

## Assessment of cold stress tolerance in maize through quantitative trait locus, genome-wide association study and transcriptome analysis

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### Abstract

Genome-wide association study (GWAS) has become a widely accepted strategy for decoding genotype phenotype associations in many species thanks to advances in next-generation sequencing (NGS) technologies. Maize is an ideal crop for GWAS and significant progress has been made in the last decade. This review summarizes current GWAS efforts in maize functional genomics research and discusses future prospects in the omics era. The general goal of GWAS is to link genotypic variations to corresponding differences in phenotype using the most appropriate statistical model in a given population. The current review also presents perspectives for optimizing GWAS design and analysis. GWAS analysis of data from RNA, protein, and metabolite-based omics studies is discussed, along with new models and new population designs that will identify causes of phenotypic variation that have been hidden to date. The detailed that low temperature in maize seedlings altogether restricts germination and seedlings' development and destabilizes the cancer prevention agent safeguard component. Cold pressure adversely influences root morphology, photosystem II (PS II) effectiveness, chlorophyll substance, and leaf region. A short scene of low temperature stress (for example, under 10 °C for 7 days) during the V6–V9 maize development stages can fundamentally defer the anthesis commencement. Among the morphological reactions by focused on maize plants, low temperature stress causes strange tuft development in maize, along these lines influencing the fertilization and grain filling measures. Hence, problematic temperatures can cause a genuine yield decrease if happening at basic conceptive stages, as plants allocate over half of their photosynthesis to foster grains during this stage until physiological development. Low temperature stress fundamentally diminishes the plant stature and absolute yield biomass of maize. Leaf improvement turns out to be delayed in chilly focused on plants because of a drawn-out cell cycle and diminished pace of mitosis. The joint and continuous efforts of the whole community will enhance our understanding of maize quantitative traits and boost crop molecular breeding designs.

**Keywords:** GWAS; functional genomics; mixed model; population design; *Zea mays*

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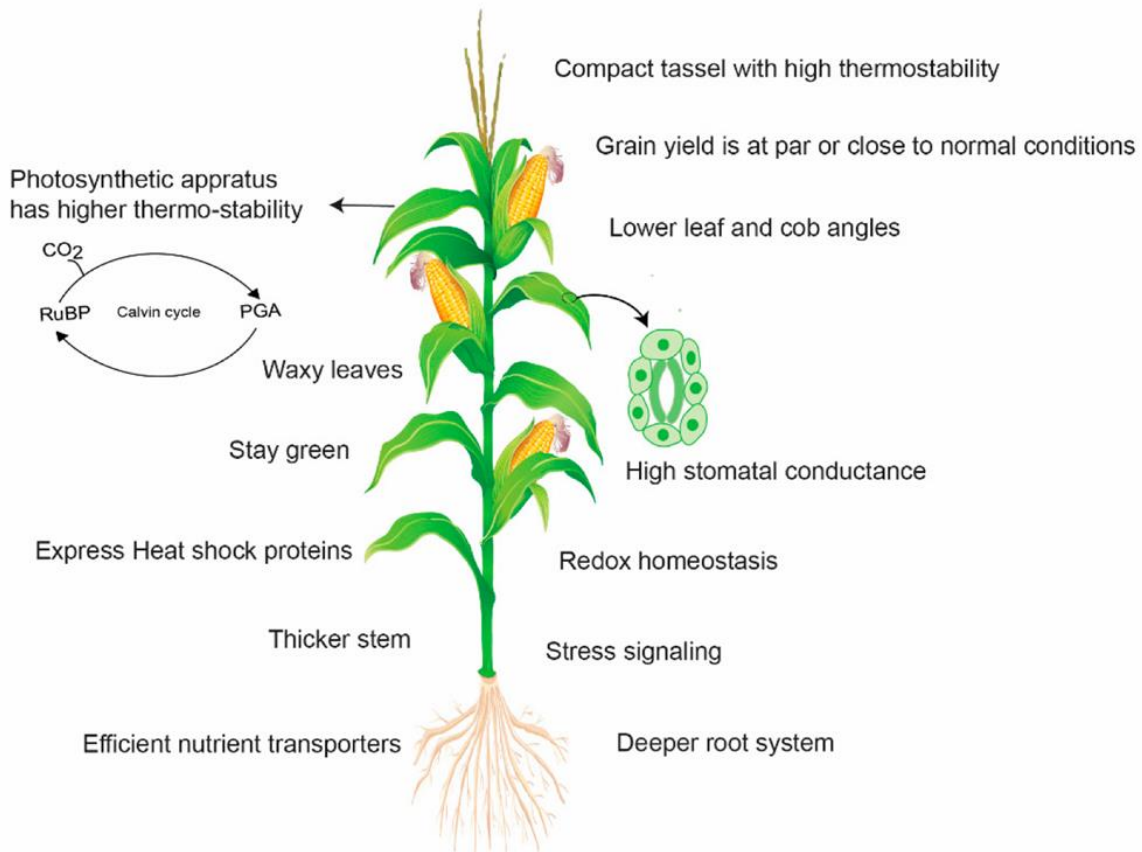
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## Introduction

In the current scenario of global climate change, the utmost desire to ensure food security is to maintain and increase agricultural production. But, due to rapid climate change, many abiotic factors such as rainfall, drought, flooding, temperature and solar radiations are severely affecting the production of cereal crops at various growth stages (Saleh *et al.*, 2008; Saud *et al.*, 2013; Saud *et al.*, 2014; Saud *et al.*, 2016; Saud *et al.*, 2017; Sajid *et al.*, 2019; Sajid *et al.*, 2020; Saud *et al.*, 2020; Unsar Naeem *et al.*, 2020). The effects of climate change on agriculture could not be ignored. Changes in precipitation and temperature as well as the increase in CO<sub>2</sub> levels leading to climate change have significant impacts on global agriculture. The decrease in the yield of agricultural products and the change in land structure cause people not to receive recompense for their labor and break their hopes (Shah *et al.*, 2013; Tariq *et al.*, 2018; Shafi *et al.*, 2020; Senol *et al.*, 2020; Saman *et al.*, 2020). World population is increasing at an alarming rate and more food is needed to satisfy the hunger of human being within existing resources (Rasheed *et al.*, 2017; Rasheed *et al.*, 2018; Rasheed *et al.*, 2019; Rasheed *et al.*, 2021a; 2021b). Maize (*Zea mays* L.) started in the Balsas River bowl of southwestern Mexico roughly 9000 years prior (Alam *et al.*, 2017). It has since spread geologically and financially, becoming perhaps the main harvests worldwide for food, feed, and fuel (Alexander *et al.*, 2009). Maize grain creation has expanded more than eight-crease in the previous century to a current yearly worldwide creation of one billion tons (An *et al.*, 2012). Mapping of quantitative trait loci (QTL) brought a revolutionary breakthrough in the world of crop production. Salinity, drought, water logging and toxicity are those abiotic stresses that affect the crop yield and production (Wajid *et al.*, 2017; Saman *et al.*, 2020; Wahid *et al.*, 2020). Notwithstanding, ceaselessly enhancing requests for maize creation has prompted the nonstop requirement for hereditary improvement of different agronomically and monetarily significant attributes (Anders *et al.*, 2015). The most monetarily significant attributes are generally acquired in a quantitative way, and the hereditary premise is ascribed to polygenes and cooperation impacts among qualities and additionally qualities and the climate (Apel *et al.*, 2004). Linkage planning dependent on an isolating populace from a cross between two guardians showing maximally various aggregates is a notable way to deal with find quantitative attribute loci (QTL) (Applequist *et al.*, 2001).

They are measurably gathered, for the most part through direct relapse and most extreme probability gauge techniques, and in light of a hereditary linkage map (Ardy *et al.*, 2002). A couple of QTLs are by and large distinguished by means of linkage planning in each trial (Atwell *et al.*, 2010). Further fine planning of QTL to an all the more barely exact hereditary position and cloning of the basic quality, as huge optional populaces are by and large needed to accomplish adequate guide goal (Atwell *et al.*, 2010; Ayers *et al.*, 2010). The huge and complex maize genome, over 85% of which comprises of dull groupings further eases back progress in QTL fine planning and cloning. Genome-wide affiliation study (GWAS) utilizing assorted populaces gives another technique to successfully fine guide QTL because of an enormous number of authentic recombination occasions that lead to the fast rot of linkage disequilibrium (Bajželj *et al.*, 2014). In general QTL mapping provides the opportunity to detect and clone the QTL of major traits in crops (Rasheed *et al.*, 2020a; 2020b; 2020c).

