $S336_{776}$ on chromosome $2B^L$ (Prabhu *et al.,* 2009). Singh *et al.* (2001) reported that the APR is considered effective resistance for rust resistance breeding. Most of the resistance genes confer resistance in the seedling stage itself, enabling the plant to resist the invasion by the fungus during the entire growing period. The APR enables the plant to withstand the extreme effect of the infecting virulent pathogen via hypersensitive reaction as a consequence of the ability of the fungus to infect the plant. It is acknowledged that leaf rust control could be most effective if APR is utilized in combination with seedling resistance in wheat breeding programs (Pretorius and Roux 1988). The most prominent such example is of durable resistance conferred by the APR gene *Lr34* (Wamishe and Milus 2004). In such an attempt, 3 pyramided wheat lines were developed to provide durable leaf rust resistance. One of them is HD 2329 (*Lr9* + *Lr24* + *Lr28*), a three-gene pyramid. Two two-gene pyramids, PBW 343 (*Lr24* + *Lr48*) and PBW 343 (*Lr28* + *Lr48*), were also developed in the prominent cultivar PBW343. The RAPD marker pair, S3450 and S336775, linked in repulsion and coupling phase, respectively, to the Lr48 locus has been utilized as a co dominant marker system (Prabhu *et al.,* 2009). As MARS response is more in case of prior knowledge of the QTL and the response decreases as the knowledge of the number of minor QTL associated with the trait decreases (Bernardo and Charcosset 2006). Tsilo *et al.* (2014) mapped genes for APR to leaf rust in a 139 recombinant inbred line MN98550-5/MN99394-1 population. Four QTL on chromosomes 2BS, 2DS, 7AL and 7DS were detected. The QTL on 2BS explained 33.6%, whereas other QTL on 2DS, 7AL and 7DS explained 15.7%, 8.1% and 34.2%, of the phenotypic variation, respectively. Deployment of these QTL in combination with other effective resistance genes will lead to effective and successful control of leaf rust.

Stripe rust resistance

Many stripe rust resistance genes are known and DNA markers are associated with them, enabling their deployment in wheat breeding programs. Many researchers have identified seedling-stage stripe rust resistance genes, i.e., *Yr5* (Smith *et al.,* 2007; Chen *et al.,* 2003; Yan *et al.,* 2003; Sun *et al.,* 2002), *Yr7* (Yao *et al.,* 2006), *Yr17* (Helguera *et al.,* 2003), *Yr10* (Smith *et al.,* 2002), *Yr9* (Shi *et al.,* 2001), *Yr15* (Peng *et al.,* 2000), *Yr26* (Ma *et al.,* 2001) and *Yr28* (Singh *et al.,* 2000), have been deployed in improving wheat germplasm. Most resistance genes originate from wheat, but some have been introduced from related cereal species, too. Many of these alien introductions have the added value of being linked to genes, such as *Yr9* linked to *Lr26/Sr31/Pm8*, which confer resistance against other fungal pathogens (Singh *et al.,* 1990) and *Yr17* linked to *Lr37/Sr38* conferring resistance to all 3 rusts. Bariana and McIntosh 1994; Robert *et al.,* 1999). Although *Yr* genes are identified on most of the wheat chromosomes, the B-genome, and in particular chromosome 2B, has maximum number of resistance genes (Luo *et al.,* 2009). Among the resistance genes detected on 2B, *Yr5* and Yr7 have been shown to be allelic (Zhang *et al.,* 2009), whereas *Yr27, Yr31, Yr41, Yr43, Yr44, YrQz (*line Qz180; Deng *et al.,* 2004) and *YrV23* (cv. Vilmorin 23; Luo *et al.,* 2009) represent potentially independent loci. Genes *Yr24, YrCH42* and *Yr26* are allelic, which are located on short arm of chromosome 1B (Li *et al.,* 2006). However, *Yr10* was shown to be independent, while *Yrl5* was linked in repulsion

with *Yr24/Yr26* (Zakari *et al.,* 2003). Also the most popular example of molecular breeding is of employing marker-assisted backcross breeding to transfer *Yr* 15 to 'Zak' (Randhawa *et al.,* 2009). Several APR genes have an important role in durable protection; for example, slow-rusting *Sr2/Yr30* complex showed durable disease resistance (Lowe *et al.,* 2011). *Yr18/Lr34/Pm38* provides an important source of partial resistance (Krattinger *et al.,* 2009). *Yr29*/*Lr46*/*Pm39* combination provides effective resistance to both powdery mildew and rusts (Rosewarne *et al.,* 2008; Lillemo *et al.,* 2008).

