

An overview of genome-wide association mapping studies in Poaceae species (Model crops: Wheat and Rice)

Muhammad Naeem (✉ naemmuaf@gmail.com)

Nigde University: Nigde Omer Halisdemir Universitesi <https://orcid.org/0000-0002-5066-3465>

Muhammad Abu Bakar Zia

Bahauddin Zakariya University Sub-Campus Layyah

Muhammad Farhan Yousaf

Nigde Omer Halisdemir Universitesi

Arslan Asim

Nigde University: Nigde Omer Halisdemir Universitesi

Research Article

Keywords: Genetic mapping, Association mapping, QTLs, Wheat, Rice

Posted Date: April 13th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1509810/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

There is a significant interest while utilizing association mapping technique to determine the genes which are accountable for numerical dissimilarity of the more complex characteristics with agronomic and evolutionary significance. Recently improvements have been made in genomic technology, which motivates for the exploitation of natural diversity, and establishment of more vigorous and strong statistical analysis methods creates association mapping technique more demanding and reasonable to plant research programs. Genome-wide association mapping technique recognizes quantitative trait loci (QTLs) by studying the marker-trait associations which could be credited to the power of linkage disequilibrium between different molecular markers and functional polymorphisms through a pool of diversified germplasm. In this review, we will describe an overview of genetic mapping and the current status of association mapping studies in cereal crops i.e., wheat and rice.

Introduction

An overview of genetic mapping in plants

The question of which genes contribute to which phenotypic characteristics/traits have been well addressed by an approach known as genetic mapping. In 1911, T.H. Morgan and his student Alfred Sturtevant, published the first genetic map, depicting the location of six sex-linked genes on the chromosome of a fruit fly. In plants, genetic mapping serves as the foundation for the identification of genomic regions underlying important plant traits such as disease resistance, salt, and drought tolerance/resistance, yield and quality characteristics (Sharlach et al., 2013; Long et al., 2013; Solis et al., 2018; Pereira et al., 2018; Barik et al., 2020). These are complex traits controlled by polygenes or minor genes and hold great economical and agricultural importance in the era of climate change, malnutrition and food security. By far polygenic traits have been proved to be challenging due to complex segregating patterns and complications in the precision mapping of all genomic regions responsible for the variation in complex traits (Doerge 2002). The evolution of species occurred in complex environments with varying conditions, both in time and space. These complex traits can also be designated as quantitative traits and are strongly influenced by fluctuating environments; for instance, heritability measured under controlled conditions (laboratory or greenhouse) often exceeds field experimentation (Anderson et al. 2014). A genetic locus/loci or more precisely a gene linked to the natural variation in quantitative trait/s is known as quantitative trait locus/loci (QTL). The hypothesis that phenotypic variation of complex traits may be linked to several structural variants or causative variants, catalyzed the genetic mapping studies in plants (Xu et al. 2017).

The identification of QTL linked to natural phenotypic variation is the main aim of genetic mapping (Xu et al. 2017). It is also referred to as meiotic mapping or linkage mapping and utilizes molecular markers in various plant species to reveal causative genomic regions, intended to determine the relative position of genes on a molecule of DNA (plasmid or chromosome), along with the distance between them. A genetic map showed a position and relative genetic distance between the markers along chromosomes, which is

analogous to a flanking region cuddled to the gene of interest (Semagn et al. 2006). In fact, a genetic map is synonymous with a highway mile-marker system created by geneticists. The highway mile marker system was created through the development of structured plant populations which showed segregation for the set of markers along with the trait of interest. The distance between the markers residing on the same chromosomes can be determined by detecting the amount of recombination in the structured plant populations. Recombination is a vital meiotic process occurring in the anther sacs and ovule of plant species involving the exchange and repair of male and female chromosomes. Higher recombination indicated that the markers are farther apart from each other (Hyten and Lee, 2016).

Numerous markers like protein markers, phenotypic markers and molecular markers are used for the construction of genetic linkage maps. The advancements in next-generation sequencing (NGS) have made available high-throughput markers for fine mapping of plant genomes at a reasonable cost. In this regard, the most common sequence variations or molecular markers that can serve as potential genetic markers include simple sequence repeats (SSRs) and single nucleotide polymorphisms (SNPs). Recently, genetic linkage mapping has expanded and got several applications such as QTL mapping, gene mapping, genome-wide association mapping (GWAS), and marker-assisted selection (MAS) (Hyten and Lee, 2016). With the availability of NGS, linkage mapping can be done to locate QTL (Quantitative trait loci) on corresponding genomes of the biparental population to facilitate MAS. Alternatively, QTLs or genomic regions can be identified by extensive genotyping of germplasm panel of breeding populations or cultivars depicting biological variation/diversity in phenotypes across fluctuating environments, with an objective to reveal marker-trait associations. The former approach is termed QTL mapping while the latter is known as genome-wide association mapping (GWAS).

Association Mapping in Wheat

According to FAOSTAT, 2020 the wheat crop stands at the second position among the most-producing cereal crops around the world (FAOSTAT, 2020). It contributes around 19% among the total production of cereal crops and delivers about 55 % of the carbohydrate which are utilized by humans all over the globe (Gupta et al. 1999; Bagge et al. 2007). Biotic and abiotic stresses effect the production of wheat and plays a significant role in the reduction of its potential yield. It's the requirement of the time to make strategies and develop a technique against these stresses, and plant breeding is one of the tools to cope with biotic and abiotic stress conditions including drought, salinity and plant diseases (Araus et al. 2008; Cooper et al. 2009). Traditional plant breeding approach is very slow and still there is a big yield difference between drought prone areas and perfect growing areas for most of the crops, comprising wheat. As drought tolerance is a very complex quantitative trait that is controlled by minor genes which are located on several chromosome regions (Barnabas et al. 2008; Fleury et al. 2010; Pinto et al. 2010; Ravi et al. 2011; Mir et al. 2012). Genetic enhancement for drought resistance necessitates to find the genomic regions related to drought tolerance and transferring the genes possess the desired characters to locally adapted cultivars. The major task for applying this approach in future breeding programs is the finding of the most appropriate targeted traits in an efficient and cost-effective method for varied water

scarcity scenarios (Passioura 2012). Recently improvements in high-throughput genotyping and phenotyping have increased the understanding of biological and molecular bases hold complex traits including drought resistance (Collins et al. 2008; Habash et al. 2009; Mir et al. 2012; Sinclair 2012). QTL mapping is an important tool for the better understanding of genomic structure of more complex characters in the plants (Holland 2007). Yet, QTL mapping technique by consuming biparental populations defines a minor portion of the genomic structure of a parameter for the reason that only two alleles on a locus can be screened at a time. Some other restrictions of biparental populations are low resolution of mapping, population specificity of identified QTL, and extensive time is necessary to generate the mapping populations. These restrictions make hurdles in the transfer of information from biparental QTL studies to the practical use in breeding programmes. Few problems belong to the biparental mapping population has been resolved with the introduction of the association mapping technique. Diverse germplasm can be used for association mapping and high resolution from AM can aid to detect QTL for many traits which make this technique most effectual and less costly than bi-parental QTL mapping approach (Bressegello and Sorrells 2006; Ersoz et al. 2009; Sorrells and Yu 2009; Waugh et al. 2009).

