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Wheat Resistance to Fusarium Head Blight and Possibilities of its Improvement using Molecular Marker-Assisted Selection

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Abstract

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Wheat, one of the world's major crops, is seriously affected by fungal diseases, especially in regions with high moisture and moderately warm temperatures. This paper reviews various molecular and conventional techniques that are used to identify genotypes with resistance alleles associated with Fusarium head blight (FHB) diseases. Quantitative trait loci (QTL) type II, designated as *Fhb1*, are frequently applied in plant breeding, and the newly recognized genes related to resistance to this fungal disease give extra insights into marker-assisted selection (MAS). Molecular markers are robust tools that may be routinely used in MAS for the mapping of resistance genes in crop breeding. FHB resistance is polygenic, and different resistance genes could be conveyed into a single genotype by MAS, which might ensure greater resistance to FHB disease. In conclusion, different researchers have used various techniques to control FHB resistance, such as MAS, gene pyramiding (through backcross), and molecular markers (association with resistance QTLs or genes).

Keywords: FHB; marker-assisted selection; quantitative trait loci; sources of resistance

Development of disease resistant cultivars is an important factor in private as well as in commercial cultivation around the world. Breeding for disease control is considered to be a reliable and environmentally friendly approach that increases yield production as well as increases selection intensity for desirable genotypes. It is also important to farmers and reduces their costs. In conclusion, numerous scientists have developed different approaches (various molecular markers, marker-assisted selection) in the last few years for the recognition of genes/QTLs of interest on wheat chromosomes. The backcross method is used for the accumulation of desired traits (disease resistance) in a genotype. Improving germplasm or breeding of cultivars often requires combining desired traits from different parental lines into single genotypes (gene pyramiding), mostly applied in resistance to diseases. Combining desired traits could be enhanced by using molecular marker techniques to recognize and promote desirable genetic combinations in the following generations. The use of molecular markers (definition, see Table 1) shortens the breeding cycle and increases the possibility of the selected traits being present in the progenies. Numerous efforts have been made by various scientists in traditional as well as molecular plant breeding to produce varieties with resistance to FHB. Collard and Mackill (2008) remarked that recombination can lead to the

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loss of genes/traits originally selected if the desired trait was in a heterozygous condition. Each FHB resistance QTL can be screened by phenotyping (inoculation with *Fusarium* spp.) or by genotyping (MAS). According to Salameh *et al.* (2011), major QTLs possibly integrated and selected for FHB resistance by using MAS in wheat breeding programs and selected breeding lines should then be evaluated phenotypically to determine the major and minor QTLs on resistance to FHB.

FHB disease life cycle

FHB is caused by fungal species in the genus *Fusarium.* The most common species causing FHB is *Fusarium graminearum.* The primary source of inoculum comes from overwintering fungus colonies in remaining crop residues (Figure 1). The fungus produces perithecia on colonized maize stubble. These perithecia release ascospores into the air which infect the wheat or barley plant. The plant is most susceptible to infection during flowering. In wheat and durum, any part or all of the head may appear bleached. These white heads are very conspicuous in a susceptible variety. The partly white and partly green heads are diagnostic of the disease in wheat. The fungus may also infect the stem (culm) immediately below the head, causing symptoms including premature bleaching of the spikelets or entire spike. Seeds from infected spikelets may be small, shrivelled, and white or chalky in appearance. FHB infected seeds are commonly referred to as tombstones.

Different mechanisms of genetic resistance to Fusarium head blight

Among the numerous control mechanisms, host plant resistance is the most effective control of plant diseases from an economic point of view in most regions of the world. Disease resistance in plants might be categorized based on the genotypic and biochemical data (monogenic or oligogenic, polygenic, acquired resistance, and post-transcriptional gene silencing). Quantitative (polygenic) resistance ensures