Molecular markers are available for many APR genes; for example, 2 marker systems were developed viz., Microsatellite, SWM10 by Bossolini *et al.,* 2006; and STS marker csLV34 by Lagudah *et al.,* 2006 for *Yr18*, but these have since been superseded by the development of 5 allele-specific markers, cssfr1- cssfr5 (Lagudah *et al.,* 2009). In addition, the *Lr34/Yr18* locus has been cloned (Krattinger *et al.,* 2009). Similarly, markers have been developed for APR genes, *i.e*., *Yr29* (Suenaga *et al.,* 2003) and *Yr30* (Spielmeyer *et al.,* 2003; Hayden *et al.,* 2004). The SSR markers linked to *Yr26* were used to transfer this gene successfully into the popular Turkish wheat cultivars, Gerek-79 and Gun-91 (Yildirim *et al.,* 2004). To know the molecular and biochemical processes involved in the plant-pathogen interaction, molecular studies focused on cloning specific resistance genes. Genes *Yr10, Yr18* and *Yr36* have been cloned (McHale *et al.,* 2006). More than 140 QTL have been identified for stripe rust resistance in wheat. About 47 regions have been identified that are effective against stripe rust and are dispersed across all chromosomes, except 5D (Rosewarne *et al.,* 2013).

Pre-harvest sprouting tolerance

A major QTL (*QPhs.ccsu* 3A.1) for pre-harvest sprouting tolerance (PHST) was identified and mapped on the long arm of chromosome 3A, which was transferred into wheat cultivar HD2329 (a pre-harvest sprouting-susceptible cultivar) from SPR8198 (a pre-harvest sprouting-tolerant cultivar) using MABC (Kulwal *et al.,* 2005). The 2 parents and the mapping population (RILs) developed from the cross were grown in 6 different environments and a linkage map (the length of the map being 279.1 cM) of chromosome 3A was prepared with 13 markers and used for QTL analysis. The major QTL, QPhs.ccsu-3A.1, was detected at a genetic distance of 183 cM (approximately) from the centromere on the long arm of chromosome 3A and the QTL explained 78.03% of the variation across environments (Kulwal *et al.,* 2005). The positive additive effects of the QTL available in the superior parent (SPR8198) can be used for MAS for the transfer of this QTL allele to obtain PHS-tolerant cultivars. Four QTL, i.e., *QPhs.caas-2BL*, *QPhs.caas-3AS.1*, *QPhs.caas-3AS.2* and *QPhs.caas-3AL*, were identified from a cross between Zhongyou 206 and CA-0431 (white grain Chinese winter wheat line showing high PHS resistance). Line CA-0431 and the identified markers *Xbarc1042* and *Xmag3319* can be used in breeding programs for improvement of PHS resistance for white kernel wheat (Miao *et al.,* 2013).

Fusarium head blight resistance

Fusarium head blight (FHB) is a severe wheat disease (Leonard and Bushnell, 2003) and contamination caused by mycotoxins (fusarium secondary metabolites) pose a big threat to both human and animal health (Van Egmond, 2004). Molecular breeding studies for FHB resistance in wheat have led to the identification of 19 QTLs (Buerstmayr *et al.,* 2009; Liu *et al.,* 2009; Loffler *et al.,* 2009), which are spread across all wheat chromosomes. A PCR-based marker, *Umn10,* linked to a major FHB resistance QTL (*Fhb1)* is located on the short arm of chromosome 3B, which explained 40% to 50% of phenotypic variance in an experiment (Rosyara *et al.,* 2009; Liu *et al.,* 2008). As a closely linked co-dominant molecular marker is an essential prerequisite for a successful Another major QTL from Wangshuibai mapped for FHB resistance is *Fhb*5, which is located on chromosome 5A (Xue *et al.,* 2011).