Mostly agronomic traits were organized by many genes, and QTLs trainings in these plants commonly use the linkage studies with F₂, DH and backcross populations. In wheat, QTL mapping studies have been performed on agronomic traits such as flowering period, grain yield, some quality traits and resistance against diseases by using these populations (Borner et al. 2002; Peng et al. 2003; Blanco et al. 1998; Khan et al. 2000; Perretant et al. 2000; Olmos et al. 2003; Otto et al. 2002; Gervais et al. 2003; Navabi et al. 2005; Toth et al. 2003; Hanocq et al. 2004). Contrarily, QTL mapping in segregating population have a lot of limitations. This includes less allele quantity and middle density of marker. Association mapping is a technique that works on the basis of linkage disequilibrium (Zondervan and Cardon 2004). Compared to conventional linkage analysis, association mapping offers the vital benefits of sampling unrelated individuals in the population for marker-assisted selection in diversified traits study in plant breeding (Risch 2000; Jannink et al. 2001). First of all, the investigational population can be a demonstrative sample of the population to which interpretation is wanted. Secondly, association mapping could be more effective in the utilization of resources and means. For example, many traits could be studied in the same population by utilizing the similar genotypic records. A greater quantity of molecular markers with polymorphic is expected to deliver improved genomic analysis than biparental mapping. In addition, phenotypic record of many years and time would be accessible deprived of extra cost in study of elite wheat lines (Rafalski 2002). Recently, it has been extensively used for the QTLs discovering in many plants' species like maize, rice and barley etc., Important SSR markers linked with the size of wheat kernel was determined by Bressegello and Sorrells (2006) in hexaploid wheat. International Maize and Wheat Improvement Centre (Jose et al. 2007) set up a multi-environmental experiment to examine the relation among stem rust, leaf rust, yellow rust, powdery mildew, and grain yield by utilizing two markers diversity array technology (DArT) marker and SSR marker. Tommasini et al. (2007) found genomic region that controls resistance against *Stagonospora nodorum* blotch by linkage analysis with SSR markers. Association mapping works on the principle of linkage disequilibrium (LD). Extent of LD

across the genome determines the strength and resolution of association mapping studies. The strength of association mapping increases when linkage disequilibrium decays quickly (Rafalski 2002). Extent of LD is varied in different species. The extent of linkage disequilibrium was about 1 cM in chromosome 2D, nearly 5 cM in the centromeric region of chromosome 5A and less than 0.5 cM in chromosome 3B of hexaploid wheat depends on SSR markers (Breseghello and Sorrells 2006; Tommasini et al. 2007). Since linkage disequilibrium is affected by many dynamics such as population history, recombination rate and mating system, it is desirable to examine it in each study.

Association mapping studies in hexaploid wheat are extended to grain yield, kernel size and milling quality of grain, the amount of glutenin content and disease resistance (Breseghello and Sorrells 2006; Jose et al. 2007). On the other hand, there are limited studies about yield related agronomic trait like spikelets per spike and grains per spike. Some examples of association mapping studies in wheat are presented in Table 1.

Table 1

Examples of Association Mapping studies in Wheat

Association mapping in Rice

Rice is a staple food crop feeding 3 billion people worldwide (FAO, 2021). The development of improved varieties providing resistance against biotic and abiotic stress factors combined with high productivity, quality and adaptability under wide range of environmental conditions are the major objectives and challenges of rice breeders worldwide (Gregoria et al., 2013). Rice genome is small having a size of 400 to 430 Mbp among major cereal crops (Eckardt, 2000). A genome size of 389 Mbp was reported by International Rice Genome Sequencing Project (IRGSP). A total of 37,544 protein coding sequences were detected along with the identification of 80,127 polymorphic sites that distinguish two rice species i.e., indica and japonica (International Rice Genome Sequencing Project, 2005). It is fortunate that the availability of sequencing technologies coupled with fully sequenced rice genome (availability of 3000 re-sequenced varieties) has created an opportunity to enhance crop productivity and quality using modern genomic tools and methods (Begum et al., 2015; McCouch et al., 2016). GWAS is a significant tool for unveiling genotypic variation associated with complex phenotypic traits. Mapping of candidate genes concerning to the desired trait of interest can be achieved efficiently through GWAS. Several methods such as GLM, MLM, FarmCPU and BLINK were employed for GWAS analysis. Though GLM helps in the identification of a greater number of QTLs compared to other methods but prone to false-positives. MLM reduce false positive rates but may causes overcorrection which reduced its power of detection. Both BLINK and FarmCPU uses multilocus model for testing markers across genome, hence possesses higher statistical power and decrease false-positives (Zhong et al., 2021). A comprehensive detail of GWAS in rice is outlined in Table 2.

Table 2

Population	Sample Size	Markers Used	Traits	References
Diverse Accessions	1596	5011 SNPs	Seedling leaf rust resistance	Li 2016
Diverse cultivars	95	95 SSRs	Kernal Size, Milling Quality	Bresegheo and Sorrells 2006
Soft Winter Wheat Accessions	95	36 SSRs	Kernal Size, Milling Quality	Flavio et al. 2006
Diverse Accessions	108	85 SSRs 40 EST-SSRs	Agronomic Traits (Plant Height, Spike Length, Spikelet per spike, Grains per Spike, 1000 grain weight)	Yao et al. 2009
Elite durum wheat accessions	189	56 SSRs	Drought + Adaptive traits and grain yield	Marco Maccaferri et al. 2011
Diverse European Elite wheat lines	207	115 SSRs	1000- Kernal weight, Protein content, Sedimentation volume, Starch concentration	Reif et al. 2011
Elite winter wheat	120	3051 DArT	Yield and grain quality	Tadesse et al., 2015
Durum Wheat	287	30155 SNPs	Agronomic traits	Mengistu et al., 2016
Spring type bread wheat cultivars	108	9646 SNP	Yield and yield related traits	Qaseem et al., 2018
Spring wheat	586	90K SNP	Grain yield and agronomic traits	Garcia et al., 2019
Advanced lines	382	2214 SNPs	Drought + agronomic traits	Ballesta et al., 2019