This affiliation planning methodology was initially applied in plants in the start of the 21<sup>st</sup> century as an up-and-comer quality affiliation (Ardy *et al.*, 2002). Concentrate in maize nonetheless, the principal affiliation learn at genome-wide scale was accounted for in maize, in 2008, in which 8590 loci in 553 world class maize inbreeds was utilized to investigate the qualities influencing unsaturated fat content in bits (Bano *et al.*, 2015). Right now, GWAS is an everyday practice instrument in the investigation of human illness and other complex attributes in numerous enormous accomplice examinations (Barnabás *et al.*, 2008). For maize, since the arrival of the B73 reference genome (Bates *et al.*, 2015). GWAS has multiplied significantly and many agronomically significant characteristics have been analyzed (Bilska-Kos *et al.*, 2017) (Figure 1).



**Figure 1.** Basic mechanism evolved during cold stress in maize plant.

These advances recommend GWAS is an amazing asset to viably and effectively distinguish genome-aggregate affiliations (Boehlein *et al.*, 2019). In this survey, we

- Audit maize practical genomics worked with by GWAS on agent attributes and a huge scope (Cai *et al.*, 2017).
- Diagram progress of new hereditary and more elevated level (over-hereditary) variety, strategy advancements, and populace plans that boost factual force (Cárcova *et al.*, 2001).
- Talk about the difficulties and openings for maize GWAS in the future (Change *et al.*, 2007).

Functional genomics in plants intends to distinguish the capacities of all qualities (Chen *et al.*, 2007). Somewhat recently, the unstable turn of events of cutting-edge sequencing (NGS) advancements, and the arrival of the maize B73 reference genome, have generally advanced maize hereditary examination into the genomics period (Chen *et al.*, 2012). Until now, different characteristics, going from sub-atomic (counting the transcriptome) to cell (i.e., metabolites), and from the individual morphological scale (agronomic, yield, or conceptive qualities) to the collaboration with various ecological variables (biotic or abiotic stress resistance), have been thoroughly examined, alongside (Cho *et al.*, 2010). various cloned qualities and a lot more proposed quality contender for comparing attributes, all utilizing a GWAS approach (Cicchino *et al.*, 2010). GWAS Helps Understand Genetic Architecture of Complex Quantitative Traits Exceptionally enormous scope GWAS examinations give new freedoms to comprehend the hereditary engineering of complex quantitative attributes (Commuri *et al.*, 2001).

### GWAS: a promising tool in maize functional genomics

The information produced to date for the most part show that a huge number of QTL are being distinguished yet each just clarifies a little piece of phenotypic variety for the greater part of the agronomic characteristics examined in maize (Deeks *et al.*, 2012). For instance, in excess of 40 QTL were planned for blossoming time (Dubouzet *et al.*, 2003). Expanding Number of Publications on Maize GWAS since the Release of the B73 Reference Genome (Edreira *et al.*, 2011). Then again, cell quality and piece organization characteristics seem to have a less muddled hereditary design, with a more modest number of bigger impact QTL to be recognized (Esim *et al.*, 2016). In one examination, a few qualities were found to clarify over 10% of the difference for bit oil fixation (Fang *et al.*, 2020). In another investigation, the related loci were discovered that clarify more than 20% of noticed change in the auxiliary metabolomics attributes of maize bits, with a middle of 7.8% (Fang *et al.*, 2017). GWAS on transcriptomic variety, likewise called articulation QTL (eQTL) planning, joins hereditary markers to articulation variety from a huge number of qualities, and has exhibited the simplex hereditary reason for quality articulation characteristics, as each eQTL regularly clarifies an enormous extent of phenotypic (articulation level) variety (Fang *et al.*, 2015).

In a new report, the statement of 14 375 qualities was estimated, and a normal of more than 15% of the difference was clarified for every quality per eQTL (Farooq *et al.*, 2008). Especially, a solitary QTL was recognized for clarifying 87.7% of quality expressional fluctuation (Farooq *et al.*, 2009). As the quality under examination travels through distinctive omic layers from the aggregate estimated in factor conditions (Foyer *et al.*, 2002) to the degree of metabolites in single cell types, or to the outflow of single qualities (Fujino *et al.*, 2010). It is normal that the number of QTL distinguished will move from profoundly quantitative to subjective or single locus (Fujino *et al.*, 2011). An expanding number of openly accessible GWAS results give the chance to limit relationship to single (Fujino *et al.*, 2004). Very much explained competitor qualities and to comprehend genome structure and constitution related with every attribute of interest (Hernández *et al.*, 2005). Early endeavors to ascertain the dissemination example of related loci at the genome-wide level tracked down those genic and almost genic districts (rather than intergenic areas) contribute most to maize attribute variety, particularly in the 50 UTR (Golub *et al.*, 2016).

Besides, non-equivalent transformed single nucleotide polymorphisms (SNPs) are the most practically enhanced, along with huge duplicate number variations (CNVs), while intergenic districts show critical consumption for utilitarian SNPs (Gourdji *et al.*, 2013). These precise investigations propose that quality guideline in articulation level should assume a critical part in phenotypic variety (Gu *et al.*, 2013). Under this speculation, the articulation scene of youthful maize parts has been widely investigated (Guan *et al.*, 2012) and the equivalent ends were reached as past discoveries on quantitative qualities; i.e., that non-equivalent SNPs are the hugest drivers of articulation guideline, with a higher number of SNP QTL affiliations (Han *et al.*, 2008).

To investigate another significant layer forming hereditary variety in maize (Hartmann *et al.*, 2000). Played out a metabolome-based GWAS in maize parts to represent the entire biochemical scene, looking for general and explicit patterns (Hasanuzzaman *et al.*, 2020). This sub-atomic level affiliation considers enjoy taken full benefits of accessible GWAS information, which help to comprehend the inborn practical genome basic attribute variety (Hayashi *et al.*, 2016). The subsequent deductions are fit for directing new or more inside and out quality distinguishing proof investigations (Hayashi *et al.*, 2015). For instance, QTL results from the metabolite study and agronomic characteristics estimated on a similar populace were mutually dissected (Hepworth *et al.*, 2002). This permitted the recognizable proof of a significant QTL influencing both the metabolic characteristic (on which it had a major impact) and the agronomic quality (on which it had a minor impact) (Hieke *et al.*, 2014). Utilizing the hint gave by the metabolic quality as an extension prompted the distinguishing proof of a quality hidden the QTL influencing the agronomic quality, and to a superior comprehension of the basic component (Hoggart *et al.*, 2008). When known metabolites are related with

obscure qualities or the other way around, great hints are accommodated novel explanations of both metabolites and qualities (Hu *et al.*, 2019).

Complex metabolic organizations can be additionally recreated or recognized as significant for a given characteristic by consolidating linkage or affiliation planning and organizations including articulation administrative networks (Huang *et al.*, 2017) and known metabolic pathways (Huang *et al.*, 2009). Joining huge datasets accumulated utilizing a wide range of conventions, particularly arising omics instruments, with high-throughput attribute affiliation examinations will accordingly speed maize useful genomic study (Huang *et al.*, 2012). An early fruitful and commonsense affiliation model is the provitamin a bio fortification of maize (Hund *et al.*, 2007). Right now, more than 250 000 youngsters experience the ill effects of visual impairment every year because of nutrient An inadequacy (VAD), and almost two billion individuals, generally in non-industrial nations, stay in danger for inadequacies for this and different micronutrients (Hunter *et al.*, 2017). Uncommon great alleles of *LcyE* and *crtRB1* were distinguished in applicant quality affiliation investigations (Hussain *et al.*, 2018).

By introgression these uncommon alleles into first class maize germplasm through sub-atomic marker helped reproducing, maize with improved levels of supportive of nutrient (Hussain *et al.*, 2019). A currently devoured by several thousands of African youngsters who might profit promptly, and accordingly the commonness of VAD is declining (Hussain *et al.*, 2019). It is one of the best sub-atomic reproducing undertakings of the Worldwide Maize Program of the International Maize and Wcold Improvement Center (CIMMYT) until this point in time (Hussain *et al.*, 2019). The streamlining of photoperiod affectability is one key factor that permits plants to adjust to new conditions in various scopes. The quality *ZmCCT* majorly affects photoperiod affectability furthermore, has been obviously analyzed in two free GWAS distributions (Hussain *et al.*, 2006). The CACTA-like transposable component in the 50 UTR locale of *ZmCCT* is the causal variation for the methylation level of the advertiser locale (Izaurrealde *et al.*, 2011). One allele lessens quality articulation, which advances early blooming, permitting maize to fill adaptively in higher scopes. Streamlining plant design is right now one of the key targets in maize reproducing (Kang *et al.*, 2008).

This incorporates upgrading tallness to decrease dwelling and to permit an expansion in plant thickness (Kawahara *et al.*, 2016). *Brachytic2* has been recognized as a serious, uncommon, and regular freak influencing plant stature (Koseki *et al.*, 2010). An uncommon and regular transformation that decently decreased plant tallness has end up being the causal variation (Kovach *et al.*, 2007). This is a new change, and is just distinguished in mild maize germplasm, which will make it simpler to figure it out its potential for yield improvement in future reproducing programs (Kuroki *et al.*, 2007). A different report distinguished the *lg1* and *lg2* loci, which were discovered to be essentially connected with upper leaf point, which related to an increment in the effectiveness of sun powered radiation catch. This effectiveness gave the *lg2* allele possibilities to essentially expand grain yield (Lei *et al.*, 2014).

