

Recent advances in genomics assisted breeding for drought stress tolerance in major cereals

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Abstract

Drought is one of the foremost threats for global cereal crop production with looming risks due to changing climatic scenarios. Among major cereals, rice wheat and maize are commonly grown worldwide for their importance as staple food as well as significance in fulfilling the nutritional requirements among the escalating human population. Drought being a complex trait is difficult to manage through conventional breeding approaches therefore, recent advances in genomics tools has resulted in précised and targeted identification of mechanisms underlying drought stress tolerance in cereals. Further, combination of customary breeding advances with the recent high throughput genomics technologies resulted in the popularization of genomics assisted breeding. There are various marker-assisted breeding (MAB) strategies to transfer or introgress trait of interest; these include marker-assisted selection (MAS); marker-assisted introgression (MAI), MA-backcrossing (MABC), MA-recurrent selection (MARS), MA-gene pyramiding (MAGP); genome-wide selection (GWS) and genomic selection (GS). In this review, recent advances for achieving drought stress tolerance in major cereals using genomics assisted breeding (GAB) has been discussed. We begin with the genetics of drought stress traits, MAB for abiotic stress tolerance with successful examples of mapped genomic regions for drought stress tolerance in rice, wheat and maize, respectively and finally MAI of genomic regions for improvement of drought tolerance in cereals. Further, in addition to MAB, genomic selection, an advanced molecular breeding technology, have pronounced potential to improve multiple traits simultaneously including drought tolerance in cereals.

Keywords: QTLs, GWAS, drought, MAS

1. Introduction

Cereals including rice, wheat and maize majorly contributed to food and animal feed globally. With expected 9.7 billion global human population by 2050, annual cereal production must be augmented so that future requirement can be met out. In addition to the fact that arable land is shrinking day by day and has led

to conversion of fertile arable lands due to urbanization. Therefore, in the present scenario, it appears hard to accomplish the projected target of growing the food production by 70 percent by 2050 (Wani and Sah, 2014). Repeated incidents of drought roughly in every five years resulted in up to 40% loss of total rice production in eastern states of India (Bhandari *et al.* 2007; Wassman

et al. 2009). Considerable accomplishments have been achieved for increasing the grain yield for most of the cereals but in the present climate change scenario, abiotic stresses particularly drought poses a severe challenge in further yield enhancement and sustaining the present yields. Abiotic stresses are key yield limiting factors with anticipated losses due to drought, waterlogging and heat disclose grave apprehension for productivity in various crops (Gosal and Wani, 2018; Ahmad *et al.*, 2019). Drought stress refers to water scarcity which persuades vivid changes at molecular and biochemical level which ultimately changes the morphological and physiological state of the plant, hence leading to reduced crop growth and yields (Sallam *et al.*, 2019). Drought being a complex trait is difficult to manage through conventional breeding approaches therefore, recent advances in genomics tools has resulted in précised and targeted identification of mechanisms underlying drought stress tolerance in cereals.

Hence, combination of customary breeding advances with the advanced genomics tools resulted in the popularization of genomics assisted breeding. Quantitative Trait Loci (QTL) and association mapping (AM) studies assisted in precise identification of various minor genes and some major genes responsible for drought tolerance in major cereals (Chen *et al.*, 2016; Wani *et al.*, 2018). Similarly, more recent advancements in omics, fine mapping and expression experiments revealed the accurate genomic position of genes governing drought tolerance and categorization of biochemical, physiological and molecular mechanism and signalling pathways responsible for the expression of drought tolerant genes. High throughput phenotyping approaches including root traits studies, water use efficiency estimation, and evapotranspiration studies have given further impetus to precision phenotyping which is a prerequisite for genomics assisted breeding. Therefore, genomics assisted breeding tools provide a prospect to accelerate the cereal drought improvement research worldwide (Tuberosa and Salvi, 2006; Wani *et al.*, 2019). For genomics assisted breeding, the first and foremost requirement is availability of tightly linked molecular markers with the trait of interest. Since drought is a complex trait, so numbers of genes/QTLs are responsible for imparting tolerance to the crop. These genes/loci need to be tagged with molecular markers using high-throughput technology. High throughput