Examples of Association Mapping studies in Rice

Phenotypic Trait	Markers	Population	Number of associated loci/QTLs	Chromosomes (Position)	References
<i>Agronomic & Yield traits</i>					
Yield and Agronomic traits	71,710 SNPs	363 elite breeding lines from IRRI	52	2, 3 (233 bp to 900 kb), 6 (47.9 kb), 7, 8, and 11 (38 bp)	Begum et al. (2015)
Agronomic traits and drought tolerance	3.6 million SNPs	517 landraces	80	2 (25.02 and 30.18 Mb), 3 (17.37 Mb), 5 (5.3 Mb), 6 (1.7-6.7 Mb), 9 (7.3 Mb), 10 (2.31 Mb) and 11 (21.16)	Huang et al. (2010)
Agronomic traits	426,337 SNPs and 67,544 indels.	176 <i>japonica</i> rice varieties	26	1, 3, 6, 7, 8 and 11	Yano et al. (2016)
Panicle architecture	411,066 SNPs	421 accessions (Rice diversity panel)	106	All chromosomes	Zhong et al. (2021)
Morphological traits of panicle	241 DArT and 25971 SNPs	159 traditional varieties	105	All chromosomes except 5	Ta et al. (2018)
<i>Abiotic traits</i>					
Cold tolerance	36727 SNPs	211 landraces	12	2 (4.4 Mbp); 3 (10.23-11.31 Mbp); 4 (11.4 Mbp); 7 (29.11 Mbp) and 9 (7.10 Mbp)	Li et al. (2021)
Chilling tolerance	148 SSRs+3 InDels+6 SNPs	202 RMC accessions	48	All chromosomes; two novel QTLs (<i>qLTSS3-4</i> and <i>qLTSS4-1</i>) positioned at 35.3 & 13.6 Mbp on chr 3 & 4, respectively.	Schläppi et al. (2017)
High temperature	14,779,691 SNPs data from 3 k database	255 Asian cultivated rice varieties	117	3 (2.96-3.82 cM), 6 (2.77 cM), 7 (3.68 cM), 9 (3.54 cM), 11	Wei et al. (2021)

				(5.01-6.72 cM), 12 (2.82, 4.80 cM)	
High temperature	2 million SNPs	98 rice accessions	2	10 and 11	Kwon et al. (2021)
Drought tolerance	21623 SNPs	180 Vietnamese landraces	17	1 (22.97-24.84 Mbp), 2 (35.13 Mbp), 5 (14.99-15.94 Mbp), 6 (17.77-17.84 Mbp), 7 (17.90-20.79 Mbp), 10 (10.28 Mbp), 11 (24.38-25.67; 66.42-68.95 Mbp)	Hoang et al. (2019)
Drought tolerance	170 SSR	114 rice genotypes	11	1, 4, 7 and 9	Verma and Sarma (2021)
Drought tolerance	4 358 600 SNPs (RiceVariation Map v2.0)	507 accessions	470	Nearly all chromosomes (<i>OsPP15</i> gene)	Guo et al. (2018)
Drought tolerance	4,358,600 SNPs	529 rice accessions	143	All chromosomes (<i>Nal1</i> and <i>OsJAZ1</i> genes)	Li et al. (2017)
Salt tolerance	> 33000 SNPs	155 varieties	151	1 (40.79-42.98 Mbp); 2 (35.26 Mbp); 6 (29.76-31.21 Mbp); 7 (19.66-19.83 Mbp); 9 (17.96 Mbp); 10 (6.12-7.32 Mbp); 12 (17.53-18.60 Mbp)	Nayyeripasand et al. (2021)
Cadmium tolerance	3.3 million SNPs	188	119	All chromosomes	Yu et al. (2021)
Sulfur deficiency	700k SNPs	98 accessions	11 (<i>low S conditions</i>)	1 (12.11 Mb), 2 (21.4 Mb), 3 (19.34, 28.01 Mb), 4 (32.96 Mb), 6 (0.29 Mb), 9 (15.01 Mb) and 11 (17.95 Mb)	Pariasca-Tanaka et al. (2020)
<i>Biotic traits</i>					
Rice Blast resistance	High density 700 K SNP	420 accessions	97	Distributed on all chromosomes	Kang et al. (2016)

(<i>Maganaporthe oryzae</i>)	array				
Rice blast (<i>Magnaporthe oryzae</i>)	High density 700 K SNP array	413 accessions	16	1, 3, 4, 5, 8, 9, 10, 11, 12	Zhu et al. (2016)
Sheath Blight resistance (<i>Rhizoctonia solani</i>)	44k SNPs	299 varieties	147 (2 reliable QTLs)	3 (16-17 Mbp); 6 (20-22.5 Mbp)	Chen et al. (2019)
Rice black-streaked dwarf virus	44k SNP array	305 accessions	13	1 (2.09-2.72 Mbp); 2 (19.54-29.73 Mbp); 3 (29.7 and 27.69-28.02 Mbp); 4 (41.72-52.55 Mbp); 6 (10.95-11.10 and 17.99-19.86 Mbp); 8 (16.3 and 19.7 Mbp); 11 (9 Mbp)	Feng et al. (2019)
Bacterial leaf streak resistance (<i>Xanthomonas oryzae</i>)	140345 SNPs	510 accessions	79	All chromosomes (majority on chr 11)	song et al. (2021)
Quality traits					
Grain protein, amylose content, alkali spreading value	22947 SNPs	217 USDA accessions	10	4 (23.52 Mbp); 6 (16.43-17.88 Mbp); 8 (18.11 Mbp); 12 (24.08 Mbp)	Song et al. (2019)
Grain appearance and milling quality	22488 SNPs	258 accessions	72	All chromosomes	Wang et al. (2017)
Cooked rice texture	700K high Density Rice Array (HDRA)	236 <i>Indica</i> accessions	97	All chromosomes	Misra et al. (2018)
Grain Starch	246,026 SNPs	115 accessions	16	1, 2, 3, 5, 6, 8, 11	Biselli et al. (2019)