At long last, a 3-Kb intergenic grouping inside the *KRN4* locus was discovered to be answerable for maize piece column number (*KRN*) variety by managing the statement of the SBP-box quality *Unbranched3* (Lesk *et al.*, 2016). The ideal allele of *KRN4* has been demonstrated to be essentially enhanced in world class mild inbreeds yet not in tropical maize germplasm (Li *et al.*, 2015). Dry spell resilience is an especially intricate quantitative quality constrained by numerous loci with little impacts (Li *et al.*, 2019). It is exceptionally impacted by the climate, and is hence viewed as hard to take apart utilizing GWAS (Li *et al.*, 2019). A progression of specialists worked on the dry spell aggregate by estimating a part attribute, seedling endurance rate submerged focused on condition, and a progression of affiliation examines distinguished positive normal variations of various qualities that could be utilized for dry spell resilience improvement in maize (Li *et al.*, 2014).

### GWAS helps understand genetic architecture of complex quantitative traits

Diminishing characteristic intricacy by correctly estimating connected metabolic qualities rather than yield itself under dry spell has moreover prompted effective GWAS analyzation of dry season related attributes in maize (Li *et al.*, 2014). In rundown, these and lot later outcomes summed up have permitted point by point investigation of explicit attributes of revenue (Li *et al.*, 2011). These examinations have end up being genuinely fast and direct on the grounds that the recognizable proof of the best great alleles effectively present in regular populaces (Liu *et al.*, 2012). Furthermore, these GWAS examines cleared the way for the most productive abuse of this regular variety, as found in the model from the crtRB1 investigation of supportive of nutrient A (Liu *et al.*, 2000). Linkage examination had recognized one QTL covering the crtRB1 district in two autonomous isolating populations with comparable phenotypic variety clarified. Further quality-based affiliation investigation recognized six normal haplotypes inside crtRB1, each with various impacts (Liu *et al.*, 2016) (Table 1).

**Table 1.** Inbred association panel

Phenotype	Population	Sample size	No. marker
Water tolerance	IAP	350	56K
Cold tolerance	IAP	125	56K
	IAP	375	56K
	Dent + Flint	306 + 292	50K

The affiliation data permitted the recognizable proof of potential guardians containing the specific haplotypes that ought to be crossed for maximal articulation of the quality (Liu *et al.*, 2016). This was functional regardless of the way that the best blend of guardians came from various affiliation boards what's more, reproducing pools, and may never have been crossed without the genomic data acquired by GWAS, accordingly demonstrating the capacity to give immediate and solid data to picking suitable guardians or potentially benefactors for rearing. In the previous few decades, GWAS has effectively distinguished great many related loci in people, creatures, and plants (Lizaso *et al.*, 2018), this has given numerous advantageous signs to further develop sickness treatments and creature or potentially crop rearing (Lobell *et al.*, 2011). Nonetheless, just a little part of phenotypic variety for a characteristic can be clarified in some random GWAS, particularly in human investigations, raising a drawn-out banter over the issue of "missing heritability" (Long *et al.*, 2010).

For instance, GWAS has recognized many human tallness related loci in a huge human accomplice informational collection, yet they just represented a little part (<5%) of absolute heritability (Lu *et al.*, 2014). On the other hand, by utilizing all genome-wide SNPs in an examination (not simply measurably huge SNPs), all things considered expanded the gauge of tallness heritability to 67% through an exemplary quantitative hereditary methodology (Lü *et al.*, 2011). These outcomes give an update that heritability may stay stowed away in genomics concentrates until the appropriate apparatuses can uncover the missing part (Lukatkin *et al.*, 2003). This part is accepted to be mostly available through the investigation of variations in qualities of minor impact in more hereditarily homogeneous foundations, by expanding variations present in populaces at low recurrence until their impact can be appropriately estimated, or by including new hereditary variations undiscovered in past investigations (Lv *et al.*, 2020; Ibrar *et al.*, 2020) (Figure 2).

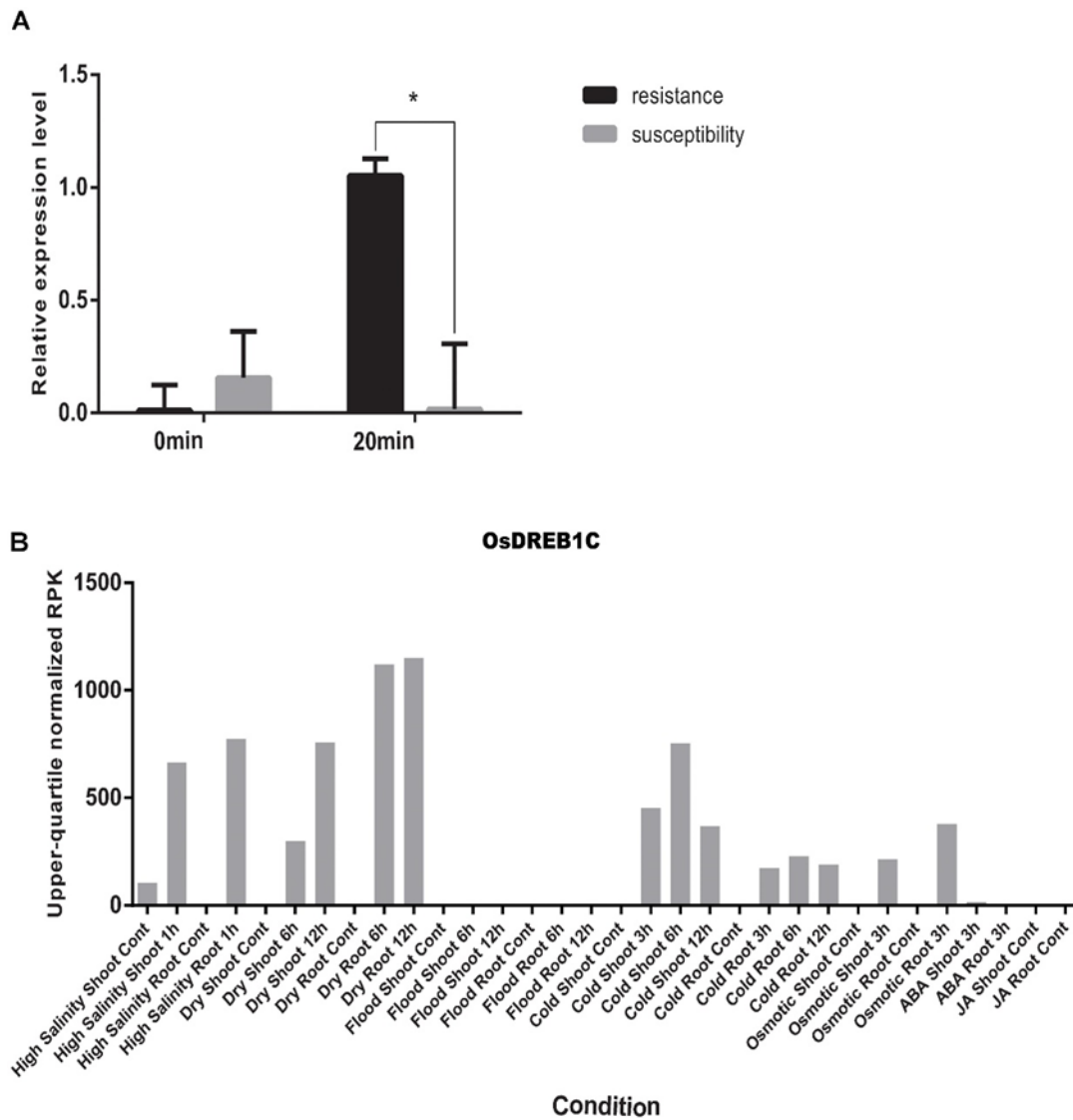


Figure 2. GWAS results showed the response of maize plant under various stress conditions

A significant distinction between plant and human frameworks is that controlled intersection tests are conceivable in the previous yet not in the last mentioned (Ma *et al.*, 2018), henceforth, plant frameworks give a doable chance to work with GWAS in intricate populace or measurable plans to improve planning power (Ma *et al.*, 2015). In the following segments, we sum up three conceivably free methodologies that, independently or mutually, may add to uncovering missing heritability in plants, particularly in maize, including novel kinds of genotypes furthermore, aggregates, measurable technique advancements, and new hereditary plans (Mao *et al.*, 2015).

It was recognized more than 1,000,000 PAVs by planning 26 million labels from 14 129 innate lines, and tracked down that this kind of variety displays advanced relationship with a wide scope of phenotypic characteristics (Michaels *et al.*, 2018). The PAVs of translated successions were to a great extent associated with articulation guideline, metabolic vacillation, also, more elevated levels of phenotypic variety and heterotic (Morell *et al.*, 2001). These major underlying improvements, including considerably bigger scope redundancies brought about by transposable components, are known to represent enormous rates of the (Moser *et al.*, 2015), substance inside the maize genome and may assume bigger parts in making phenotypic variety than single-nucleotide variations (SNVs); nonetheless, in light of the fact that a significant number of the bigger scope

changes are in high LD with flanking SNV, it is hard to appoint the phenotypic changes to either solely (Nazir *et al.*, 2020).