Table 1. Definition of terms used in the paper

Host plant resistance	Host plant resistance pertains to a plant's ability that protects from and reduces the pathogen invasions
Adult plant resistance	Resistance visible only at the adult stage of a plant, i.e. at the generative phase (in contrast with seedling resistance). Adult plant resistance can be inherited mono- or oligogenically. Adult plant resistance need not be durable.
Durable resistance	Resistance that remains effective for a long period when applied on a large scale in a region that is undergoing regular epidemics of the pathogen.
Marker-assisted selection	A marker (morphological, biochemical, or one based on DNA/RNA variation) is used for indirect selection of a gene/QTL.
Molecular marker	Specific fragments of DNA with a known location on the chromosome that can be identified within the whole genome and reveal neutral sites of variation. Markers that are in close linkage with a particular gene/QTL of interest can be used for MAS.
Mapping	Assigning markers, genes, and/or QTL in the order indicating the relative distances among them, and assigning them to their linkage groups on the basis of their recombination values from all pairwise combinations.
Recombinant inbred lines (RILs)	RILs are a collection of strains that can be used to map quantitative trait loci. Parent strains are crossed to create recombinants that are then inbred to isogenicity, resulting in a permanent resource for trait mapping and analysis.
Near-isogenic line	Near-isogenic line is constructed by the way of backcross methods. The donor parent carrying the gene of interest is crossed with a recurrent parent to produce a heterozygous F_1, and then repeatedly back-crossing the offspring to the recurrent parent (BC1, BC2, etc.), retaining the donor gene or trait in each successive generation. Marker-assisted selection (MAS) can be used to increase the efficiency of NIL development by screening individuals for the presence of the target locus (gene) in each generation and the absence of extraneous donor DNA throughout the rest of the genome to speed up the return to the recurrent parent type.

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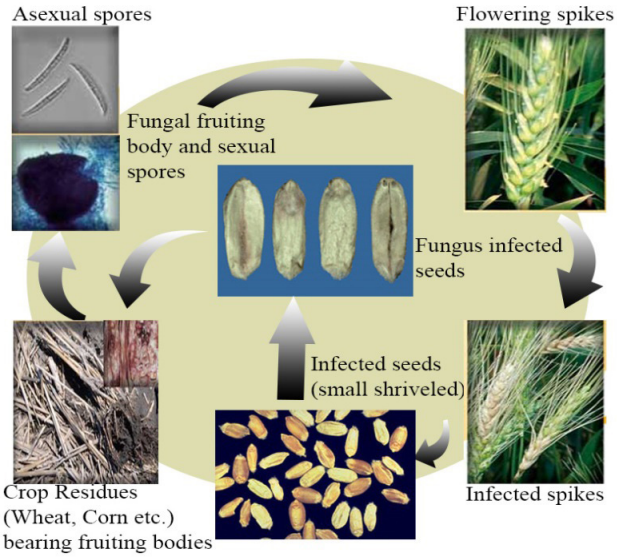

Figure 1. Fusarium head blight disease cycle

durable resistance to the disease in the host plant, and physiological responses are the most significant factor for FHB resistance. Resistance to FHB has been categorized into five resistance types: (a) preliminary contamination (Type I) (Schroeder & Christensen 1963), (b) spread of fungal contamination through the spike (Type II) (Schroeder & Christensen 1963), (c) resistance to mycotoxin accumulation observed by Miller *et al.* (1985), (d) kernel damage (Mesterházy 1995), (e) resistance to yield loss (Mesterházy 1995). Yu *et al.* (2008) observed that the host plant is the most resistant to FHB when multiple mechanisms of resistance are present such as resistance to preliminary contamination, spread of fungal contamination and mycotoxin accumulation. Physiological responses are the most important factor for FHB resistance to the pathogen. When high numbers of plants are subjected to high levels of disease pressure, selection of surviving plants is an excellent source of disease resistance. Such types of plants have genetic resistance to the disease that can be transferred to susceptible cultivars by hybridization techniques. Cultivation of resistant and moderately resistant wheat cultivars against FHB is listed in Table 2.

Quantitative resistance loci associated with FHB

QRL *Fhb1*, a major locus for resistance to FHB, was mapped to chromosome 3B of the resistant wheat cultivar Sumai 3 (Zhuang *et al.* 2013). Anderson *et al.* (2001) confirmed both the phenotypic effects and the chromosome positions of the quantitative resistance loci in a second mapping of wheat plants.