High density panel of markers covering the whole genome can be used successfully for the detection of recombination density points in unrelated populations (Zhu et al., 2008). High density polymorphic 71,710 SNPs were genotyped using genotyping by sequencing (GBS) technique and further utilized to perform GWAS in 363 elite panel of breeding lines from International Rice Research Institute (IRRI). 52 QTLs were identified and found to be associated with yield and yield components such as flowering time,

grain length, width, plant height and rice grain yield. Plant height and flowering time were linked with the candidate gene named *OsMADS50* positioned on chr 3, which is a known activator of flowering in rice and also termed as pleiotropic gene (Lee et al., 2004; Begum et al., 2015). A high-density haplotype map was constructed using approximately 3.6 million SNPs through a sequencing of 517 rice landraces (*Oryza sativa indica*). The information was further used to perform GWAS regarding 14 agronomic traits. 56 significant SNPs were detected that are tightly linked to already identified genes in rice on chr 3, 5, 6 and 7. The peak signals were identified for apiculus colour, pericarp colour, Gelatinization temperature, amylose content, grain width and grain length (Huang et al., 2010). 29 stable QTLs were identified on nearly all 12 chromosomes except 5 using 241 DaRT and 25971 SNPs in a set of 159 traditional rice varieties. These QTLs were associated with genes that control panicle development and architecture such as *LONELY GUY* (*LOG*), *TAWAWA1* (*TAW1*) and *RICE DOF DAILY FLUCTUATIONS 1* (*RDD1*) (Ta et al., 2018). It is common to select alleles of the same gene during crop domestication and breeding resulting in allelic heterogeneity. To deal with spurious associations, gene-based association analysis proves to be effective. In rice, chromosome 8 contains a crucial causal gene (*LOC_Os08g37890*) for awnless phenotype detected through gene-based association analysis facilitated by whole genome sequencing. This method followed by gene expression profiling eliminates spurious associations that are meant to happen through allelic heterogeneity (Yano et al., 2016). It is pertinent to discuss here the power of GWAS combined with GPWAS (Genome-Phenome wide association mapping) to unveil significant QTLs and genes linked with panicle architecture in rice. 23 candidate genes were identified by employing both these techniques using 411,066 SNPs covering 62.40% (23,623 out of 37,860) genes in rice (Zhong et al., 2021). A candidate gene (*Os07g0669700*) on chr 7 with gene annotation of potassium transporter 7 (*OsHAK7*) was associated with total spikelet number per plant (TSNP). Loss of function *OsHAK7* mutant causes a decrease in panicle length, grain yield and seed setting in comparison to wild type (Chen et al., 2015). *Os01g0140100* was TSNP linked overlapped gene identified by both GWAS and GPWAS that is crucial for rice fertility. Potassium transporter gene (*Os02g0809800*; *OsPHO1;2*) detected by GPWAS technique was known to regulate number of panicles, grain number per panicle, 1000-grain weight and yield per plant in rice (Zhong et al., 2021).

A study conducted by Schläppi et al. (2017) concluded that japonica rice accessions possess a high tendency to tolerate chilling environment as compared to indica accessions. Mapping of QTLs using GWAS approach was done based on five chilling tolerance indices (namely low temperature germinability (LTG), plumule growth rate after cold germination (PGCG), seedling survivability at low temperature (LTSS), plumule recovery growth after cold exposure (PGC) and survival at low temperature (LTS)). 48 QTLs were identified on nearly all 12 chromosomes. *qLTG10-2* located on chr 10 (21.1 Mbp) confer chilling tolerance due to the overexpression of associated candidate gene *MYBS3* in rice (Su et al., 2010). Similarly, *qPCGC9-2* is present within the candidate gene *OsWRKY76*, which showed tolerance against cold during overexpression studies (Yokotani et al., 2013). Schläppi et al. (2017) identified two novel QTLs (*qLTSS4-1* and *qLTSS3-4*) associated with seedling chilling tolerance, which provides a good indicator of field performance of transplanted rice seedlings. An important QTL linked with recovery of plumule after exposure to cold stress was found on chromosome 6 (*qPGC6-1*). This particular QTL was

found to be associated with cold stress gene OsDREB1C. It is pertinent to recall here that DREB transcription factor family is highly responsive in improving tolerance to drought and low temperature conditions (Chawade et al., 2013). Chilling acclimation has been achieved through genes such as OsCAF1B and ABA receptor OsPYL/RCAR5. These annotated genes were associated with QTLs located on chr 3 (qLTG3c), 4 (qLTG4), 5 (qLVG5), 7 (qLVG7-1) and 12 (qCTGERM12-2). Overexpression of these genes enhanced survival rate and decrease the leakage of electrolytes in transgenic lines subjected to cold stress (Verma et al., 2019; Fang et al., 2021). Population structure analysis conducted by Li et al. (2021) also confirmed that japonica rice was more tolerant against cold as compared to indica rice in a GWAS study carried for 211 rice landraces. Using MLM with a robust set of 36,727 SNPs, twelve QTLs were associated with cold tolerance at bud burst stage (seedling survival rate). Seven novel QTLs were identified and among those qSSR9 was the most significant SNP explaining the maximum phenotypic variation ($R^2 = 0.14$). This QTL was localized on chr 9 comprising of 39 underlying candidate genes. Further, candidate gene analysis elucidates that among 39 genes, 5 were colocalized with cold tolerance genes such as COLD1, LTG1, Ctb1, OsbZIP73 and OsWRKY71, respectively. Therefore, the region located on chr 9 is favourable for mining of alleles and genetic resources to be used for breeding new rice varieties characterized with cold tolerance (Li et al., 2021). In rice, chromosome 9 contains a QTL named qSR_ind9-3 associated with a gene Ugp1 that confers tolerance to heat stress at the seedling and heading stage. GWAS revealed two more significant QTLs i.e., qDW_ind8 (3.09 Mb–3.29 Mb) and qFW_ind8 (3.09 Mb–3.29 Mb) positioned on chromosome 8. This region was linked to dry and fresh weight of rice controlling biomass under high temperature stress environments. Interestingly, in rice the LD is between 100 to 200 kb. A 200 kb interval in qFW_ind6, qFW6 (chr 6), and qDW_ind7, qDW7 (chr 7) carries important candidate genes conferring resistant to heat at the seedling stage (Wei et al., 2021). Functional genomic study of these genes will further disclose their molecular mechanisms. Kwon et al. (2021) were of the view that chromosomes 10 and 11 bear two significant QTLs (qHTS10 and qHTS11) associated with spikelet fertility under high temperature (marker for tolerance to high temperature) revealed in a set of 98 rice accessions using GWAS technique. Haplotype analysis showed 39 candidate genes located within these two QTLs. Interestingly only one gene (Os10g0177200: EF-HAND 2 domain containing protein) demonstrated significant difference among the haplotypes. This candidate gene encodes Ca²⁺ binding proteins (CBP) having a helix-loop-helix structure conferring resistance against stress environments (cold and heat) through the movement of Ca²⁺ ions within the cell (Zeng et al., 2017). RM212 and RM252 markers identified through association mapping technique have been linked with drought tolerant traits in rice (Verma and Sarma, 2021). QTLs such as qDTY1.1, qDTY2.2, qDTY2.3, qDTY3.1, qDTY3.2, qDTY6.1, and qDTY12.1 regulates grain yield under drought stress (Li et al., 2017; Hoang et al., 2019). Candidate gene analysis demonstrates the efficiency of two genes (Nal1 and OsJAZ1) controlling root traits improving drought avoidance in rice (Li et al., 2017).