Higher-request or over-genomic varieties, for example, changes or contrasts in articulation levels, have end up being extraordinary assets as "sub-atomic aggregates" (Neiff *et al.*, 2016). Along these lines, we recommend that they could likewise be viewed as free "sub-atomic genotypes" that are not basically in LD with genomic variety. It utilized articulation PAV as the "genotype" and tracked down this sort of marker playing huge jobs in articulation guideline, metabolome variety, also, morphological characteristic variety. By changing articulation level into double variety, (Neild *et al.*, 2009), utilized high versus low articulation (comparative with the middle worth) as variety to uncover the commitment of differentially communicated qualities to their comparing cell and agronomic characteristic fluctuation (Panison *et al.*, 2016) (Table 2).

**Table 2.** Performance comparison of different methods in mixed linear model GWAS

Year	Method	Positive semidefinite matrix requirement	Strategy for increasing computational speed			Computational speed	Statistical power
			Approximate/Two-step approach	Matrix optimization	Low-rank matrix		
2006	Standard MLM					Low	High
2007	GRAMMAR		+			Very fast	Intermediate
2008	EMMA	+		+		Intermediate	High
2010	EMMAX	+	+	+		Fast	High/Intermediate
2010	P3D,M CMLM		+		+	Fast	High/Intermediate
2011	FaST-LMM	+		+		Fast	High
2012	GEMMA	+		+		Fast	High
2012	FaST-LMM-Select	+		+	+	Very fast	High
2014	ECMLM		+		+		High/Intermediate
2014	SUPER	+		+	+	Fast	High
2014							

Results demonstrate that transcriptomic variety is predominant and works at the administrative level (Paterson *et al.*, 2013), and show a few benefits that are integral with SNP-characteristic affiliation contemplates: (1) they reflect variety in both hereditary and epigenetic administrative components; (2) they give extra proof to fine guide QTL; (3) they help to comprehend sub-atomic systems and develop administrative organizations (Paterson *et al.*, 2003). Sub-atomic aggregates over the genome level would now be able to be immediately estimated with high-throughput and minimal expense stages, and can be utilized on one or the other side of the planning condition (Perrea *et al.*, 2016) this could fill in missing data when at least one factors were thought about reciprocally. The epigenomic code gives another basic layer in choosing the destiny of a cell or a life form. Epigenetic changes can be autonomous from genomic variety and react (*in vivo* and *in vitro*) to climate changes, going with phenotypic inconstancy (Piepho *et al.*, 2007).

Ongoing advances in populace epigenomics in a small bunch of animal types have zeroed in on unraveling the hereditary premise, actually in regards to the epigenetic adjustment as "attributes" (Pugh *et al.*, 2010). With respect to epigenome as the "genotypic" side of the condition would be important, like the transcriptome examined above, and, along with other omics investigations of the proteome and metabolome, this sort of over-genomic variety could be applied as sub-atomic markers to analyze downstream aggregates. Since the epigenome and transcriptome are nearer to their phenotypic results than the genome does, they additionally hold the guarantee of recovering missing heritability. The recognizable proof of varieties in these

new "genotypes" at the populace level for species with enormous genomes like maize, at present is still nontrivial, as it doesn't think about tissue and formative stage contrasts (Qin *et al.*, 2008).

Besides, as various as genomic varieties with paired or restricted quantities of alleles can be, variety for new omics qualities are quantitative and range alterable, along these lines making traditional and clear planning strategies inadmissible for new omics information (Rafique *et al.*, 2019). It was recommended a minimal expense catch based bisulfite approach for powerfully and dependably breaking down DNA methylation for pre-characterized genomic areas. It was proposed a contingent Gaussian Bayesian strategy to derive conceivable connections between discrete what's more, consistent qualities under an organization technique, which might be promising for affiliation planning also (Raza *et al.*, 2019). A direct relapse model representing populace design and relatedness grid while breaking down more elevated level omics information, quantitative GWAS (qGWAS), has as of late been proposed to tackle the constant genotype issue, and has been utilized to investigate the administrative organization (Read *et al.*, 2001).

Future advancements in sequencing advances ought to be thought about correspondingly with new logical strategies centered on more significant level variety to all the more completely enlighten the covered-up secrets at the most minimal omics levels (Reeves *et al.*, 2001). Inventive GWAS METHODS IMPROVE Planning POWER To evaluate how qualities or QTL impact phenotypic variety, early GWAS essentially relapsed the marker variable against the aggregate, and furthermore utilized control foundation commotion with covariates to preclude bogus relationship due exclusively to populace structure in normal populaces of plants (Riva-Roveda *et al.*, 2016). Nonetheless, in a characteristic populace, the people consistently share complex tribal relatedness, generally due to broad intercrossing endeavors in crop rearing (Robinson *et al.*, 2010). The one-measurement size of induced subpopulations for GWAS is for the most part deficient to control the covariance connections between individual combines in multi-dimensional scales, also, the degree of inclination relies upon the quality fundamentally (Ruan *et al.*, 2013).

In animal breeding programs, the blended model methodology is regularly used to choose great people in a rearing populace in light of rearing qualities, assessed utilizing a family based hereditary relatedness network (GRM) between individual sets of creatures (Ruan *et al.*, 2005). Although apparently clear (Rymen *et al.*, 2007). It is infeasible to straightforwardly apply the creature blended model to plant GWAS, in light of the fact that harvest rearing family records are at times erroneous and regularly totally obscure. A brought together blended model technique that substitutes the inaccessible family based GRM with a marker-based GRM was an effective answer for all the while represent populace structure and the difference covariance lattice in GWAS (Saito *et al.*, 2010) (Figure 3).

In the accompanying segment, we call this the standard Mixed Linear Model (MLM) strategy (Saito *et al.*, 2004) and we sum up key focuses and inspirations of late enhancements in GWAS strategies. Variety of Mixed Models for Improving GWAS Power Measurably talking, it is direct to further develop power by means of expanding test size. Notwithstanding, the standard MLM technique is wasteful for huge informational indexes (those with a huge number of people), in view of the computational weight important for mathematical streamlining (Sánchez *et al.*, 2014). In a first endeavor to work on the speed of GWAS estimations, the productive blended model affiliation (EMMA) technique improves on network tasks through ghastly decay (Sandhu *et al.*, 2018). Be that as it may, this "accurate technique" of tackling blended model conditions with entire genome markers in an iterative style is of restricted esteem when testing a large number of markers to recognize all recombination occasions. Other assorted new strategies with various suppositions have been proposed for investigation with persistently expanding test size and marker thickness, and subtleties of these new strategies are momentarily presented underneath (Sang *et al.*, 2007).

A decent compromise between computational speed and factual force can be made by just assessing model boundaries once and then, at that point continually testing markers iteratively utilizing a rough strategy, commonly including the P3D (populace boundary recently resolved) and the remaining methodology. The P3D approach, counting P3D (Schauberger *et al.*, 2017) gives comparable advantages to the remaining methodology, (for example, genome-wide fast affiliation utilizing blended model and relapse (Segura *et al.*,

2012) nonetheless, the P3D and lingering approaches are actually unique. The lingering approach fits the residuals from a decreased blended model as the reliant variable to test marker importance utilizing a straight relapse, though P3D fits the unique aggregate as the reliant variable and tests marker importance under a blended model in with fixed difference boundaries got from the decreased model (Shen *et al.*, 2007).