Table 2. Cultivation of resistant and moderately resistant wheat cultivars in the world

Cultivar name	Area of origin	Nature	Cultivar name	Area of origin	Nature
Huoshaobairimai	China	resistant	Chokwang	Korea	moderately resistant
Asozaira III	Japan	resistant	Sotome A	Japan	moderately resistant
Nobeokabozu	Japan	resistant	Nobeokabozu Komugi	Japan	moderately resistant
Asozairai	Japan	resistant	Yanglazi	China	moderately resistant
Huangfangzhu	China	resistant	Wannin 2	China	moderately resistant
Huangcandou	China	resistant	Hongjianzi	China	moderately resistant
Baisanyuehuang	China	resistant	Qiangshuihuang	China	moderately resistant
Yangmai 1	China	resistant	Huishanyangmai	China	moderately resistant
Wangshuibai	China	resistant	Shinchunaga	Japan	moderately resistant
Mutanchiang	China	resistant	Sobakomugi 1C	Japan	moderately resistant
Haiyanzhong	China	resistant	Yangmai 4	China	moderately resistant
Taiwan Wheat	China	resistant	Jiangdongmen	China	moderately resistant
Caizihuang	China	resistant	Xinghuabaiyuhua	China	moderately resistant
Ernie	USA	resistant	Youbaomai	China	moderately resistant
Sumai 3	China	resistant	Yangmai 158	China	moderately resistant
JACEO	Europe	resistant	GK ROZI	Europe	resistant

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Pumphrey *et al.* (2007) performed additional confirmatory experiments on other varieties of wheat and further validated the *Fhb1* resistance. Using tightly linked markers along with 13 existing breeding populations, Pumphrey *et al.* (2007) developed 19 pairs of near-isogenic lines for the resistant Sumai 3 allele at QRL *Fhb1*. They observed that the near-isogenic lines exhibited substantial decreases in the intensity of the disease (Haberle *et al.* 2009). Haberle *et al.* (2009), who mapped the prime FHB quantitative resistance loci positioned on chromosome 1B and, along with 3 other quantitative resistance loci located on chromosomes 2B, 6A, and 7B in case of European winter wheat, concluded that these loci are appropriate targets for marker-assisted selection.

Marker-assisted breeding

Application of large numbers of markers in the molecular breeding during the last few years and the use of such markers in desired plant selection have proved inadequate (Xu & Crouch 2008). Scientists have recognized three useful stages in which MAS should be helpful in plant breeding: (a) selection at earlier developmental stages, (b) genotyping increasing the reliability of plant selection, (c) complex traits more easily assessed in comparison with conventional phenotyping (Collard & Mackill 2008). The development and efficiency of QTL transfer from donor to recipient could be hindered if the genetic background of the recipient parent does not interact favourably with the donor QTL. Markers tightly linked with QTL should be used to improve the transfer of resistance genes from donor parent to recurrent parent (backcross method). The successful development of markers in this way can be used by many plant breeders to simplify desired trait selections. The report of Sharma *et al.* (1995) indicated that transfer, mapping and validation of Barley Yellow Dwarf Virus resistance in wheat grass *Thinopyrum intermedium* (Host) can be transferred to common wheat, where the resistance is not naturally found. The *Bvd2* gene located on the alien segment is polymorphic in most wheat cultivars and reduced recombination with the wheat homoeologous region maintains a close linkage between the markers and gene. Molecular markers are a valuable approach for making selection when trait screening does not reflect the true target environment (Campbell & Lipps 1998). Marker based selection is the most efficient for phenotypic selection, where the trait heritability is high, and the validated marker is subsequently used in selection where heritability is low (Dudley 1993). The cultivation of resistant varieties is the most economical approach to control FHB disease in wheat. Traditional methods for wheat breeding require substantial time and effort, because evaluations of resistance require laborious inoculation and evaluation procedures. Kelly (1995) combined one resistance gene into adapted wheat genotypes using conventional breeding, but it is laborious and difficult to identify desirable plants in segregating populations. Anderson (2007) reported that molecular mapping and MAS are modern tools that help in the exploitation and combining of different resistance genes into a single cultivar within a short period of time. Molecular markers are useful for discovery of new plant genotypes in segregating wheat populations (Liu *et al.* 2000). Roelfs (1988) reported that resistance based on the generation of lines with a combination of more resistance genes is a recommended approach to offer long durable resistance. FHB resistance genes/QTLs (QTLs of type I resistance on chromosomes 3A and 5A and type II resistance QTLs on chromosomes 3B, 6B, 7A) have been combined into a single wheat genotype using MAS (Figure 2).