GWAS identified 11 SNPs associated with sheath blight (SB) resistance in rice diversity panel of 299 varieties using 44k SNPs. Two reliable QTLs (qSB3 and qSB6) localized on chr 3 and chr 6 were found to be linked with SB resistance (Chen et al., 2019). Using 700k SNPs in an unrelated population of 420 rice accessions, GWAS identified 97 non-redundant loci associated with blast resistance (Magnaporthe

oryzae). Chromosome 9 contains LABR_64 locus associated with broad-spectrum blast resistance against all five tested blast isolates in several different subpopulations of rice (Kang et al., 2016). This locus colocalizes with previously known resistance locus Pi5 that requires two NBS-LRR (nucleotide-binding site leucine-rich repeat) genes i.e., Pia and Pikm, also found in R genes (1). It might explain the broad-spectrum biotic resistance of this particular locus. Bacterial leaf streak (BLS) is a devastating rice disease caused by *Xanthomonas oryzae* pv. *Oryzicola*. GWAS performed on 510 rice accessions revealed 69 QTLs associated with BLS with a peak signal on chromosome 11 followed by chr 1 and chr 5. Important QTLs includes qnBLS5.1, qnBLS9.1 and qnBLS11.17 corresponding to genes LOC_Os11g47600 and LOC_Os11g47680 which perform functional roles under stress conditions (Xie et al., 2021). Similarly, GWAS identified important QTLs associated with quality characteristics of rice as outlined in Table 2. Significant marker trait associations were detected on chr 1, 5 and 6 related to starch and amylose contents (Biselli et al., 2019). A major QTL corresponding to rice textural attributes such as adhesiveness and amylose content were positioned on chromosome 6 (Misra et al., 2018). A total of 19 candidate genes including GS3 and TUD and 17 QTLs including two previously mapped QTLs (qGRL7.1 and qPGWC7) were discovered by Wang et al. (2017) affecting rice milling properties and grain appearance. GWAS approach played a crucial role in development of tolerant/resistance rice varieties and paved a way for next generation breeding using selection markers. In addition to marker assisted based breeding, candidate genes provide valuable information for functional characterization and development of molecular tool kit for continued rice improvement.

Conclusion And Perspectives

We have reviewed the progress in genetic mapping techniques and association mapping studies conducted in *Poaceae* species to dissect the genomic and molecular origins of numerical characteristics. A lot of mapping studies have been conducted in wheat and rice which have certified the recognition of thousands of QTLs some of which are of keen interest for breeding point of view. Mapping with segregating populations is an effective method for comparing two alleles with low resolution. In contrast, association mapping can assess a wide range of variables alleles with high resolvability. According to our understanding, these two approaches are mutually beneficial and a successful combination will allow for the dissection of quantitative traits all the way down to the single-gene level. The selection of germplasm holds prime significance in association mapping, quality of genotypic and phenotypic data, along with application of appropriate statistical analysis for the detection and confirmation of marker-phenotype associations.

Declarations

Acknowledgements

The authors acknowledged Amir Maqbool (PhD) and Syed Ali Zafar (MSc), for assisting in proofreading of this publication.

Author contributions

All authors contributed equally to the research and composition involved with this publication.

Funding

Nothing declared.

Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest. The authors of this review article have no professional, personal, or financial competing interests of any kind relating to this publication.

References

1. Anderson JT, Wagner MR, Rushworth CA, Prasad KVSK, Mitchell-Olds T (2014) The evolution of quantitative traits in complex environments. *Heredity* 112(1):4-12
2. Araus JI, Slafer GA, royo C, Serret MD (2008) Breeding for yield potential and stress adaptation in cereals. *Crit rev Plant Sci* 27:377–412
3. Bagge M, Xia XC, Lubberstedt T (2007) Functional markers in wheat commentary. *Curr Opin Plant Biol* 10:211–216
4. Ballesta P, Mora F, Del Pozo A (2019) Association mapping of drought tolerance indices in wheat: QTL-rich regions on chromosome 4A. *Scientia Agricola* 77
5. Barik SR, Pandit E, Mohanty SP, Nayak DK, Pradhan SK (2020) Genetic mapping of physiological traits associated with terminal stage drought tolerance in rice. *BMC Genetics* 21(1): 1-12
6. Barnabas B, Jager K, Feher A (2008) The effect of drought and heat stress on reproductive processes in cereals. *Plant Cell Environ* 31:11–38
7. Begum H, Spindel JE, Lalusin A, Borromeo T, Gregorio G, Hernandez, McCouch SR (2015) Genome-wide association mapping for yield and other agronomic traits in an elite breeding population of tropical rice (*Oryza sativa*). *PloS One* 10(3):e0119873
8. Biselli C, Volante A, Desiderio F, Tondelli A, Gianinetti A, Finocchiaro F, Valè G (2019) GWAS for starch-related parameters in japonica rice (*Oryza sativa* L.). *Plants* 8(8):292
9. Biselli C, Volante A, Desiderio F, Tondelli A, Gianinetti A, Finocchiaro F, Valè G (2019) GWAS for starch-related parameters in japonica rice (*Oryza sativa* L.). *Plants* 8(8):292