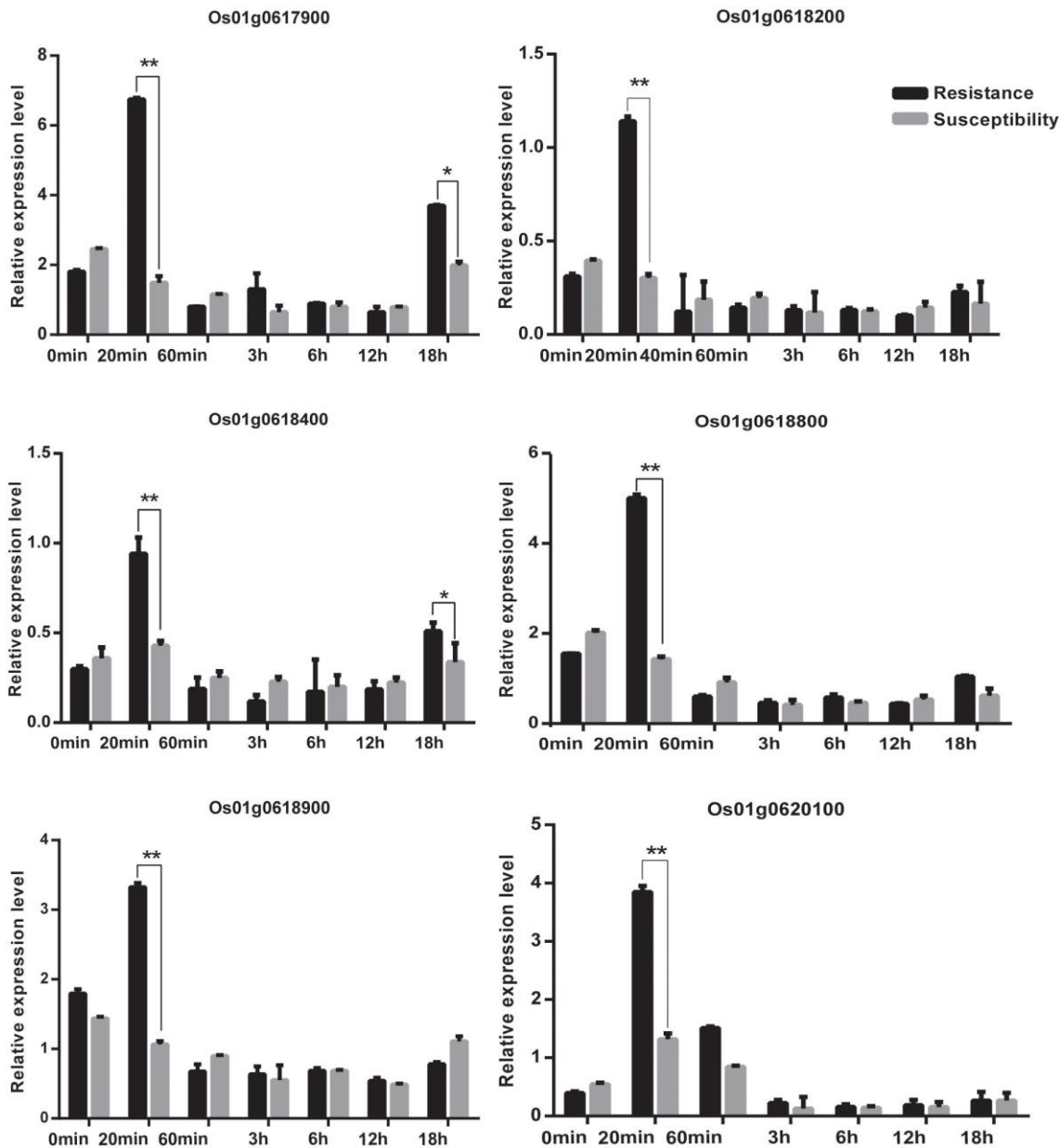


Figure 3. Expression pattern of different genes under cold stress in maize

### GWAS on molecular phenotypes yields genome annotation and insights into mechanisms

Accepting polygenic legacy, rough techniques have end up being a productive answer for accelerate GWAS for large scale informational indexes meaning to expand planning power. In truth, be that as it may, it's anything but conceivable to know deduced how exact the estimated techniques will be (Shim *et al.*, 2017). Two free calculations were proposed to work on the speed of the specific strategy by improvement of the blended model condition, and these are named the calculated frightfully changed straight blended model (FaST-LMM)

(Siebers *et al.*, 2017) and the genome-wide productive blended model affiliation (GEMMA) calculation (Song *et al.*, 2017). Momentarily, the worked on precise techniques regularly center around modifying the mixed model conditions that refactor the customary probability work of the blended model to a structure comparable to the probability of a direct relapse model. This advancement improves on the multidimensional boundaries assessment into a one-dimensional mathematical enhancement issue, significantly lessening computational weight for every cycle (Steward *et al.*, 2018).

These techniques work at even more prominent rates than the surmised strategies in enormous scope GWAS. To tackle a blended model condition, figuring cost is expanded generally because of the network tasks that gauge arbitrary impacts, which are corresponding to the cubed test size. Thus, it ought to be feasible to additionally further develop GWAS speed by utilizing a low-position framework in the blended model. In creature reproducing, creatures' rearing worth can be anticipated by their sire beginnings; consequently, creature connections can be assessed by sire covariance lattices (this is named the family-based sire model). Also, (Su *et al.*, 2016) initially proposed a low-position network based blended model approach, which they called the packed MLM (CMLM). This model uses the GRM between sets of gatherings to supplant the GRM between sets of people as the irregular impact. The CMLM technique was additionally streamlined by including another boundary to characterize calculations for computing GRM between gatherings, named enhanced CMLM (ECMLM) (Suh *et al.*, 2010).

On the other hand, (Sun *et al.*, 2018) represent an extraordinary failure rank framework strategy inside Quick LMM, which actually manages an individual-sets GRM grid, however, to appraise it utilizing a lot more modest subset of markers rather than by utilizing every one of them (Sun *et al.*, 2017). The best markers to assess the low-position GSM framework has not however been resolved. Under the supposition of the blended model comparable to a Bayesian direct relapse model, the all-encompassing form of FaST-LMM calculation, FaST-LMM-Select, endeavors to pick the best markers relying upon the affiliations with a normal characteristic (Sun *et al.*, 2013).

Momentarily, direct relapse is first and foremost led to arrange all markers rising by  $p$  esteems; the ideal subset of compelling markers is then controlled by searching for least genomic control file esteem, a boundary to appraise the genomic swellings because of foundation commotion, which is ordinarily utilized in human infection GWAS contemplates (Tamura *et al.*, 2011). For each tried marker, the GSM network is iteratively set up by utilizing distinguished persuasive markers previously precluding the tried markers (and all markers inside 2 cM) (Tao *et al.*, 2007). Past FaST-LMM-Select, a comparative in any case, more modern calculation, called Settlement of MLM under Progressively Exclusive Relationship (SUPER), gives another arrangement by treating the number and content of powerful markers as hereditary boundaries of blended model capacities for explicit attributes.

Streamlining of the probability would then be required to increment factual power and lessen bogus positives (Tao *et al.*, 2012). New GWAS Methods for Multi-variation Test of Rare Variations Customary GWAS techniques, including those referenced previously, accept the normal illness brought about by normal variations model (CDCV) (Tao *et al.*, 2016). Due to this predisposition, and since uncommon variations have such low measurable force, it is common to sift through uncommon variations before any GWAS. Be that as it may, uncommon alleles might be the reason for the phenotypic variation of interest. Along these lines, this is one wellspring of the missing heritability, in light of the fact that an absence of adequate force won't permit distinguishing proof of uncommon causal variations except if their impact on the aggregate is very enormous (Thakur *et al.*, 2010).

Also, the instance of different uncommon utilitarian variations in close by positions can conceivably trigger circuitous affiliations (engineered affiliation); these might be in places that are mega bases away from utilitarian variations (Thompson *et al.*, 2007). Manufactured affiliations brought about by long-range LD blocks cause low GWAS goal also, increment hardships in pinpointing causal qualities dependent on GWAS signals (Tian *et al.*, 2017). In species filled in extremely enormous numbers, as of late arose uncommon

variations were found to be exceptionally pervasive, and hence naturally accepted to play fundamental capacities on attribute varieties this was shown exactly to be valid (Tian *et al.*, 2019).

More vigorous proof will follow as genotyping advancements quickly advance, which empowers a more complete appraisal of uncommon variations with particularly enormous example sizes and their jobs in complex qualities (Tominaga *et al.*, 2008). At the point when at least two free causal variations, each with immaterial impact, existing together in an acquired area (e.g., recombinant receptacle or LD block), it is genuinely far-fetched that any single variation will be identified, however would be feasible to be distinguished by mutually testing the variations collectively in a multi-variation test (Ummenhofer *et al.*, 2017). Multi-variation techniques, which profit with uncommon variation discovery requests (and possibly stay away from manufactured affiliations), are presently accessible to address various unlinked causal variations, and have been checked.

These techniques expect either fixed or irregular impacts. On the premise of fixed-impact supposition for tried variations, trouble tests propose the data from multi-variations are fallen into a new measurable score that tests the relationship between the score also, an attribute (Vos *et al.*, 2005). For the premise of arbitrary suspicion, variance component tests have been proposed, and blended models are used to test the probability proportion for a gathering of multi-variations treated as irregular impact factors with free typical dispersions. Another choice to examine connected free causal variations is the haplotype-based affiliation examination. This halfway resolves the issue of manufactured affiliation by means of the distinguishing proof of the meaning of allelic series or hereditary heterogeneity ascribed to numerous utilitarian polymorphisms in a genomic (or gene based) locale (Wang *et al.*, 2017).