The essential requirements in crop breeding for marker-assisted selections are: (a) tightly linked markers (maximum distance 1cM) with the trait of interest; (b) available molecular markers for screening

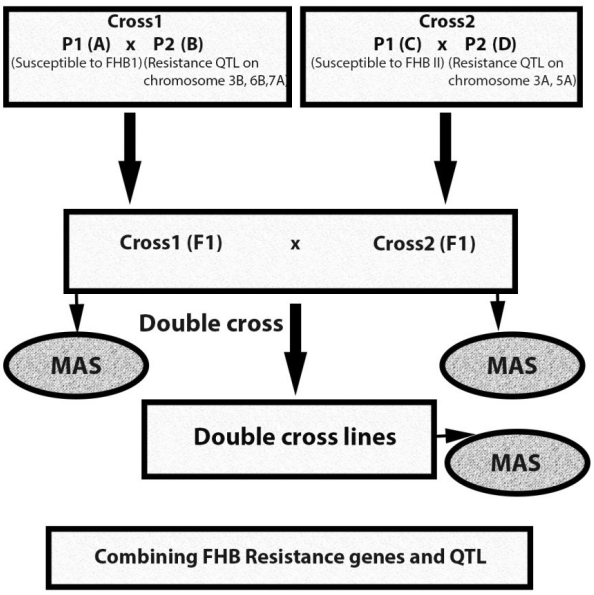

Figure 2. Combining FHB resistance genes and QTL into a single wheat genotype using MAS

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large populations, and (c) accurate technique used for screening across laboratories. Collard *et al.* (2005) reported that MAS may increase efficiency and effectiveness in plant breeding by combining many genes simultaneously into a single genotype. The most frequently used markers are microsatellite markers and their high level of polymorphism makes them very useful as markers for selection in experimental breeding. The markers of restriction fragment length polymorphisms (RFLPs) are codominant in nature and might be easy to use, but the use of radioactive radiation limits their utility in plant breeding programs. Another limitation of random amplified polymorphic DNAs (RAPDs) and RFLPs is a low level of polymorphism with failure in recognition of QTLs related to FHB resistance.

Results on genetic markers were published in the past in which several genes were correlated with resistance to Fusarium head blight on chromosomes of wheat. Bai *et al.* (1995) used 1120 RAPD markers on F_6 RIL (recombinant inbred lines) resulting from the cross between Clark and Ning 7840 wheat cultivars, but among of them, only five markers were associated with FHB resistance. From this, 110 double haploid lines were categorized into two classifications based on four RAPD markers linked to FHB resistance, which exhibited significant variations for Fusarium head blight intensity between the two groups. Bai *et al.* (1999) conducted an experiment on RIL as F_5, F_6, F_7 and F_{10} resulting from hybridization between Ning 7840 (resistant) and Clark (susceptible) and these RIL were evaluated in a greenhouse for the infection of Fusarium head blight in spike. About 300 amplified fragment length polymorphism (AFLP) primers were applied to F_9 plants of 133 RILs for polymorphism using bulked segregant analysis. Among them, only 20 AFLP markers exhibited one polymorphic DNA band in two distinct bulks. Significant associations were observed between the 11 AFLP markers for Fusarium head blight resistance and 53% of variability was shown by markers. Anderson *et al.* (1998) performed experiments on 112 F_5 RILs inoculated with *Fusarium graminearum* conidia and analysed the resultant population by RFLP analysis. Significant associations were observed between the five QTLs for FHB resistance. Buerstmayr *et al.* (2011) introduced a resistant wheat cultivar by the hybridization of *T. macha* and *T. aestivum* and applied various types of RFLP markers to the population for polymorphism of plant morphological traits. Liu *et al*. (2009) conducted a meta-analysis study with 245 QTLs for resistance to Fusarium head blight. Loffler *et al.* (2009) carried out a similar study and the mean location of each cluster was provided. Buerstmayr *et al.* (2009) reported that these two meta-analyses represented a rich source of information for different QTLs associated with the FHB disease. Buerstmayr *et al.* (2009) reviewed more than 100 QTLs for FHB resistance through linkage mapping in wheat. They reported that these QTLs were localized across all 21 chromosomes, except for chromosome 7D. However other researchers, Cativelli *et al.* (2013), identified QTL for type II resistance on chromosome 7D.