10. Blanco A, Bellomo MP, Lotti C, Maniglio T, Pasqualone A, Simeone R, Troccoli A, Di Fonzo N (1998) Genetic mapping of sedimentation volume across environments using recombinant inbred lines of durum wheat. *Plant Breed* 117:413–417 doi: 10.1111/j.1439-0523. 1998.tb01965.x
11. Borner A, Schumann E, Furste A, Coster H, Leithold B, Roder S, Weber E (2002) Mapping of quantitative trait loci determining agronomic important characters in hexaploid wheat (*Triticum aestivum* L.). *Theor Appl Genet* 105:921–936 doi:10.1007/s00122-002-0994-1
12. Breseghello F, Sorrells ME (2006) Association Mapping of Kernel Size and Milling Quality in Wheat (*Triticum aestivum* L.) Cultivars. *Genetics Society of America* DOI: 10.1534/genetics.105.044586.
13. Breseghello F, Sorrells ME (2006b) Association mapping of kernel size and milling quality in wheat (*Triticum aestivum* L.) cultivars. *Genetics* 172:1165–1177
14. Chakraborty M, Emerson JJ, Macdonald SJ, Long AD (2019) Structural variants exhibit widespread allelic heterogeneity and shape variation in complex traits. *Nat Comm* 10(1):1-11
15. Chawade A, Lindlöf A, Olsson B, Olsson O (2013) Global expression profiling of low temperature induced genes in the chilling tolerant japonica rice Jumli Marshi. *PLoS One* 8(12): e81729
16. Chen Z, Feng Z, Kang H, Zhao J, Chen T, Li Q, Zuo S (2019) Identification of new resistance loci against sheath blight disease in rice through genome-wide association study. *Rice Sci* 26(1):21-31
17. Collins NC, Shirley NJ, Saeed M, Pallotta M, Gustafson JP (2008) An AlMT1 gene cluster controlling aluminum tolerance at the Alt4 locus of rye (*Secale cereale* L.). *Genetics* 179:669–682
18. Cooper M, van eeuwijk FA, Hammer Gl, Podlich DW, Messina C (2009) Modeling QTL for complex traits: detection and context for plant breeding. *Curr Opin Plant Biol* 12:231–240.
19. Doerge RW (2002) Mapping and analysis of quantitative trait loci in experimental populations. *Nat Rev Genet* 3(1):43-52
20. Eckardt N A (2000) Sequencing the rice genome. *The Plant cell* 12(11):2011–2017
21. Ersoz E, Yu J, Buckler ES (2009) Applications of linkage disequilibrium and association mapping in maize. In: Kriz AI, Iarkins BA (eds) *Molecular genetic approaches to maize improvement*. *Biotechnol Agric Forest* 173(63)
22. Fang J C, Tsai Y C, Chou W L, Liu H Y, Chang C C, Wu S J, Lu C A (2021) A CCR4-associated factor 1, OsCAF1B, confers tolerance of low-temperature stress to rice seedlings. *Plant Mol Bio* 105(1):177-192
23. FAO. *Increasing Crop Production Sustainably. The Perspective of Biological Processes Food and Agriculture Organization of the United Nations, Rome (2021)*.
24. Feng Z, Kang H, Li M, Zou L, Wang X, Zhao J, Zuo S (2019) Identification of new rice cultivars and resistance loci against rice black-streaked dwarf virus disease through genome-wide association study. *Rice* 12(1):1-13
25. Fleury D, Jefferies S, Kuchel H, Langridge P (2010) Genetic and genomic tools to improve drought tolerance in wheat. *J Exp Bot* 61:3211–3222

26. Garcia M, Eckermann P, Haefele S, Satija S, Sznajder B, Timmins A, Fleury D (2019) Genome-wide association mapping of grain yield in a diverse collection of spring wheat (*Triticum aestivum* L.) evaluated in southern Australia. PLoS one 14(2):e0211730
27. Gervais L, Dedryver F, Morlais JY, Bodusseau V, Negre S, Bilous M, Groos C, Trottet M (2003) Mapping of quantitative trait loci for field resistance to Fusarium head blight in a European winter wheat. Theor Appl Genet 106:961-970
28. Gregorio GB, Islam MR, Vergara GV, Thirumeni S (2013) Recent advances in rice science to design salinity and other abiotic stress tolerant rice varieties. Sabrao J Breed Genet 45(1):31-41
29. Guo Z, Yang W, Chang Y, Ma X, Tu H, Xiong F, Xiong L (2018) Genome-wide association studies of image traits reveal genetic architecture of drought resistance in rice. Mol Plant 11(6):789-805
30. Gupta PK, Varshney RK, Sharma PC, Ramesh B (1999) Molecular markers and their applications in wheat breeding. Plant Breed 118:369–390
31. Habash DZ, Kehel Z, nachit M (2009) Genomic approaches for designing durum wheat ready for climate change with a focus on drought. J Exp Bot 60:2805–2815
32. Hanocq E, Niarquin M, Heumez E, Rousset M, Gouis J (2004) Detection and mapping of QTL for earliness components in a bread wheat recombinant inbred lines population. Theor Appl Genet 110:106–115 doi:10.1007/s00122-004-1799-1
33. Hoang GT, Van Dinh L, Nguyen TT, Ta NK, Gathignol F, Mai CD, Gantet P (2019) Genome-wide association study of a panel of Vietnamese rice landraces reveals new QTLs for tolerance to water deficit during the vegetative phase. Rice 12(1):1-20
34. Huang X, Sang T, Zhao Q, Feng Q, Zhao Y, Li C, Zhu C, Lu T, Zhang Z, Li M, Fan D (2010) Genome-wide association studies of 14 agronomic traits in rice landraces. Nat Genet 42(11):961.
35. Huang XH, Wei XH, Sang T, Zhao Q, Feng Q, Zhao Y, Li CY, Zhu CR, Lu TT, Zhang ZW, Li M, Fan DL, Guo YL, Wang AH, Wang L, Deng, Li WJ, Lu YQ, Weng QJ, Liu KY, Huang T, Zhou TY, Jing YF, Li W, Lin Z, Buckler ES, Qian Q, Zhang QF, Han B (2010) Genome-wide association studies of 14 agronomic traits in rice landraces. Nat Genet 42:961-967
36. Hyten David L, Lee Donald J (2016) Plant Genetic Mapping Techniques. In: eLS. John Wiley & Sons, Ltd: Chichester
37. Jannink JL, Bink M, Jansen RC (2001) Using complex plant pedigrees to map valuable genes. Trends Plant Sci 6:337–342 doi:10.1016/S1360-1385(01)02017-9
38. Jose C, Juan B, Susanne D, Mateo V, Sybil A, Herrera F, Morten L, Ravi PS, Richard T, Marilyn W, Jorge F, Matthew R, Jonathan HC, Rodomiro O (2007) Association analysis of historical bread wheat germplasm using additive genetic covariance of relatives and population structure. Genetics 177(3):1889–1913 doi: 10.1534/genetics.107.078659
39. Kang H, Wang Y, Peng S, Zhang Y, Xiao Y, Wang D, Wang G L (2016) Dissection of the genetic architecture of rice resistance to the blast fungus Magnaporthe oryzae. Mol Plant Pathol 17(6):959-972