advancements in molecular marker technology have provided a wider range of molecular markers like *RFLP*: Restriction Fragment Length Polymorphism, *RAPD*: Random Amplified Polymorphic DNA, *AFLP*: Amplified fragment length polymorphism, *CAPS*: Cleaved Amplified Polymorphic Sequences, *SCAR*: Sequence Characterized Amplified Region, *ISSR*: Inter Simple Sequence Repeats, *SSR*: Simple Sequence Repeats or Microsatellites, *STS*: Sequence-Tagged Sites, *SRAP*: Sequence Related Amplified polymorphism, *TRAP*: Target Region Amplification Polymorphism, *DArT*: Diversity Arrays Technology, *SNP*: Single-Nucleotide Polymorphism, etc., however SNPs are marker of choice in today's next generation sequencing era. Molecular markers offer an alternative approach to plant breeders to significantly improve elite cultivars for imparting resistance to biotic and abiotic stresses including drought, etc. very rapidly and precisely in addition to conventional selection schemes (Moose and Mumm, 2008; Rana *et al.*, 2019). Molecular markers linked to the targeted trait/QTLs can be used for crop improvement endeavours using GAB programmes. There are various MAB strategies to transfer or introgress trait of interest; these include MAS; MABC; MAGP; MARS; GWS, and GS. This review first begins with the genetics of drought stress traits, then MAB for abiotic stress tolerance with successful examples of genomic regions mapped for drought stress tolerance and finally MAI of genomic regions pertaining to drought tolerance among cereals.

2. Genetics of drought stress traits in cereals

Drought is a complex trait owing to its polygenic nature and low heritability. The gene action and combining ability studies are used to discover the mode of gene action for various agronomic traits under stress and optimum conditions. For example, leaf temperature, kernels per ear, 100-grain weight and grain yield plant⁻¹ in maize are governed by additive as well as non-additive gene action (Wu, 1987; Muraya *et al.*, 2006; Iqbal *et al.*, 2007; Hussain *et al.* 2009). ASI, Anthesis-Silking Interval, being one of the most important drought stress trait in maize is defined as the widened interval of anthesis and silking. The cause behind high ASI is slow rate of ear growth relative to tassel and therefore delayed silk emergence. Low ASI is usually preferred as it helps in better synchronization of male and female flowering plants and therefore ensuring better seed setting. Similarly, in wheat, both additive and

non-additive gene action are responsible for grain yield related traits under stress, but with predominance of non-additive gene action and medium heritability (Mia *et al.* 2017). Drought tolerance in rice is considered as a quantitative trait considering its complex nature and array of crop phenotypes linked with it (Mitra 2001). In rice, the leaf rolling trait was governed by single gene (Singh and MacKill 1991). In another study, a gene *Drt1* was found to have multiple phenotypic expressions on root system, plant height, pigmentation and awning behavior in drought tolerant lines when exposed to stress (Tomar and Prasad (1996). There are multiple reasons why these genes governing drought tolerance have not been able to map in a breeding population and among them the important ones being the environmental influence and poor heritability (Vinod *et al.*, 2019). Hence, QTL mapping is suggested to be a viable option for dissecting genetics for drought tolerance (Price *et al.*, 2002). Once mapped, the Loci closely related to the genes governing drought stress traits can be efficiently used for improving drought tolerance of mega varieties or popular cultivars which are good in quality traits but are susceptible to drought stress (Kumar *et al.*, 2013; Sandhu *et al.*, 2018; Muthu *et al.*, 2020). In conclusion, the conventional breeding led to limited success in drought stress tolerance owing to its complex nature and limitations of conventional breeding approach. Therefore, genetic dissection of drought tolerance is important for developing elite drought tolerant cultivars using conventional and molecular plant breeding techniques.

3. MAB for abiotic stress tolerance in major crop plants

The advent of molecular markers initiated the era of genetic mapping studies. The traits associated with drought tolerance are governed by genomic regions known as QTL. A lot of QTL mapping studies have been carried out for drought tolerance in cereals (Table 1). However, most of the identified QTLs are of minor effect and less stable (Choudhary *et al.* 2019; Gupta *et al.* 2020). For example, in wheat, over 50 interval mapping studies conducted globally resulted into > 1200 QTL (Gupta *et al.* 2020). The maximum numbers of QTLs have been reported for thousand grain weight followed by grain yield under drought stress and optimum moisture conditions. In case of physiological traits, chlorophyll content followed by

water soluble carbohydrates were maximum targeted traits for QTL identification. However, only 70 QTLs were found to be major effect with PVE ~>20%, and out of these 19 QTL were found to be stable as they were detected in $\geq 50\%$ environments. The next section of the review highlights the progress and recent advances mapping of QTLs, meta QTL analysis and introgression of QTLs in rice, wheat and maize, respectively.