Gene pyramiding

Singh *et al.* (2011) reviewed the use of MAS for FHB resistance associated breeding in case of the wheat population. Along similar lines, Wilde *et al.* (2007) discussed the utility of MAS by combining two CM-82036 based QTLs located on chromosomes 3B and 5A with one that had been donated by the Frontana cultivar and was located on chromosome 3A. Yet another study by Shi *et al.* (2008) discussed the same for multiple FHB resistance. Wilde *et al.* (2008) and Miedaner *et al.* (2009) combined the QTLs *Qfhs.lfl-6AL* and *Qfhs.lfl-7BS* derived from the wheat variety Dream with the QTL from the line G16-92 which is present on the chromosome 2BL. The double cross population generated was subjected to FHB infection and subjected to comparison with respect to phenotype as well as marker selection. Miedaner *et al.* (2009) concluded that the effectiveness of singular QTLs for inducing resistance to FHB is low, hence it is imperative to combine multiple alleles using MAS so as to augment resistance.

Gene pyramiding is the accumulating of several traits of interest from various parental lines into a single variety. Joshi and Nayak (2010) applied molecular markers to select lines having genes of interest and made crosses to accumulate desired traits into a single genotype. Durable disease resistance refers to pyramiding the multiple resistance of monogenic and polygenic allele in a variety, which is an approach to enhance the level of disease resistance (Figure 3). Gene pyramiding programs comprise three stages. The first stage involves the selection of parents having a desirable gene (Joshi & Nayak 2010). In the second step, successive backcrossing to one of the parents results in the accumulation of desired genes (Joshi & Nayak 2010). The third stage involves

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consecutively selfing to generate homozygous plants with desired traits (Joshi & Nayak 2010). Rudd *et al.* (2001) developed the wheat cultivar Sumai3 from moderately resistant parents; along similar lines they developed Ernie from moderately susceptible parents that exhibited a transgressive segregation for resistance to the FHB disease. Sumai 3, which has type II FHB resistance, and Frontana, which has type I FHB resistance, were pyramided in RCATL33 as a soft red winter wheat (Tamburic-Ilincic *et al.* 2006).

Backcross breeding

Molecular markers have been widely used for improving backcrossing efficiency for the purpose of marker-assisted building of disease resistance, generation of quality improved genotypes as well as for improved abiotic stress tolerance. In principle backcrossing involves using a donor line to assemble a target trait that is controlled by a single gene into a highly adapted recipient line. Molecular markers can be used at the level of each backcross cycle to identify the target trait having the closest fit to the recurrent parent genotype.