Molecular breeding for abiotic stresses in wheat

Heat tolerance

Global temperature is predicted to increase by about 2 to 4 ˚C by the end of the 21st century (IPCC 2007). In cereal crops, heat stress accelerates plant development, including flowering time, and reduces anther dehiscence, pollen fertility rate, and grain filling, as well as the overall yield (Dwiyanti and Yamada 2013). Heat stress thresholds differ among plant species and cultivars (Wahid *et al.,* 2007; Prasad *et al.,* 2006). Heat tolerance is a quantitative trait, with complex nature and controlled by a number of genes/QTL, with interactions among QTL and QTL interaction with the environment (QTL × QTL interaction; QTL × environment and QTL × QTL × environment interactions) (Kumar *et al.,* 2013). Nevertheless, several stable QTL for heat tolerance in wheat have been reported for various parameters, such as grain filling duration (GFD) (Mason *et al.,* 2010; Yang *et al.,* 2002a), senescence-related traits (Vijayalakshmi *et al.,* 2010). The QTL were identified on different chromosomes, i.e., 2B, 7B and 7D, using a cross between NW1014 (heat-tolerant) and HUW468 (heat-susceptible). These QTL governed the heat susceptibility index (HSI) for grain fill duration (HSIGFD); heat susceptibility index (HSI) for thousand grain weight (HSITGW) and canopy temperature depression (CTD) (Paliwal *et al.,* 2012).

Drought tolerance

A marker map (EST-STS/SSR) constructed by Kirigwi *et al.* (2007) from 127 RILs from a cross between Dharwar Dry (drought tolerant) and Sitta (drought susceptible). Kirigwi *et al.* (2007) reported a QTL for grain yield on the long arm of chromosome 4A. This QTL had impact on grains m^2, grain-fill rate, grain yield, spike density, biomass production and drought susceptibility index. Microsatellite locus Xwmc89 was associated with all significant QTL covering a 7.7 cM region and generally explained the largest proportion of phenotypic variation. The alleles associated with enhanced performance under drought stress were contributed by Dharwar Dry. Microsatellite marker wmc89 may be useful for MAS to enhance drought tolerance (Kirigwi *et al.,* 2007). Kumar *et al.,* 2012 identified several QTL for drought, i.e., *QLt.ksu-1D, QFv/Fm.ksu-3B, QChl.ksu-3B* and *QGyp.ksu-4A*, in cross between 'C306' and 'HUW206' for Lt (low flag leaf temperature under stress) on short arm of chromosome 1D; for potential quantum efficiency of photosystem (PS) II (Fv/Fm), chlorophyll content under stress, co-localized on chromosome 3B and for grain yield per plant on chromosome 4A.

Molecular breeding for biotic stresses in maize

Biotic stresses, including downy mildews, banded leaf sheath blight, turcicum leaf blight, stem borers and abiotic stresses, i.e., drought, water logging and nutrient deficiencies and toxicity in soils have widespread yield-reducing effects on maize (Gerpacio and Pingali 2007). Many studies have reported identification and mapping of QTL associated with resilience, but practical applications of such QTL in resilience development are scarce. Identifying QTL that express uniformly across different genetic backgrounds would complement efforts in resilience development programs. Below are mentioned certain QTL that have been utilized in such programs.

Downy mildew resistance

Development of resistance to downy mildew, especially for *Peronosclerospora sorghi*, *P. zeae, P. maydis, P. heteropogoni* and *P. philippinensis*, is given high priority throughout the world (Prasanna *et al.,* 2010b). Several QTL governing downy-mildew resistance have been identified and a significant one has been mapped on chromosome 6 using a set of 135 RILs developed from a cross between Ki3 (resistant) and CML139 (susceptible) (George *et al.,* 2003). In an Asian Maize Biotechnology Network (AMBIONET) study, these same 135 RIL families were evaluated for downy mildew reaction (during year 2000 and 2001) at different