3.1 Mapping of genomic regions for drought stress tolerance in Rice:

One of the major limitations in rice production under rainfed conditions is the drought stress. Hence, detection and transfer of reliable QTLs for imparting drought tolerance into region specific elite cultivars could be an efficient plan to deal with the low rice production from drought affected areas. In rice, many QTLs for drought tolerance have been reported so far but the advancement on MABC based introgression of the recognized QTLs has not happened to its satisfaction (Table1). Prince *et al.* 2015 mapped three QTLs (*RM8085*, *I12S* and *RM6836*) for physiological and yield traits using RIL population (IR20 x Nootripathu). These QTLs may be efficiently exploited for introgression into elite lines for targeting drought affected zones. Similarly, for mapping deep rooting trait, SNP based genotyping platform was used on RILs and AM (Association mapping) panel to mapped six QTLs (Lou *et al.* 2015). Meanwhile, 10 QTLs for physiological and productivity linked traits were observed by Sangodele *et al.* (2014) under drought stress using backcross inbred lines (Swarna x WAB 450). However, Lang *et al.* 2013 utilized BC₂F₂ population of OM1490 x WAB880-1-38-18-20-P1-HB and reported 4 QTLs for root length and root dry weight. These QTLs for dry root weight exhibited a phenotypic variation in the range of 20.7% to 30.8%. Bhattarai *et al.* (2018) used GBS-based saturated linkage map to identify drought responsive QTLs during vegetative growth. This study, based on evaluation of RILs developed from Cocodrie and N-22, identified 14 additive QTLs for various root and shoot traits. Maximum number of these QTLs were mapped on Chromosome 1 indicating it as potential carrier of drought stress tolerance. Recently, Hoang *et al.* (2019) conducted GWAS studies for mapping of different drought responsive and recovery traits using 180 rice landraces panel from Vietnam and 21,623 SNPs marker. The study revealed 17 different QTLs for various traits including leaf relative water, its slope and drought sensitivity score.

Table 1. List of selected examples of QTLs identified for drought stress tolerance in major cereals