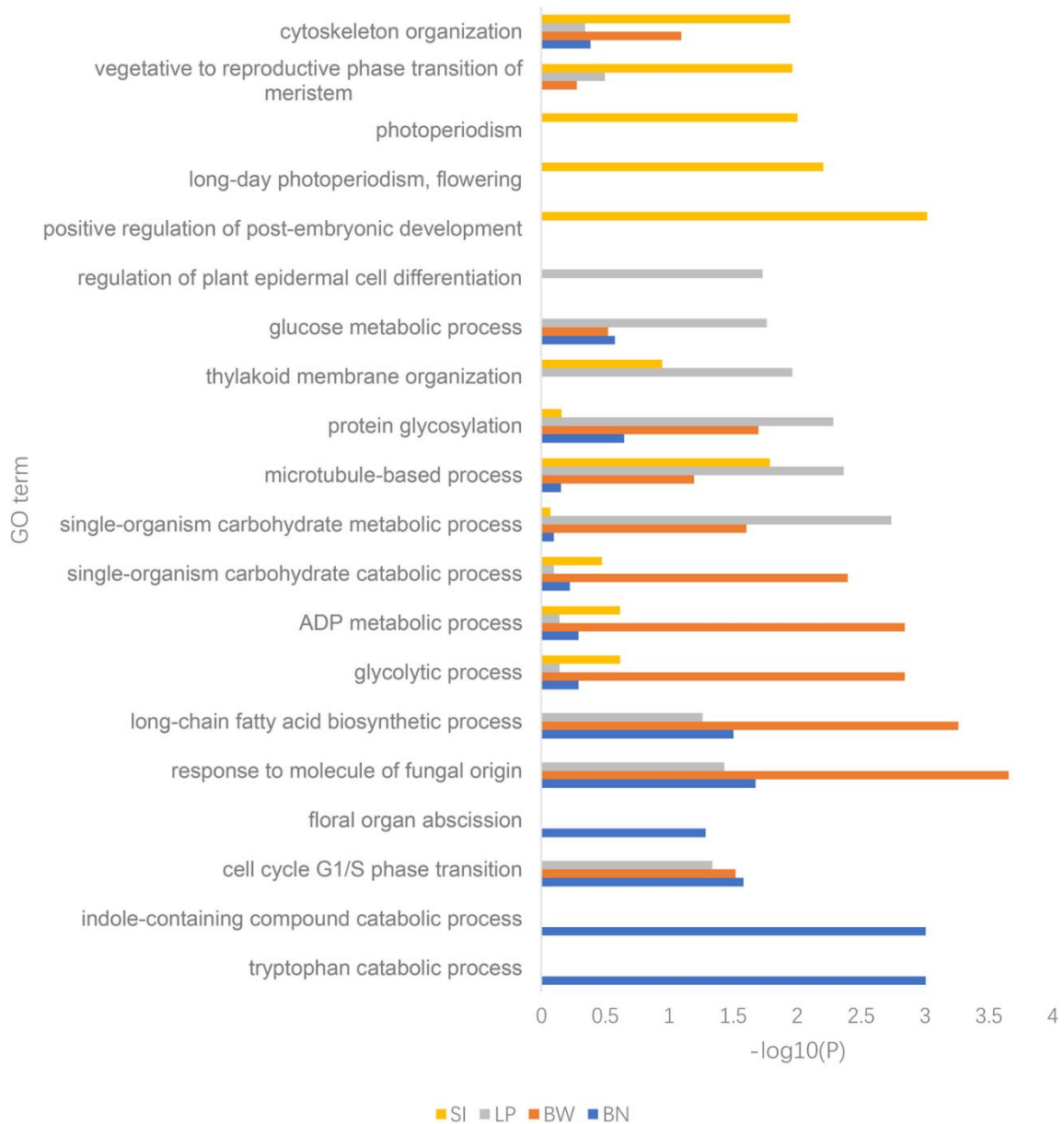
### **GWAS success in enhancing maize breeding by identifying beneficial alleles**

Environmental change is compromising food security across the globe Alam *et al.* (2017). Harvest yield should increment by 25-70% continuously 2050 without squeezing biological system working (Alexander *et al.*, 2009; An *et al.*, 2012). Since the 1960s, the yield improvement pace of significant food crops (rice, and maize) has eased back down (Anders *et al.*, 2015), and current yield patterns are not adequate to meet future necessities (Apel *et al.*, 2004). Also, enhancements in crop usefulness should be achievable in a profoundly irregular environment. More and strengthened limit climatic occasions (dry spell, cold wave, ice, hefty precipitation, storms, and so forth) are expected in the future (Applequist *et al.*, 2001; Ardy *et al.*, 2002). These uncommon climatic limits will contrarily impact plant development and improvement, environment administrations, and human solace (Atwell *et al.*, 2010). Maize (*Zea mays* L.) crop gives 19.5% of worldwide caloric admission from all sources (Atwell *et al.*, 2010; Ayers *et al.*, 2010). Moreover, it has additionally become a significant mechanical item. Notwithstanding, temperature limits (event of high and low temperatures during the development time frame) are compromising the yield supportability of maize. Maize plants are delicate to warm pressure (>30 °C) and there is a solid decrease in grain yield as plants face cold pressure over this limit for a delayed span (Bajželj *et al.*, 2014).

The ideal development of maize crop needs unique temperatures during day and night and over the entire developing season. During sunlight, the ideal temperature shifts from 25 to 33 °C, though during the evening, ideal temperature differs from 17 to 23 °C; the mean ideal temperature for the entire developing season is 20-22 °C (Bano *et al.*, 2015). Maize plants sprout best at 25-28 °C (Barnabás *et al.*, 2008). The conceptive stage is the touchiest to imperfect and supra-ideal temperatures. A swing from the ideal temperature causing high-temperature stress essentially diminishes the development rate and grain yield through a decline in seed setting proportion and unsettling influence of a few physiological cycles. The base and most extreme edge temperatures at different development and formative phases of maize crop. It is extended that until 2050, 45% of the worldwide maize creation region is probably going to confront a mean scene of five days of the greatest temperature >35 °C during the regenerative stage yearly (Bates *et al.*, 2015).

This is essential to note as a simple 1 °C ascend in mean occasional temperature can cut the monetary yield of maize crop by 3-13 % (Bilska-Kos *et al.*, 2017). A high temperature at basic advancement stages may likewise weaken the nature of maize grains (Boehlein *et al.*, 2019). Diminished seed setting in summer maize (ZD958 planted in Hebei, China, in 2018) presented to warm pressure at the fertilization stage. The temperature surpassed 35 °C at the hour of dust shed, influencing the dust gathering by at first arose silks at the foundation of the ear when contrasted with the tip of the ear for late-arising silks. Despite the fact that maize crop is initially from the (sub-) jungles, its development has moved to areas with mild environments. Efficiency misfortune under low temperature principally happens in view of a solid decrease in metabolite transport and photosynthetic movement (Sandhu *et al.*, 2018). As a general rule, low temperature adversely influences vaporous trade, water use proficiency, morphology, and physiology (Perrea *et al.*, 2016, Reeves *et al.*, 2001). Ranchers sow maize right on time to get away from cold pressure at the regenerative stage, yet plants are presented to low soil temperature (under 10 °C) during early seedling foundation.

During this stage, soil temperature firmly impacts leaf improvement as the shoot zenith is situated extremely close to the dirt surface. In this way, to adapt to temperature limits in maize creation, a thorough arrangement of changes in social just as in atomic procedures, (for example, rearing environment tough genotypes) and a worked-on comprehension of the hereditary, physiological, and sub-atomic reactions to temperature limits are required. Harvest plants normally experience distinctive biotic and abiotic focuses at the same time that cause numerous morphological and physiological irritations, bringing about hindered plant development and diminished grain yields (Cho *et al.*, 2010; Chen *et al.*, 2012) (Figure 4).



**Figure 4.** An overview of different processes initiated in maize during cold stress

Moreover, the maize plant just executes sped up endosperm advancement under raised day-and evening time temperature, not just under day-time warming (Tian *et al.*, 2017), recommending that warmth stress sway changes extraordinarily with the hour of day and seriousness of stress. It clarifies the impact of warm weight on conceptive improvement in maize. Physio-metabolic: Inadequate photosynthates in cold-focused on plants are frequently considered as a significant restricting element for yield (Goddard *et al.*, 2009). By the by, considering the C<sub>4</sub> organic chemistry of maize crop, ordinarily, photosynthate supply isn't restricting (Tominaga *et al.*, 2008). Subsequently, the essential driver of yield misfortune under raised temperatures for the maize crop during the grain filling period is the sped up formative cycle.