locations, i.e., Mandya (southern India) against sorghum downy mildew (*P. sorghi*); at Suwan (Thailand) against sorghum downy mildew (*P. zeae*); at Maros (Indonesia) against Java downy mildew (*P. maydis*); at Udaipur (western India) against Rajasthan downy mildew (*P. heteropogoni*); and at Southern Mindanao (Philippines) against Philippine downy mildew (*P. philippinensis*). Selection of QTL using genetic markers can be effective if a significant association is found between them. The AMBIONET study identified 3 SSR markers, i.e., *umc11, umc23a* and *umc113*, which were linked tightly to the QTL on chromosome 6, suggesting their possible use for MAS (Prasanna and Hoisington 2003). Also in India, a QTL each on chromosomes 3 and 6 was identified and validated from backcross mapping population developed from a cross between NAI116 (sorghum downy mildew resistant) and CM139 (susceptible) (Nair *et al.,* 2005). Identification and subsequent mapping of major QTL helps in developing better DNA marker-trait associations (Collard and Mackill 2008), which can be utilized for successful application of MAS for the development of disease-resilience in susceptible cultivars.

Turcicum leaf blight and polysora rust

Molecular-marker-assisted pyramiding of major genes governing resistance to turcicum leaf blight and polysora rust in elite 5 Indian inbred lines, i.e., CM137, CM138, CM139, CM140 and CM212, has been achieved at IARI (Prasanna *et al.,* 2010a; Prasanna *et al.,* 2009b). Turcicum leaf blight-resistance genes, i.e., *Htn1*and *Ht2*, along with a QTL (*RppQ*) for polysora rust from 4 resistant donors, i.e., NAI 147, SKV 21, NAI 112 and SKV18, were pyramided together by generating 7 different backcross populations. An SSR polymorphism survey was carried out on the selected donor and recipient parents covering all 10 chromosomes. Foreground selection (MABC) for different resistance gene combinations was carried out in BC_1F_1 and BC_2F_2 generations using SSR markers (viz., umc1293, bnlg128 and umc1249), along with background selection for accelerated recovery of recurrent parent genome in BC_1F_1 and BC_2F_1 progenies. Phenotypic screening under artificial inoculation of BC_2F_1 and BC_2F_3 with local isolates was carried out at Hawalbagh (Almora) and Nagenahalli against turcicum leaf blight and against polysora rust at Nagenahalli. Differential responses of the genotypes to turcicum leaf blight at Hawalbagh and Naganahalli were revealed. The MABC enabled the development of BC_2F_4 progenies with resistance to both the diseases, which led to the development of turcicum leaf blight- and polysora rust-resistant maize hybrids in India (Prasanna *et al.,* 2009b).

Northern corn leaf blight resistance

Studies on resistance revealed the complex genetic nature of northern corn leaf blight (NCLB), with many QTL distributed genome wide (Van Inghelandt *et al.,* 2012; Poland *et al.,* 2011). Genomic selection in maize for prediction of NCLB resistance was employed by Technow *et al.* (2013) by using G-BLUP model to predict genotypic values of 100 dent and 97 flint lines, which were genotyped with high-density SNP markers and phenotyped for NCLB resistance *per se*.

Maize rough dwarf disease

Three major strains of virus cause maize rough dwarf disease (MRDD), which includes Mal de Rio Cuarto virus in South America, maize rough dwarf virus in Europe and rice black-streak dwarf virus in East Asia. Thus, it is a complex trait and resistance against it involves numerous QTL. The main approach for reducing yield losses from these viruses is to breed and deploy resilient maize cultivars. Mapping of a major QTL (*qMrdd)* to a 1.2 Mb region by Tao *et al.* (2013) would enable introgression of *qMrdd1*-based resistance into susceptible but elite and well-adapted hybrids and hence would minimize MRDD-related crop losses.