Quantitative Trait Loci	Mapping Population	Parents	Genoty-ping Markers	Environment	Chromosome	References
Rice						
4 QTLs (root length and root dry weight)	BC ₂ F ₂	OM1490 × WAB880-1-38-18-20-PL-HB	SSRs	Green house	2, 3, 4, 8, 9, 10 and 12	Lang <i>et al.</i> 2013
15 QTLs (1000 grain weight, Leaf temperature, Relative water content, Grain weight per plant, Relative water content, Productive tillers, Grain number per plant, Panicle weight, Productive tillers and Spikelet fertility)	B a c k c r o s s derived Inbred Lines (BIL)	Swarna × WAB 450	SSR	Poly house	1, 2, 3, 7, 8 and 9	Sangodelle <i>et al.</i> 2014
6 QTLs (ratio of deep rooting)	RILS	Zhenshan97B × IRAT109	SNP	Field	1, 2, 4, 7, and 10	Lou <i>et al.</i> 2015
3 QTLs (physiological and yield traits)	RILs	IR20 × Nootripathu	SSRs	Field	1, 4 and 6	Prince <i>et al.</i> 2015
A novel gene <i>OxHL1</i>	RIL	Zhenshan97B × IRAT109	G e n e microarray	Hydroponic	11	Zhou <i>et al.</i> 2016
3 stable QTLs for tiller formation	D o u b l e d Haplloid (DH) population	Samgang Nagdong	SSRs and STSs	Green house and Field	2,6 and 11	Kim <i>et al.</i> 2017
14 QTLs for root length, shoot length, fresh root mass, fresh shoot mass, number of tillers, dry root mass, dry shoot mass, and root-shoot ratio	RIL	Cocodrie × N-22	SNPs	Poly house	1, 3, 4, 8 and 12	B h a t t a r a i <i>et al.</i> 2018
1 QTL for reproductive stage	190 RILs	CR 143-2-2 × Krishnahamsa	SSR	Field	9	Barik <i>et al.</i> 2018
34 QTLs budding, early seedling stage, leaf withering degree and leaf rolling index	RILs F ₁₀	IAPAR-9/Akihikari × IAPAR-9/	SSR	Hydroponic (PEG stress) and Field trial	1, 3, 4, 5, 9, 10 and 11	Han <i>et al.</i> 2018
5 stable QTLs under reproductive stage (leaf rolling, leaf drying, harvest index, spikelet fertility, and relative water content)	190 F7 RIL	Liaoyan241 × CR 143-2-2 × Krishnahamsa	SSR	R a i n - o u t shelter (RoS)	8, 9 and 12	Barik <i>et al.</i> 2019
17 QTLs for leaf relative water content, for slope of relative water content, drought sensitivity score, recovery ability and relative crop growth rate	Panel of 180 Vietnamese rice landraces	-	SNPs	Greenhouse	1, 5, 6, 7, 8, 10, 11	Hoang <i>et al.</i> 2019
4 QTLs Grain yield under droughts stress and physiological trait photosynthetic rate	101 BILs of rice (BC ₁ F ₃)	Norungan × TKM9	SSR	Field	1, 12, 4,	Ramchander <i>et al.</i> 2016
21 QTLs Plant, Tillers per plant, Culm length, Leaf dry weight, Stem dry weight, Total shoot dry weight, Leaf drying score, Total water uptake, Leaf area, Total root dry weight, Deep root length, Deep root volume, Deep root surface area, Deep root diameter	418 F ₂ population	Super Basmati × IR55419-04	SSR	Greenhouse	1, 6, 11, 2, 3, 4, 9	Sabar <i>et al.</i> 2019
3 stable QTLs (Grain yield under droughts stress	BC ₁ F ₃	Swarna*2 × Dular	SNP	Field	1, 3, 6	Yadav <i>et al.</i> , 2019
3 stable QTLs (Grain yield under drought stress)	BC ₁ F ₃	IR11N121*2 × AUS 196	SNP	Field	1, 2, 11	
Wheat						
20 major and minor QTLs (1000 grain weight, grain weight per spike, number of grains per spike, spike weight, spike harvest index and harvest index)	F ₃ and F ₄	Oste-Gata Massara-1 ×	SSR	Field	3B, 7B, 1B, 2B, 1B and 3B	G o l a b a d i <i>et al.</i> 2011

6 QTLs (seminal root angle and seminal root number)	DHs	SeriM82 × Hartog	DArT and SSR	Gel chambers	2A, 3D, 6A, 5D, 4A, 1B, 3A, 3B, 6B	Christopher <i>et al.</i> 2013
22 QTLs (coleoptile length, seedling height, longest root length, root number, seedling fresh weight, stem and leaves fresh weight, root fresh weight, seedling dry weight, stem and leaves dry weight, root dry weight, root to shoot fresh weight ratio, root-to-shoot dry weight ratio)	RILs	Weimai 8 × Luohan 2 Weimai 8 × Yannong 19	SSR, ISSR, STS, SRAP and RAPD	Laboratory	1B, 2A, 2B, 3B, 4A, 5D, 6A, 6D, 7B, and 7D.	Zhang <i>et al.</i> 2013
13 main QTLs (ABA content)	F ₄	YecoraRojo × Pavon 76	TRAP, SRAP and SSR	Field	3B, 4A, and 5A	Barakat <i>et al.</i> 2015
4 QTLs (net photosynthesis, water content and cell membrane stability)	F ₂	Chakwal-86 × 6544-6	SSR	Hydroponics	2A	Malik <i>et al.</i> 2015
3QTLs (yield and biomass)	NILs	Wild emmer wheat (<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>) and durum (<i>T. turgidum</i> ssp. <i>durum</i>) and bread wheat (<i>Taestivum</i>)	SNP	Net house	1BL, 2BS and 7AS	Merchuk-Ovnat <i>et al.</i> 2016
225 QTLs spike number per plant and kernel number per spike and thousand-kernel weight	131 RILs	Chuan 35050 × Shannong 483	DArTs, SSRs, and ESTSSRs.	Field	3A, 1A, 7A, 1D	Xu <i>et al.</i> 2017
1,000-kernel weight and kernels per spike	A d v a n c e d cultivar	-	SNP (GBS)	Field	4A	Ballesta <i>et al.</i> 2020
46 QTLs for Normalized Difference Vegetation Index, leaf chlorophyll content, leaf rolling and dry biomass	GWAS Panel	248 accessions of durum wheat	GWAS	field trial	1A, 1B, 2B, 4B, 5B, 6B, and 7B	Condorelli <i>et al.</i> 2018
4 Major QTLs for spike length and grain per spike	84 DH population	Opata × SH349	SSR	Field	2D, 1B, 7A and 5A	Fatima <i>et al.</i> 2018
Grain yield and its components	Durum panel of 208 lines	-	D A r T s e q SNPs	Field	2A and 2B	Sukumaran <i>et al.</i> 2018
3 Major QTLs for reproductive growth	166 DH population	Cranbrook × Halberd	90K SNP chip	Hydroponics	5A, 3A and 2A	D o l f e r u s <i>et al.</i> 2019
7 stable QTLs flag leaf area, flag leaf length, flag leaf width and cell membrane stability	206 RILs F _{9,10}	WL711 × C306	chip	Field	2DS and 3BS	K h a n n a - Chopra <i>et al.</i> 2019
22 QTLs Yield related traits	277 wheat accessions and 150 DH	-	SNPs and SSRs	Field	2B, 6B, 6A, 5B, 2D, 6D	Li <i>et al.</i> 2019
17 QTLs	276 RIL population	SYN-D × Weebill	DArTseq and 90 K SNP	field	2D, 2A, 1A, 6D, 7A and 5B	Liu <i>et al.</i> 2019
590 QTLs	Panel elite European varieties (210)	-	280 K SNP chip	Field	2B and 4A	Touzy <i>et al.</i> 2019
128 QTL grain yield, thousand grain weight (TGW), days to heading and grain filling duration	233 DH lines	Excalibur × Kukri	SSR, DArT, GBS markers, SNP, ISBP and gene-based	Field	1B	Tura <i>et al.</i> 2019