40. Khan A, Prokunier DJ, Humphreys GD, Tranquilli G, Schlatter AR, Marcucci-Poltri S, Froberg R, Dubcovsky J (2000) Development of PCR-based marker for a high grain protein content gene from *Triticum turgidum* ssp. *dicoccoides* transferred to bread wheat. *Crop Sci* 40:518–524
41. Kwon Y, Ham T H, Kim J, Lee G, Lee Y, Lee J (2021) Genome Wide Association Study of Rice (*Oryza sativa* L.) during Heading Stage under a High Temperature. *Plant Breed Biotechnol* 9(2):104-111
42. Lee SY, Kim J, Han JJ, Han MJ, An GH (2004) Functional analyses of the flowering time gene OsMADS50, the putative SUPPRESSOR OF OVEREXPRESSION OF CO 1/AGAMOUS-LIKE 20 (SOC1/AGL20) ortholog in rice. *Plant J* 38:754–764. pmid:15144377
43. Li C, Liu J, Bian J, Jin T, Zou B, Liu S, Bian J (2021) Identification of cold tolerance QTLs at the bud burst stage in 211 rice landraces by GWAS. *BMC Plant Biol* 21(1):1-11
44. Li G, Xu X, Bai G, Carver BF, Hunger R, Bonman JM, Kolmer J, Dong H (2016) Genome-Wide Association Mapping Reveals Novel QTL for Seedling Leaf Rust Resistance in a Worldwide Collection of Winter Wheat. *Plant Genome* 9
45. Li X, Guo Z, Lv Y, Cen X, Ding X, Wu H, Xiong L (2017) Genetic control of the root system in rice under normal and drought stress conditions by genome-wide association study. *PLoS Genet* 13(7):e1006889
46. Long NV, Dolstra O, Malosetti M, Kilian B, Graner A, Visser RG, van der Linden CG (2013) Association mapping of salt tolerance in barley (*Hordeum vulgare* L.). *Theor Appl Genet* 126(9):2335-2351
47. Maccaferri M, Sanguineti MC, Demontis A, El-Ahmed A, del Moral LG, Maalouf F, Nachit M, Nserallah N, Ouabbou H, Rhouma S, Royo C, Villegas D Tuberosa R (2011) Association mapping in durum wheat grown across a broad range of water regimes. *J Exp Bot* 62(2):409–438
48. McCouch S R, Wright M H, Tung C W, Maron L G, McNally K L, Fitzgerald M, Singh N, DeClerck G, Agosto-Perez F, Korniliev P, Greenberg A J (2016) Open access resources for genome-wide association mapping in rice. *Nat Comm* 7(1):1-14
49. Mengistu DK, Kidane YG, Catellani M, Frascaroli E, Fadda C, Pè ME, Dell'Acqua M (2016) High-density molecular characterization and association mapping in Ethiopian durum wheat landraces reveals high diversity and potential for wheat breeding. *Plant Biotechnol J* 14(9):1800-1812
50. Mir R, Zaman-Allah M, Sreenivasulu N, Trethowan rR Varshney R (2012) Integrated genomics, physiology and breeding approaches for improving drought tolerance in crops. *Theor Appl Genet* doi:10.1007/s00122-012-1904-9
51. Misra G, Badoni S, Domingo CJ, Cuevas RPO, Llorente C, Mbanjo EGN, Sreenivasulu N (2018) Deciphering the genetic architecture of cooked rice texture. *Front Plant Sci* (9) :1405
52. Navabi A, Tewari JP, Singh RP, McCallum B, Laroche A, Briggs KG (2005) Inheritance and QTL analysis of durable resistance to stripe and leaf rusts in an Australian cultivar, *Triticum aestivum* 'Cook'. *Genome* 48:97–107 doi:10.1139/g04-100
53. Nayyeripasand L, Garoosi G A, Ahmadikhah A (2021) Genome-wide association study (GWAS) to identify salt-tolerance QTLs carrying novel candidate genes in rice during early vegetative stage. *Rice* 14(1):1-21

54. Olmos S, Distelfeld A, Chicaiza O, Schlatter AR, Fahima T, Echenique V, Dulxovsky J (2003) Precise mapping of a locus affecting grain protein content in durum wheat. *Theor Appl Genet* 107:1243–1251 doi:10.1007/s00122-003-1377-y
55. Otto CD, Kianian SF, Elias EM, Stack RW, Joppa LR (2002) Genetic dissection of a major Fusarium head blight QTL in tetraploid wheat. *Plant Mol Biol* 48:625–632 doi:10.1023/A:1014821 929830
56. Pariasca-Tanaka J, Baertschi C, Wissuwa M (2020) Identification of loci through genome-wide association studies to improve tolerance to sulfur deficiency in rice. *Front Plant Sci* 10:1668
57. Passioura JB (2012) Phenotyping for drought tolerance in grain crops: when is it useful to breeders? *Funct Plant Biol* 39:851–859
58. Peng JH, Ronin Y, Fahima T, Roder MS, Li YC, Nevo E, Korol A (2003) Domestication quantitative trait loci in *Triticum dicoccoides*, the progenitor of wheat. *Proc Natl Acad Sci USA* 100:2489–2494 doi:10.1073/pnas.252763199
59. Pereira L, Ruggieri V, Pérez S, Alexiou K G, Fernández M, Jahrmann T, Garcia-Mas J (2018) QTL mapping of melon fruit quality traits using a high-density GBS-based genetic map. *BMC Plant Bio* 18(1):324
60. Perretant M, Cadalen T, Charmet G, Sourdille P, Nicolas P, Boeuf C, Tixier MH, Branlard G, Bernard S, Bernard M (2000) QTL analysis of bread-making quality in wheat using a doubled haploid population. *Theor Appl Genet* 100:1167–1175 doi: 10.1007/s001220051420
61. Pinto RS, reynolds MP, Mathews KI, McIntyre CI, Olivares-Villegas JJ, Chapman SC (2010) Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. *Theor Appl Genet* 121:1001–1021
62. Qaseem MF, Qureshi R, Muqaddasi QH, Shaheen H, Kousar R. Röder MS (2018) Genome-wide association mapping in bread wheat subjected to independent and combined high temperature and drought stress. *PLoS One* 13(6):e0199121
63. Rafalski A (2002) Applications of single nucleotide polymorphisms in crop genetics. *Curr Opin Plant Biol* 5:94–100 doi: 10.1016/S1369-5266(02)00240-6
64. Rafalski A (2002) Applications of single nucleotide polymorphisms in crop genetics. *Curr Opin Plant Biol* 5:94–100 doi: 10.1016/S1369-5266(02)00240-6
65. Reif JC, Gowda M, Maurer HP, Longin CFH, Korzun V, Ebmeyer E, Bothe R, Pietsch C, Wurschum T (2011) Association mapping for quality traits in soft winter wheat. *Theor Appl Genet* 122:961–970 DOI 10.1007/s00122-010-1502-7.
66. Risch NJ (2000) Searching for genetic determinants in the new millennium. *Nature* 405:847–856 doi:10.1038/35015718
67. Schläppi MR, Jackson AK, Eizenga GC, Wang A, Chu C, Shi Y, Boykin DL (2017) Assessment of five chilling tolerance traits and GWAS mapping in rice using the USDA mini-core collection. *Front Plant Sci* 8(957)
68. Semagn K, Bjørnstad Å, Ndjondjop MN (2006) Principles, requirements and prospects of genetic mapping in plants. *African J Biotechnol* 5(25)