Molecular breeding for abiotic stresses in maize

Drought tolerance

Maize is sensitive to drought mainly during reproductive stages. Studies on drought tolerance focused on genetic basis of root architecture, yield components and synchrony between anthesis and silking (Ribaut *et al.,* 2009). The MABC procedure was used to incorporate several QTL alleles for short anthesis-silking interval (ASI) from Ac7643 (drought-tolerant) donor to CML247 (susceptible) (Ribaut and Ragot ,2007). A major QTL, identified as Root-ABA1, which is related to root development, along with abscisic acid levels in leaf under water stress, is also associated with stomatal conductance (Giuliani *et al.,* 2005). Major QTL for deep roots have been identified in maize (Trachsel *et al.,* 2009). A study on maize drought tolerance detected 239 QTL from 22 experiments under water stress and 160 QTL under control conditions (Hao *et al.,* 2009). Later 39 consensus QTLs under water stress and 36 consensus QTLs under control conditions were identified (Hao *et al.,* 2009). Genes related to stress response (i.e., NCED, a carotenoid cleavage enzyme and CBF1/DREB transcription factors) were identified within the detected meta-QTL. Recent trends and advances in molecular breeding have enabled detection of QTL and alleles associated with tolerance to drought. Such experiments in India and China (Prasanna *et al.,* 2009a; Hao *et al.,* 2008; Xiao *et al.,* 2005) have led to the identification of QTL on different chromosomes (Prasanna *et al.,* 2009a). Several QTL identified from RILs, located on chromosomes 1, 2, 8 and 10, were found to influence specific traits under drought stress. Also, a digenic epistatic QTL for kernel number per ear under drought stress was identified (Prasanna *et al.,* 2010b). Analysis of a mapping population ($F_{2:3}$) derived from a cross between drought-tolerant line X178 and a drought-susceptible line B73 [at the Chinese Academy of Agricultural Sciences (CAAS)] (Xiao *et al.,* 2005; Hao *et al.,* 2008) at different locations in central and southern China resulted in detection of a major QTL for ASI (anthesis-silking interval) and ear number per plant under drought stress on chromosome 1 (bin 1.03) and chromosome 9 (bins 9.03-9.05), which correspond to some major QTL identified in different experiments on drought stress worldwide (Tuberosa *et al.,* 2007). Such 'consensus QTL' identified in maize for drought tolerance would be utilized in marker-assisted breeding programs as good candidates to improve maize production and productivity under drought conditions (Prasanna *et al.,* 2010b).

Several informative markers, e.g., SSR markers, have been identified for drought tolerance in maize (Gemenet *et al.,* 2010; Shiri 2011). These informative markers could be further validated and potentially deployed in molecular breeding for developing drought tolerance in maize. Numerous QTL regulating morpho-physiological component traits, i.e., leaf greenness, plant senescence, and root capacitance under drought, and for grain yield have been reported in maize (Messmer *et al.,* 2009, 2011; Li *et al.,* 2010, 2011). Almeida *et al.* (2013) evaluated 3 tropical bi-parental (CML444 x MALAWI; CML440 x CML504; CML444 x CML441) populations under well-watered and water-stress treatments in Kenya, Mexico and Zimbabwe to identify genomic regions responsible for grain yield and ASI. Meta-QTL analysis identified one genomic region for ASI and 7 regions for grain yield. From meta-QTL (mQTL) analysis, 7 genomic regions for grain yield and one genomic region for ASI were identified, of which 6 mQTL on chromosomes 1, 4, 5 and 10 for grain yield were constitutively expressed across environments and one mQTL on chromosome 7 for grain yield and one on chromosome 3 for ASI were found to be 'adaptive' to stress. An 'adaptive' QTL is one detected only in a specific environment, such as under water stress conditions, whereas a 'constitutive' QTL is consistently detected across most environments (Collins *et al.,* 2008). The SNP markers were developed via high throughput assays for delimiting the physical intervals of these mQTL (Almeida *et al.,* 2013). These mQTL regions can be effectively used in MAS and MARS programs for developing drought tolerance.

Excess soil moisture tolerance in maize

Excess soil moisture (ESM) affects over 18 per cent of the total maize production area in South and Southeast Asia, causing production losses of