Maize						
QTLs	Phenotypes	RILs	Parents	Markers	Field	References
17 QTLs (Leaf chlorophyll, Plant senescence, Electric root capacitance.		RILs	CML444 × SC-Malawi	SSRs	Field	Messmer <i>et al.</i> 2011
43 QTLs (QTLs associated with grain yield, leaf width, plant height, ear height, leaf number, tassel branch number and tassel length)		F ₂	B73 × DTP79	RFLPs, SSRs and AFLPs	Field	Nikolic <i>et al.</i> 2011
22 QTLs (sugar concentration, root density, root dry weight, total biomass, relative water content, and leaf abscisic acid content)		F _{2:3}	DTP79 × B73	RFLP	Green House	Rahman <i>et al.</i> 2011
25 QTLs (ASI, plant height, grain yield, ear height and ear setting)		F _{2:3}	D5 × 7924	SSRs	Rain shelter	Zhu <i>et al.</i> 2011
64 QTLs (Grain yield, number of kernels per row, number of rows per ear, ear length, ASI, visually-scored drought score, relative water content, osmotic potential and relative sugar content)		F _{2:3}	B73 × DTP79	RFLPs, SSRs and AFLPs	Field	Nikolic <i>et al.</i> 2012
45 QTLs (grain yield per plant and yield components)		F _{2:3}	B73 × DTP79	SSRs	Field	Nikolic <i>et al.</i> 2013
145 QTLs (Grain yield, ASI), 7 mQTL for grain yield and 1 mQTL for ASI		RILs	CML444 × MALAWI	SNPs	Field	Almeida <i>et al.</i> 2013
203 QTLs (ASI, ears per plant, stay-green and plant-to-ear height ratio)		F _{2:3}	CML440 × CML504	SNPs and SSRs	Field	Almeida <i>et al.</i> 2014
169 QTLs (Grain yield per plant, ear length, kernel number per row, ear weight and hundred kernel weight)		F _{2:3}	CML444 × CML441	SNPs	Field	Li <i>et al.</i> 2016
63 QTLs for early vigor, ears per plant, short ASI, early flowering, stay green		BC _{1F_{2:3}}	DTPWC9-F104-5-4-1-1-B-B (DTPWC9F104) × La Posta Secuia C7-F64-2-6-2-1-B-B (LPSC7F64)	SNPs	Field	Trachsel <i>et al.</i> 2016
9 QTLs final grain yield, total number of ears, kernel number, plant height and ASI		201 inbred lines	-	SNPs	Field	Wang <i>et al.</i> 2016
12 QTLs for ASI, ear weight and number of kernels per cob		160 RILs	CM123 × CM140	SSRs	Rain out shelter	Kaur 2017
12 stable QTLs for tassel primary branch number and ear number per plant		F _{2:3} populations	Langhuang × TS141 and Chang7-2 × TS141	SSRs	Field	Zhao <i>et al.</i> 2017
167 QTLs for ear length, ear diameter, ear weight, kernel weight per ear, and hundred-kernel weight		213 F _{2:3} families	H082183 × Lv28	55K SNP	Field	Abdelghany <i>et al.</i> 2019
19 candidate genes for Grain Yield and Flowering Time		300 tropical and subtropical inbred lines	-	SNPs	Field	Yuan <i>et al.</i> 2019