## Transcription

To further identify candidate resistance genes positioned around the GWAS-identified loci, the resistant rice variety, NSIC RC154, and the susceptible variety CT 9737-6-1-3P-M (both confirmed) were grown and inoculated with the more virulent *Xoo* race P6 in a greenhouse by the leaf-clipping method (Hoggar *et al.*, 2008). From each rice variety, leaves sample were obtained at 12, 24, 48, and 72 hpi, respectively, and each treatment has three replicates. Control samples of non-inoculated, fresh leaves of seedlings at 12 h were also collected. Place all leaf samples in liquid nitrogen and stored at -80 °C for their RNA isolation. Total RNA was isolated with the Plant Total RNA Isolation Kit (Sangon Biotech, Shanghai, China), according to the manufacturer's instructions. We used the NEBNext Ultra™ RNA Library Prep Kit for Illumina (NEB, USA) for RNA-Seq libraries construction. The Illumina Hi-Seq platform was used sequencing, and 125-bp paired-end reads were generated. Among raw data, the reads having a low-quality score and those containing adaptor sequences and stretches of -Ns were removed. An index of the Nipponbare rice reference genome was built using Bowtie v2.2.3, to which the above paired-end reads were aligned using TopHat v2.0.12 (Hussain *et al.*, 2006; Izaurrealde *et al.*, 2011; Hussain *et al.*, 2019). To count the number of reads mapped to each gene, HTSeq v0.6.1 software was used (Kang *et al.*, 2008). The expression value of each gene was present based on FPKM (fragments per kilobase of transcript sequence per million) that calculated using Cuffdiff software (v2.2.1).

The differential expression analysis of two treatments (each treatment contains three biological replicates) was carried out in R, using the “DESeq” package (v1.18.0) (Kawahara *et al.*, 2016). Differential expression levels of gene in the two treatments sample comparisons were determined based on the negative binomial distribution. Benjamini and Hochberg's approach was used to adjust *P*-values for controlling the false discovery rate (FDR). Genes with the log twofold change  $> 1$  and adjusted *P*-values of  $< 0.05$  were designated as differentially expressed (Koseki *et al.*, 2010).

### GWAS may enlighten the debate over “missing heritability

Grain yield diminishes when yield arrangement activities are led sooner than typical. Key protein exercises, for example, ADP-glucose pyrophosphorylase (engaged with starch biosynthesis) are additionally restricted at various levels, including both the transcriptional and post-transcriptional levels (Fujino *et al.*, 2004). Strikingly, a high temperature at the grain filling stage lessens amyloplast biogenesis and endosperm cell division, causing abatement in the grain size (Edreira *et al.*, 2011). Starch amasses in the creating grain through a perplexing organization of compounds (sucrose synthase, solvent starch synthase) directing this pathway (Gourdji *et al.*, 2013). Warmth stress restricts these chemical exercises and weakens starch gathering during the grain filling and solidifying measure (Gu *et al.*, 2013). High temperature ( $>30$  °C) intrudes on the ordinary amyloplast replication cycle and cell division in grains, in this way contracting sink size (Hernández *et al.*, 2005). Moreover, high temperature influences the physicochemical properties (starch, protein, and solvent sugar substance) of waxy maize during the grain filling measure, coming about in grains with unsatisfactory quality (Han *et al.*, 2008).

Warmth stress additionally upsets the ordinary physiological cycles needed for ideal maize development and improvement. Diminished biomass absorption and grain fetus removal are the key physiological cycles bringing about decreased grain number in cold-focused on plants (Fang *et al.*, 2017; Hartmann *et al.*, 2000). Warmth stress up to 36 °C essentially diminished the radiation use effectiveness (Hasanuzzaman *et al.*, 2020), and less dynamic nitrogen and carbon digestion systems add to a decline in dry matter collection (Hayashi *et al.*, 2016). The conversation above proposes that radiation use proficiency, biomass collection, and the source-sink proportion are the urgent determinants of conclusive grain yield and the gather record under cold pressure conditions. Taken together, cold pressure contrarily impacts dusts reasonability and silks' receptivity, prompting a critical reduction in seed set and monetary yield. Maize is a chilly delicate plant, and frequently, yield is restricted in cool, sticky areas (e.g., Central Europe).

In these areas, when maize crop is presented to cold pressure, the development rate will in general diminish while development span is delayed. In this manner, low temperature debilitates the seedling and may likewise stop the grain filling rashly toward the finish of the development cycle (Hoggart *et al.*, 2008; Fujino *et al.*, 2011; Hieke *et al.*, 2014), bringing about lower and conflicting grain creation in uneven and mild regions. Injury to plant cells or tissue under chilling pressure during the early seedling stage or low temperatures at the conceptive stage in maize may shift contingent on the pressure term and its degree. Low temperature stress, described by plant openness to a temperature range under 10 °C for an adequate span, can interfere with the ordinary interaction of yield development, beginning from the early seedling stage to the later conceptive stages (Wang *et al.*, 2019).

Physio-metabolic: A temperature around 8-10 °C postpones seedling development and causes a decrease in the root/shoot proportion and chlorophyll content during the early development cycle in maize (Hussain *et al.*, 2019), while a temperature from 4 to 10 °C may stifle chlorophyll combination and causes a serious decrease in photosystem II (PS II) movement (Hussain *et al.*, 2019). Low temperature stress contrarily impacts chloroplast and thylakoid structures, chemical exercises, and the Calvin cycle by lessening metabolite transport (Yan *et al.*, 2009). While examining cell divider properties under chilling pressure (12–14 °C), Cell divider gelatin content and gelatin methylesterase action become lower in a cool delicate maize half breed (Zhang *et al.*, 2019). Different physiological and biochemical problems can be seen in photosynthetic apparatus, cell layers, and compound exercises under low temperature stress (Yang *et al.*, 2019).

Chen *et al.* (2012) announced a critical ascent in malondialdehyde (MDA) substance and cell layer porousness because of chilling injury at the early seedling stage, with diminished substance of water, proline, and chlorophyll in maize leaves (Huang *et al.*, 2017). Low temperature stress additionally makes shoots and roots large scale supplement (N, P, K, Ca, Mg) inadequate by restricting metabolite transport (Kawahara *et al.*, 2016). In any case, when maize plants are presented to chilling temperatures of 7-10 °C, they produce flagging mixtures (e.g., nitric oxide and abscisic corrosive) in safeguard (Koseki *et al.*, 2010). Low temperature stress makes harm macromolecules, cell designs, and layers because of the over-the-top creation of responsive oxygen species (ROS) (Cho *et al.*, 2010; Fujino *et al.*, 2011; Kovach *et al.*, 2007). In safeguard, plants produce more cell reinforcement chemicals including superoxide dismutase (SOD), peroxidase (POD), and proline (Yu *et al.*, 2006; Segura *et al.*, 2012).

Low temperature stress at grain filling can adjust the starch synthesis in grains by lessening the amylose content, eventually diminishing water dissolvability and starch growing force and expanding gelatinization temperatures (Han *et al.*, 2008). Temperatures under 15 °C during the late conceptive stage decrease the exercises of the photosynthetic mechanical assembly just as paces of sucrose phosphate synthase, phosphoenol pyruvate carboxylase, and sucrose synthase. It will in general destabilize the absorption interaction, bringing about debilitated grain quality with unacceptable quality parts and poor actual grain surface (Lei *et al.*, 2014; Fahad *et al.*, 2017; Fahad *et al.*, 2021a; Fahad *et al.*, 2021b; Fahad *et al.*, 2021c; Fahad *et al.*, 2021e). Aggregately, low temperature stress lessens the germination rate, development rate, and the photosynthetic rate, bringing about helpless yield. A schematic portrayal of the different impacts and components of warmth and cold stress. To adapt to the malicious impacts of temperature limits, it is unavoidable to receive different agronomic and reproducing options alongside cutting edge genomic apparatuses. Here, we talk about different techniques to battle temperature limits in maize trimming frameworks.

Environment keen agronomic practices for a particular trimming framework incorporate practices that assist ranchers with adjusting environment stresses or potentially decline efficiency misfortune. These practices are turning out to be progressively essential to alleviate the unfriendly impacts of temperature limits (Li *et al.*, 2015; Lesk *et al.*, 2016; Sajid *et al.*, 2020; Mohammad *et al.*, 2020; Mohammad *et al.*, 2020a). Change in planting time may help plants get away from the temperature outrageous stage at basic development stages (Li *et al.*, 2019). In the North China Plain, maize crops have been faced with scenes of chilling and warmth stresses lately. Adjustment in planting time decreased the yield misfortunes altogether by limiting the danger of warmth

and chilling harm during the silking and grain filling stages, individually (Foyer *et al.*, 2002; Senol *et al.*, 2020; Amjad *et al.*, 2020).

### **Variation above the genomic level can function in a complementary manner**

While changing to longer seasons, cultivars likewise improved the grain yield (going from 13% to 38%) by effectively alleviating the grave impacts of expanded warming patterns of thirty years (Li *et al.*, 2019). In semi-bone-dry regions (e.g., Sub-Saharan African nations), odds of maize crop disappointment are exceptionally high due to the unforgiving environment. There, the innovation of dry soil planting (DSP) is extremely viable to accomplish sufficient grain yield (Li *et al.*, 2014). Ranchers plant seeds not long before the stormy season in dry soil. Since seeds will be in soil at the hour of downpour, they can begin the germination cycle in a flash subsequent to getting dampness. Such innovations can be reinforced with man-made reasoning all the more precisely foreseeing the stormy season (Li *et al.*, 2014). Appropriation of cultivars with more warm time prerequisites can likewise essentially expand the yield by the deferral in development and broadened conceptive development span (Li, *et al.*, 2011). Along these lines, ranchers need to adjust to the future environment by streamlining the planting date, maize earliness, and dry soil planting and choosing cultivars with more warm time necessities as indicated by their neighborhood pedoclimatic conditions.