25 to 30 per cent annually (Zaidi *et al.,* 2010). In India, water-logging is the second most serious constraint for crop production after drought. Significant QTL have been identified for water-logging tolerance at seedling stage (Qiu *et al.,* 2007). Mano *et al.* (2005) identified QTL on chromosomes 3, 7 and 8 for adventitious root formation under ESM conditions from an F_2 population of a cross between a maize inbred line (B64) and teosinte (*Zea mays* ssp. *Huehuetenangensis*). Similarly, Mano *et al.* (2009) identified QTL controlling constitutive aerenchyma formation under flooding conditions on chromosomes 1, 5 and 8 from a cross between another teosinte accession (*Zea mays* spp. *Nicaraguensis*) and maize inbred line B73. The production of NILs with such QTL in maize would be beneficial for improvement of tolerance towards excess soil moisture. A QTL analysis to map the genes controlling adventitious root formation on the soil surface (ARF-SS) under flooding conditions was undertaken in the seedlings of 317 BC_3F_1 progenies derived from a cross between elite maize Mi29 and teosinte (*Zea nicaraguensis*) (Mano *et al.,* 2009). From interval mapping analysis and single point regression, the QTL for ARF-SS were detected on chromosomes 3 (bin 3.04), 7 (bin 7.04) and 8 (bin 8.03) (Mano *et al.,* 2009). Six QTL (*ph6-1, sdw4-1, sdw7-1, tdw4-1, tdw7-1 and rl1-2,*) were identified at seedling stage, which were associated with plant height, shoot dry weight, total dry weight root length and root dry weight. These QTL were detected at 3 stages i.e., the period during 0 to 3 days of water logging, 3 to 6 days of water logging and the period during 6 to 9 days of water logging by Osman *et al.* (2013) After mapping of micro-RNAs and expressed sequence tag markers, 7 candidate genes were observed to co-localize with the identified QTL on chromosomes 1, 4, 6, 7 and 9 and hence these may be good candidate genes for ESM tolerance, which may be utilized in breeding programs.

CONCLUSION

Molecular breeding offers numerous opportunities for plant breeders to develop cultivars with resilience to diseases with precision and rapidly. Molecular breeding approaches, such as MAS, MABC, MARS and genomic selection, have expanded the tool-kit of plant breeders and provided them with various new avenues and opportunities. These approaches have been adopted successfully in almost every crop listed in Table 1. We have covered some of the most successful examples from rice, wheat and maize for developing resilience to different biotic and abiotic stresses. Molecular breeding is an efficient approach for enhancing genetic gain per crop cycle. Molecular breeding and conventional breeding are complementary in most breeding programs, as there are various issues and bottlenecks that hinder molecular breeding strategies, especially in developing countries. These bottlenecks may include high cost, non-availability and complexity of molecular platforms, poor reliability of marker profiling and scoring, limited number of markers and degree of polymorphism, gene/QTL x environment effects, lack of equipment, resources and technical expertise as well as lack of application gap. Thus, to meet these challenges in molecular breeding, platforms (policies) need to be developed to reduce cost and to optimize MARS and genomic selection procedures to identify high-yielding, resilient and stable genotypes (with low genotype x environment x marker interaction). The emergence of public-private partnership platforms for accessing molecular breeding tools with support services and ever-increasing demand for improved disease-resilient varieties to counter the food crisis throughout the globe predict that molecular breeding strategies will have a significant impact on crop improvement programs prevailing in developing countries.

Table 1. List of examples of molecular breeding for developing resilience to diseases in major cereals.

Cereal	Trait(s)	Gene/QTL		Remarks	Reference
Rice	Blast resistance	*Pi*39	Fine mapped	On Chr. 12, Associated with RM27933-RM27940	Liu *et al*. 2007
		Pi1, Piz-5, Pi1, Pita	Pyramiding in F2 generation	Associated with RFLP, STS	Hittalmani *et al*. 2000
	Bacterial blight resistance	*xa13*	Mapped	On Chr. 8 associated with markers E6A, SR6, SR11	Chu *et al.,* 2006
		*Xa*27	Mapped	On Chr. 6 associated with M964-M1197	Gu *et al.,* 2005
	BB resistance and plant height	*xa1, Xa21 and sd1*	Utilized in MABC	Incorporated into Basmati370 and Basmati 386	Bhatia *et al.,* 2011
	Green rice leafhopper resistance	*Grh5*	Mapped	On chr. 8, associated with RM3754-RM3761	Fujita *et al.,* 2006
	Deep roots	QTL on chromosomes 1, 2, 7 and 9	Utilized in MABC	Using RFLP and SSR (forground) SSR (background)	Shen *et al.,* 2001
	Submergence tolerance	*Sub1*	Mapped	On Chr. 9 associated with markers c1232, RZ698	Xu *et al.,* 2006
	Salt stress	*qST1, qST3,*	Mapped	On Chr. 1, 3 associated with markers RZ569A, RZ596	Lee *et al.,* 2007
		QTL	Mapped	On Chr. 2,3,7 associated with markers C1408	Takehisa *et al.,* 2004
	Fe toxicity	*LB1*	Mapped	On Chr. 1,2,4 associated with markers RM315, RM6, RM252	Wan, Zhai, & Wan 2005
	Rice yellow mottle virus	*Rymv*	Mapped	On chr. 4, associated with RM273-RM252	Albar *et al.,* 2003
	Drought	QTL	Identified	Kalinga III x Azucena for root length	Steele *et al.,* 2006
			Identified	Vandana x WayRarem for reproductive stage drought and grain yield	Bernier *et al.,* 2007
			Identified	Akihikari x IRAT109 for specific water use and water use efficiency (WUE)	Kato *et al.,* 2008.
			Identified	Low land rice cv. Shennong 265 × Upland rice cv. Haogelao for Photosynthesis parameters using backcross (ILs) mapping population	Gu *et al.,* 2012
Wheat	Powdery mildew	*Pm2 Pm4a*	Pyramiding in F2	Using RFLP	Liu *et al.,* 2000
	Leaf rust	*Lr*1, *Lr*9, *Lr*24, *Lr*47	Marker assisted introgression	Using STS, SCAR, CAPS	Nocente, Gazza, & Pasquini 2007
	PHST	1 QTL	MABC	Using SSR, EST	Torada *et al.,* 2008
	FHB	Fhb1 and Qfhs.ifa-5A	Transferred by MABC	From spring wheat line CM82036 to European winter lines	Salameh *et al.,* 2011