Source : Modified after Wani *et al.*, 2018

3.2 Mapping of genomic regions for drought stress tolerance in wheat:

Wheat production is limited by the drought stress, especially in the rainfed ecologies globally. Hence, the identification of QTLs for drought stress tolerance is an important step for development of drought tolerant cultivars in wheat. Root architectural traits have significant role in imparting drought stress tolerance to plants. Christopher *et al.* 2013 mapped 4 QTLs, for seminal root angle and 2 for seminal root number in a Serim82 and Hartog based doubled haploid (DH) population. Zhang *et al.* 2013 mapped six major QTLs for drought stress tolerance associated traits. Merchuk-Ovnat *et al.* 2016 used wild emmer wheat as source of tolerance to develop RILs and mapped three QTLs pertaining to yield and biomass on chromosomes 1BL, 2BS and 7AS. Later, 13 QTLs for abscisic acid content were identified by Barakat *et al.* (2015) in F_4 population (YecoraRojo and Pavon 76). Similarly, Malik *et al.* 2015 identified four QTLs for photosynthesis, cell membrane stability and RWC on chromosome 2A in F_2 population (Chakwal-86 (tolerant) \times 6544-6). In mapping study on DH population (based on cross of RAC875 and Kukri) under drought stress, Shahinnia *et al.* 2016 identified four main stable QTLs for drought tolerance, two QTLs each for grain yield and kernel width/thickness ratio. Dolferus *et al.* 2019 used a DH population (Cranbrook \times Halberd) and QTLs for spike grain numbers on chromosome 5A and 2A. Further, Liu *et al.* (2019) used 276 RILs derived from cross between a parent of synthetic origin (SYN-D: Croc 1 / *Aegilops squarrosa* (224) // Opata) and an elite line, Weebill 1. The study used SNP markers and reported 71 QTLs, of which eight were common among heat, drought and heat and drought stresses. In addition to this, five QTL hotspots for yield and associated traits were identified under all stresses in chromosomes 2A, 3D, 6D (two) and 7B. The parental line, SYN-D provided 37 QTLs, and rest being provided by Weebill 1. In a recent multi-location study by Tura *et al.* (2020), main-effect genomic region pertaining to yield QTL (*QYld.aww-1B.2*) was fine-mapped to 2.9 cM region which corresponds to physical distance of 2.2 Mbp with 39 predicted genes. Such fine mapped QTLs can be easily targeted for introgression studies. GWAS studies help in the establishment of marker traits associations (MTAs) and MTAs identified in the same cluster of SNP linkage disequilibrium can be converted to QTL (Condorelli *et al.* 2018; Touzy *et al.* 2019). Gahlaut *et al.* (2019) identified 46 candidate genes for drought tolerance associated traits using MTAs in a GWAS study.

3.3 Mapping of genomic regions for drought stress tolerance in maize: Maize, being a rainfed crop is quite prone to face the drought stress affecting the global maize production