Three QTLs, *Fhb1* and *Qfhs.ifa-5A* that had been mapped in CM-82036 along with *Qfhs.ifa-3A* previously mapped in Frontana, were accumulated into susceptible spring wheat varieties (Nandu, Munk). Introgression of two or three closely linked DNA markers per QTL led to the development of superior spring wheat lines bearing all three QTLs individually as well as all combinations thereof (Miedaner *et al.* 2006, Wilde *et al.* 2007). In another example, Von der Ohe *et al.* (2010) introgressed two FHB-resistance QTLs (*Fhb1*, *Qfhs.ifa-5A*) from a spring wheat line into winter wheat. Finally, all backcross generations resulted in specific lines containing three flanking markers for *Fhb1* and two markers for *Qfhs.ifa-5A*. The lines were selected again after the first two selfing generations for the homozygous target QTL and thereafter assigned to the following four marker classes: (a) *Qfhs.ifa-5A* (*AAbb*), (b) *Fhb1* (*aaBB*), (c) both QTLs present (*AABB*), and (d) neither QTL present (*aabb*). This categorization comprised 25 and 15 lines in the Anthus and Opus backcross populations, respectively. Additionally, selected BC_3F_2 derived bulks in $BC_3F_{2:3}$ were generated twice, which resulted in the generation of $BC_3F_{2:5}$ phenotypes evaluated in the field (Von der Ohe *et al.* 2010).

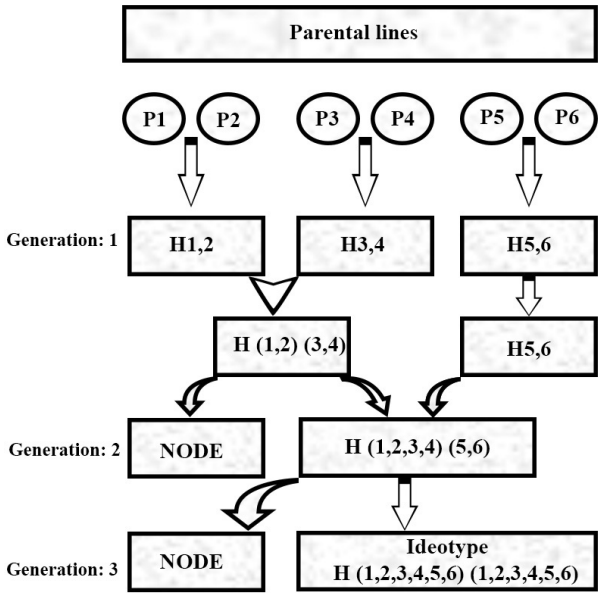

Figure 3. Schematic representation of gene pyramiding

Future developments

The available literature showed that molecular markers have been extensively used for mapping and tagging of hundreds of various important genes/QTLs in wheat for disease resistance. Disease resistance, especially to FHB, using MAS techniques in wheat breeding might be revolutionized in the next years by technological improvements. The use of molecular markers has led to possible characterization of the target genes and the identification of their positions on linkage maps. Moreover, the use of such markers from the gene sequences might be helpful in future in recognition and utilization of newer genes in wheat improvement for disease resistance. Plant breeding experiments require the screening of large segregating populations routinely over generations and introgression of such resistance genes into a single genotype might ensure the development of durable disease resistance cultivars in the future. However, screening a large number of samples manually is an extremely difficult task for the plant breeders and the application of MAS practically in plant breeding would allow easier handling and screening of large populations for disease resistance. The use of PCR based markers of sequence-tagged site (STS) and sequence characterized amplified region (SCAR) will be a key to the success of MAS in crop improvement.

CONCLUSIONS

FHB is a destructive disease that reduces grain yield and quality of wheat. In breeding for resistance

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against this disease, there is still a need for developing new and improved wheat cultivars. Combining associated resistance genes into a single genotype can lead to durable resistance against FHB. Molecular markers are now successfully used to identify genotypes for resistance genes associated with several diseases of wheat. Marker-assisted selection is one of the modern techniques that are being practiced to transfer simple traits that are not easy to score such as disease resistance traits. Hence, both traditional breeding methods and molecular techniques used simultaneously allow the selection of new wheat genotypes carrying desirable traits within a shorter period of time. Many QTLs on various chromosomes for FHB resistance have been combined by genotypic selection into a single genotype. The review concluded that MAS could be utilized in the selection of traits of interest against FHB. As a breeding tool, gene pyramiding is important for germplasm improvement and pyramiding requires a small population which increases the chance of obtaining the desired genotype.

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