Cereal	Trait(s)	Gene/QTL		Remarks	Reference
	Durable resistance to the rust	slow-rusting genes identified from five wheat populations	Genomic selection (GS) in (PBW343/Juchi, PBW343/Pavon76, PBW343/Muu, PBW343/Kingbird and PBW343/K-Nyangumi)	Using 1400 Diversity Arrays Technology markers and (LASSO), (BL), (RR) and support vector regression with linear or radial basis function kernel models	Ornella *et al.,* 2012
	Drought	QTL	Identified	Beaver x Soissons for flag leaf senescene	Verma *et al.,* 2004
			Identified	SQ1 x Chinese Spring for root length, WUE, grain yield	Quarrie *et al.,* 2005
			Identified	Seri M82 × Babax for Various productivity and physiological traits (RILs)	McIntyre *et al.,* 2010; Suzuky *et al.,* 2010
		QLt.ksu-1D	Identified	In C306' x 'HUW206 for Lt (low flag leaf temperature under stress) on short arm of chromosome 1D.	Kumar *et al.,* 2012
		QFv/Fm.ksu-3B and *QChl.ksu-3B*	Identified	In C306' x 'HUW206 for Fv/Fm and Chl controlling quantum efficiency of PS II and chlorophyll content under stress were co-localized on chromosome 3B.	
		QGyp.ksu-4A	Identified	In C306' x 'HUW206 for Grain yield per plant on chromosome 4A	
	Drought and heat	QTL for Canopy Temperature (CT), Chlorophyll (Chl), Yield	Mapped	On chromosome 2B, 5A, 4A, 1B	Pinto *et al.,* 2010
		QTL for Stay-green trait	Mapped	On chromosome 7B, 7D, 3B	Kumar *et al.,* 2010
Maize	Drought tolerance	Root-abscisic acid 1 (Root-*ABA1*)	Identified	Os420 x IABO78	Landi *et al.,* 2007
	Drought	QTL	Identified	Lo964 x Lo1016 for root traits and yield	Tuberosa *et al.,* 2002
			Identified	F2 x F252 for silking data, grain yield	Moreau, Charcosset, & Gallais 2004
			Identified	CML444 × SC-Malawi for Plant senescence, relative leaf chlorophyll contents and root capacitance (RILs)	Messmer *et al.,* 2011
	Chilling tolerance	8 QTL	Identified	From ETH-DH7 × ETH-DL3, for Photosynthesis traits which influence chlorophyll fluorescence, CO_2 exchange rate (CER) and/or photosynthetic pigments	Jompuk *et al.,* 2005
	Borer resistance	QTL on chromosomes 7, 9 and 10	MABC	Using RFLP	Willcox *et al.,* 2002
	Northern corn leaf blight (NCLB)	100 dent and 97 flint lines	Genomic Selection	Using BLUP model and high-density SNP marker data	Technow, Burgerand, & Melchinger 2013

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