and hence economic losses. A number of mapping studies revealed significant QTLs for drought stress tolerance traits in maize. Almeida *et al.* 2013 used three populations (RILs and two $F_{2,3}$) for evaluation under drought stress and optimal conditions and mapped 83 and 62 QTLs for grain yield and ASI, respectively. The study also reported six stable metaQTLs on chromosomes 1, 4, 5 and 10 for grain yield along with two adaptive metaQTLs (each for grain yield and ASI) for drought stress conditions. Using the same population, Almeida *et al.* 2014, mapped cluster of QTLs for drought associated morpho-physiological traits such as staygreenness, ears per plant etc. on different chromosomes. Zhao *et al.* 2018 identified 21 stable QTLs under moisture stress conditions. In addition, the study also identified 36 meta-QTLs using the compiled information of 26 population under 52 well-watered and 38 drought stress environments. Recently, Abdelghany *et al.* 2019 identified 167 QTLs under six drought stress environments for ear length; diameter; weight, kernel weight per ear, and hundred-kernel weight located on chromosome number 1, 2, 3, 4, 5, 7, 8, 9 and 10 using 213 $F_{2,3}$ families (cross of H082183 (drought-tolerant) and Lv28). In another metaQTL study, 20 meta-QTLs were identified in 19 populations. Interestingly, 34 candidate genes in the corresponding mQTL regions were found to be associated with the inflorescence development and drought resistance regulation (Zhao *et al.* 2017). In a GWAS study, Li *et al.* 2016 used a panel of 5000 inbred lines and identified SNP associations with 354 candidate genes. Out of these, 52 exhibited differential expression in B73 line under the optimal and drought stress environments (Li *et al.* 2016).

4. Marker assisted introgression for improvement of drought stress tolerance

Drought tolerance, being polygenic in nature and availability of only limited major and stable QTLs, can be improved by introgression of major QTLs via MABC or combining favourable major and minor effect QTLs via MAGP and MARS. In rice, development of Nepalese drought tolerant variety, Sabitri is one of the successful examples of MABC (Dixit *et al.* 2017). Similarly, MAGP has been utilized in rice to develop drought-tolerant pyramided lines (MR219) which have productivity potential of >1500 kg ha⁻¹ under water limited environments (Shamsuddin *et al.* 2016). In another MAGP study, FUNAABOR-2 variety was pyramided with two QTLs named *qDTY12.1* and *qDTY2.3*. The pyramided lines exhibited higher yields over the lines with single or no QTL that indicates towards the significant positive interactions of pyramided QTLs to

impart drought tolerance at reproductive stage (Anyaoaha *et al.* 2019). Hence, the positive interaction among QTLs in different backgrounds can help in combining multiple QTLs for drought stress together and even with biotic stress QTLs (Sandhu *et al.* 2018). For example, Muthu *et al.* 2020 developed multiples stress tolerant version of Improved White Ponni (IWP) by introgression of different major effect QTLs, *viz.* *qDTY_{1.1}* and *qDTY2.1* for drought tolerance, *Saltol* for salinity tolerance, and *Sub1* for submergence tolerance. In wheat, MABC was carried out for introgression of QTLs related to drought tolerance governing traits such as chlorophyll content, grain yield and thousand kernel weight into elite varieties of India, HD2733 and GW322 varieties (Jain *et al.* 2014). Recently, MABC was carried out for introgression of major drought tolerant QTL for yield, *Qyld.csdh.7AL* into elite Indian wheat cultivars namely HUW234, HUW468, K307 and DBW17. The introgressed lines exhibited low stress sensitivity index which was validated with their higher yields under rainfed condition (Gautam *et al.* 2020). Ribaut and Ragot (2007) tested the efficiency of MAS approaches in maize and revealed the efficiency of selecting 10-20 genotypes during MABC cycle for higher genetic gains. However, considering the majority of minor effect QTLs for drought tolerance, Bankole *et al.* 2017 suggested the use of MARS for development of drought tolerant inbred lines. Later, Cerrudo *et al.* 2018 recommended the use of QTL-MAS in forward breeding for accumulation of desirable alleles with strong additive QTL in early selection cycles while GS-MAS recommended for accumulation of favourable alleles with smaller additive effects. Further, GS studies carried out by Shikha *et al.* (2017) in maize, revealed the involvement of drought-responsive transcription factors governing the regulation of stomatal closure, root development, hormonal signaling and photosynthesis.

5. Conclusion and future prospects

For mapping of drought tolerance, being a polygenic trait, breeders must use high throughput phenomics tools in addition to high-throughput genomics, since we have achieved a lot in terms of genomics technologies. Once tightly linked genomic regions with stability and consistency will be identified, then only effects should be on their introgression using various molecular breeding strategies via MABC, MAGP and MARS. Finally, genomic selection, an advanced molecular breeding technology, having great potential should be used in crop improvement endeavours to improve multiple traits simultaneously including drought tolerance in cereals.

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