69. Sharlach M, Dahlbeck D, Liu L, Chiu J, Jiménez-Gómez J M, Kimura S, Jones, JB (2013) Fine genetic mapping of RXopJ4, a bacterial spot disease resistance locus from *Solanum pennellii* LA716. *Theor Appl Genet* 126(3):601-609
70. Sinclair TR (2012) Is transpiration efficiency a viable plant trait in breeding for crop improvement? *Funct Plant Biol* 39:359–365
71. Solis J, Gutierrez A, Mangu V, Sanchez E, Bedre R, Linscombe S, Baisakh N (2018) Genetic mapping of quantitative trait loci for grain yield under drought in rice under controlled greenhouse conditions. *Front Chem* 5(129)
72. Song J, Arif M, Zhang M, Sze MSH, Zhang HB (2019) Phenotypic and molecular dissection of grain quality using the USDA rice mini-core collection. *Food Chem* 284:312-322
73. Sorrells M, Yu J (2009) linkage disequilibrium and association mapping in the Triticeae. In: Feuillet C, Muehlbauer GJ (eds) *Genetics and genomics of the triticeae, plant genetics and genomics: Crops and Models* 7:655–683 doi:10.1007/978-387-77489-3_22
74. Su CF, Wang YC, Hsieh T H, Lu CA, Tseng T H, Yu SM (2010) A novel MYBS3-dependent pathway confers cold tolerance in rice. *Plant Physiol* 153(1):145-158
75. T, Bertoli DJ, Knapp SJ, Varshney RK (2011) Identification of several small main-effect QTLs and a large number of epistatic QTLs for drought tolerance in groundnut (*Arachis hypogaea* L.). *Theor Appl Genet* 122:1119–1132
76. Ta K N, Khong N G, Ha T L, Nguyen D T, Mai D C, Hoang T G, Jouannic S (2018) A genome-wide association study using a Vietnamese landrace panel of rice (*Oryza sativa*) reveals new QTLs controlling panicle morphological traits. *BMC Plant Biol* 18(1):1-15
77. Tadesse W, Ogonnaya FC, Jighly A, Sanchez-Garcia M, Sohail Q, Rajaram S, Baum M (2015) Genome-wide association mapping of yield and grain quality traits in winter wheat genotypes. *PLoS One* 10(10):e0141339
78. Tommasini L, Schnurbusch T, Fossati D, Mascher F, Keller B (2007) Association mapping of *Stagonospora nodorum* blotch resistance in modern European winter wheat varieties. *Theor Appl Genet* 115:697–708 doi:10.1007/s00122-007-0601-6
79. Toth B, Galiba G, Feher E, Sutka J, Snape JW (2003) Mapping genes affecting flowering time and frost resistance on chromosome 5B of wheat. *Theor Appl Genet* 107:509–514 doi:10.1007/s00122003-1275-3
80. Verma H, Sarma R N (2021) Identification of markers for root traits related to drought tolerance using traditional rice germplasm. *Mol Biotechnol* 63(12):1280-1292
81. Verma RK, Santosh Kumar, Yadav VV, Pushkar SK, Rao MV, Chinnusamy V (2019) Overexpression of ABA receptor *PYL 10* gene confers drought and cold tolerance to *indica* rice. *Front Plant Sci* 1488
82. Wang X, Pang Y, Wang C, Chen K, Zhu Y, Shen C, Li Z (2017) New candidate genes affecting rice grain appearance and milling quality detected by genome-wide and gene-based association analyses. *Front Plant Sci* 7:1998

83. Wang X, Pang Y, Zhang J, Wu Z, Chen K, Ali J, Ye G, Xu J, Li Z (2017) Genome-wide and gene-based association mapping for rice eating and cooking characteristics and protein content. *Sci Rep* 7:17203 DOI:10.1038/s41598-017-17347-5.
84. Waugh R Jannink JL, Muehlbauer GJ, Ramsay L (2009) The emergence of whole genome association scans in barley. *Curr Opin Plant Biol* 12:218–222 doi:10.1016/j.jpbi200812007
85. Wei Z, Yuan Q, Lin H, Li X, Zhang C, Gao H, Shang L (2021) Linkage analysis, GWAS, transcriptome analysis to identify candidate genes for rice seedlings in response to high temperature stress. *BMC Plant Biol* 21(1):1-13
86. Xie L, Zheng C, Li W, Pu M, Zhou G, Sun W, Xie X (2021) Mapping and identification a salt-tolerant QTL in a salt-resistant rice landrace, Haidao86. *J Plant Growth Regul* 1-12
87. Xu J, Driedonks N, Rutten MJ, Vriezen WH, de Boer GJ, Rieu I (2017) Mapping quantitative trait loci for heat tolerance of reproductive traits in tomato (*Solanum lycopersicum*). *Mol Breed* 37(5):58
88. Xu Y, Li P, Yang Z, Xu C (2017) Genetic mapping of quantitative trait loci in crops. *The Crop J* 5(2):175-184
89. Yano K, Yamamoto E, Aya K (2016) Genome-wide association study using whole-genome sequencing rapidly identifies new genes influencing agronomic traits in rice. *Nat Genet* 48:927–934.
90. Yao J, Wang L, Liu L, Zhao C, Zheng Y (2009) Association mapping of agronomic traits on chromosome 2A of wheat. *Genetica* 137:67–75 DOI 10.1007/s10709-009-9351-5.
91. Yokotani N, Sato Y, Tanabe S, Chujo T, Shimizu T, Okada K, Nishizawa Y (2013) WRKY76 is a rice transcriptional repressor playing opposite roles in blast disease resistance and cold stress tolerance. *J Exp Bot* 64(16):5085-5097
92. Yu J, Liu C, Lin H, Zhang B, Li X, Yuan Q, Shang L (2021) Loci and natural alleles for cadmium-mediated growth responses revealed by a genome wide association study and transcriptome analysis in rice. *BMC Plant Biol* 21(1):1-15
93. Zeng L, Zhu T, Gao Y, Wang Y, Ning C, Björn L O, Li S (2017) Effects of Ca addition on the uptake, translocation, and distribution of Cd in *Arabidopsis thaliana*. *Ecotoxicol Environ Saf* 139: 228-237
94. Zhong H, Liu S, Meng X, Sun T, Deng Y, Kong W, Li Y (2021) Uncovering the genetic mechanisms regulating panicle architecture in rice with GPWAS and GWAS. *BMC Genomics* 22(1):1-13
95. Zhu C, Gore M, Buckler ES, Yu J (2008) Status and prospects of association mapping in plants. *The plant genome* 1(1):5-20
96. Zhu CS Gore M, Buckler ES, Yu JM (2008) Status and prospects of association mapping in plants *Plant Genome* 1:5-20
97. Zhu D, Kang H, Li Z, Liu M, Zhu X, Wang Y, Wang D (2016) A genome-wide association mapping study of field resistance to *Magnaporthe Oryzae* in Rice. *Rice* 9(44)
98. Zondervan KT, Cardon LR (2004) The complex interplay among factors that influence allelic association. *Nat Rev Genet* 5:89– 100 doi:10.1038/nrg1270