### **Reproducing for cold tolerance**

Distinguishing proof of reasonable guardians is fundamental for any reproducing program, remembering the destinations of the investigation. For example, the determination of high-yielding warmth lenient assortments to be utilized as guardians is a pre-essential to begin a reproducing program focused on the improvement of high-temperature-open minded maize cultivars. Here, we enroll a few maize genotypes including ingrained lines and half and halves that showed critical warmth resistance and, in this manner, can fill in as significant reproducing materials to introgress cold resilience in world class maize cultivars. Also, the recognizable proof of key determination lists is urgent for the choice of lenient cultivars or wild species. Leaf terminating, tuft impact, decoration sterility (TS), anthesis-silking stretch (ASI), and senescence are contrarily related, while dust shedding length (PSD), seed setting rate (SSP), and chlorophyll content are decidedly associated lists with grain yield in maize under cold pressure (Farooq *et al.*, 2009). As of late, it was tracked down that high temperature influences the carbon dioxide swapping scale (CER) in maize, which contrarily influences crop development rate, grain number, and last grain yield (Fang *et al.*, 2020; Muhammad *et al.*, 2020).

Photosynthesis wellness is basic in choosing the exhibition of maize crops under cold pressure conditions (Atwell *et al.*, 2010). Supporting a good pace of photosynthesis action under cold pressure is fundamental to diminish efficiency misfortune (Piepho *et al.*, 2007; Perrea *et al.*, 2016). A few pointers of photosynthesis wellness have been accounted for, for example, chlorophyll substance, carotenoids, and stay-green plant engineering which are decidedly associated with the pace of photosynthesis (Portolés *et al.*, 2007). Standardized contrast vegetative record (NDVI), in view of the trademark reflectance highlights of maize covering, is a proficient marker of the stay-green quality (Pugh *et al.*, 2010; Fazli *et al.*, 2020; Md *et al.*, 2020). In this way, utilizing these qualities in rearing projects of warmth lenient high-yielding maize cultivars can increment regenerative achievement, photosynthesis proficiency (NDVI), and other yield-related attributes under cold pressure.

Wild family members and far off guardians in intra-explicit crosses are extremely valuable assets to introgress novel qualities for maize improvement. Teosinte, an ancestor of developed maize, harbors a ton of commendable qualities to endure a blend of various anxieties. Teosinte is very much adjusted to the high temperature climate as it shows somewhat lower harm and supports chlorophyll content under cold pressure (36 to 45 °C) and portrays higher endurance limit even at 55 °C (Qin *et al.*, 2008; Gopakumar *et al.*, 2020). In this way, it can fill in as an expected hotspot for maize improvement programs. In any case, it was inadequately misused for the distinguishing proof and introgression of such qualities. Before, an exertion was made to

recognize a warmth open minded assortment of teosinte called "Florida" and effectively introgressed cold resilience from teosinte to developed corn (Rafique *et al.*, 2019; Md *et al.*, 2020).

As per another report, between sub specific mixtures of teosinte × maize was created, which showed expanded thermo-capacity to bear a few developments and yield-related characteristics (Qin *et al.*, 2008). In this way, the misuse of wild family members and far off guardians in intra-explicit crosses could demonstrate an extremely valuable asset to introgress novel qualities for maize improvement. The potential systems engaged with yield misfortune aversion by cold-open minded maize. The maize crop is very delicate to low temperatures and requires genuinely high temperatures for ideal development and creation. To stay away from incessant scenes of warmth and dry season during the conceptive stage, ranchers develop this harvest early (Commuri *et al.*, 2001; Raza *et al.*, 2019; Farah *et al.*, 2020; Sadam *et al.*, 2020). Notwithstanding, early developed maize is regularly presented to chilling pressure, which may prompt low harvest execution because of helpless germination or absence of seedling endurance (Read *et al.*, 2001; Unsar Naeem *et al.*, 2020).

**Table 3.** Summary of the characteristics of three multi-parent population designs in maize

Character	Population A	Population B	Population C
Cross pattern	Interconnect	Interconnect	Disconnect
Genetic diversity	High	High	High
Founder contribution	Extremely imbalanced	Balanced	Approximate balanced
Population size	Large	Intermediate	Large/very large
Algorithm complexity	Low	High	Intermediate
Recombinant events	Intermediate	High	Intermediate
Developmental cost	High	Very high	Low
Collaborative research	Possible	No	Suitable

Sweet corn is considerably more delicate to low temperatures contrasted and field maize. Achieve high development rates and lively seedlings under low temperatures to adjust maize for early planting (Reeves *et al.*, 2001). Enormous variety is available in maize germplasm for variation to cold resilience, particularly in intriguing maize populaces (Riva-Roveda *et al.*, 2016). Maize cultivars of mild districts (e.g., Europe) have been broadly utilized in chilling resistance reproducing programs dependent on great harvest execution (Hussain *et al.*, 2019). Here, we present a few cold-open minded maize cultivars created all throughout the planet that could be used in rearing projects. Mid-parent execution is a helpless pointer of mixture choice for cold resistance, and testcross execution ought to be utilized as a solid marker for quantitative quality locus (QTL) planning to foster stable markers (Robinson *et al.*, 2010). Recognizable proof of dependable choice records for cold resistance is critical to screen germplasm for the reproducing programs (Cho *et al.*, 2010). A few attributes like photosynthetic rate, stomatal conductance, quantum proficiency, dry matter creation, leaf weight and region, and water use productivity are acceptable choice records to acknowledge cold resistance in maize (Hoggart *et al.*, 2008).

Hence, the recognizable proofs of cold-open minded germplasm dependent on solid determination lists can proficiently further develop execution. Hereditarily adjusted yields (GMCs) could fill in as a helpful asset for novel characteristics (Saito *et al.*, 2004; Saito *et al.*, 2010). In ongoing many years, fast advancement in plant sub-atomic science has sped up the pace of harvest improvement. A few methodologies including quantitative attribute locus (QTL) planning, transcriptomics, marker-helped determination (MAS), map-based quality cloning, and genome altering, (for example, grouped consistently interspaced short palindromic rehash ((CRISPR)/CRISPR-related 9, Cas9) have been used for choice and improvement of plant characteristics in a few yields.

### Marker-assisted selection (MAS)

Molecular techniques are helpful to improve any specific trait of plant (Rasheed *et al.*, 2021c). Pyramiding helpful qualities followed by the determination of advantageous plant material has been quite difficult for plant raisers. It is almost difficult to pyramid different alluring qualities through traditional reproducing because of linkage. Marker-helped choice (MAS) fundamentally worked on the productivity just as diminished the time required for complex characteristic determination like dry spell, salt, cold, and warmth resilience (Sánchez *et al.*, 2014). Different qualities control cold resistance attributes in maize crops. After the disclosure of various atomic markers for cold and warmth resistance in maize, it is currently conceivable to screen the open-minded germplasm at the early development stage, saving time, work, and space (Hayashi *et al.*, 2016; Sandhu *et al.*, 2018; Ayman *et al.*, 2020). Single nucleotide polymorphisms (SNPs) are ordinarily utilized atomic markers because of their plenitude in the genome, simple location examination, and co-predominance nature (Atwell *et al.*, 2010). A few SNPs related with qualities administering warmth and cold resilience were recognized, which could be utilized in MAS to speed up the determination interaction and accelerate generally reproducing programs (Fujino *et al.*, 2010; Zia-ur-Rehman *et al.*, 2020).

### Future perspective

Roots and shoots evolved together for nearly 3.5 million years. However, owing to directional selection for yield in the past century, root attributes were completely neglected in breeding programs, unless the improvement was indirect. Therefore, a future breeding dimension should focus simultaneously on the recruitment of lost root system variations for yield and sustainability. Several studies reported that root system attributes enhance shoot architecture for yield and drought fitness in cereals, reflecting that root should be the foremost breeding target of the future.

The natural genetic diversity in differential root system architecture may be useful to understand drought adaptation mechanisms and improve cultivars by generating beneficial root architecture. To date, studies have reported and validated QTLs associated with root system traits, such as root length, biomass, number, angle, volume, diameter, density, and xylem vessel size, under drought stress conditions. More importantly, the diversity of the wild relatives of crops showed remarkable root system variations that have great potential in drought stress adaptation. Here, we summarized a considerable amount of donor genotypes, including wild relatives (Supplementary Table S1), but very limited strategies have been undertaken to exploit these lines in resilient breeding programs. These promising donor parents need to be introgressed into elite backgrounds to enhance the stress-adaptive potential of the cultivated gene pool.

The enhancement of root-related drought stress adaptation by applying classical breeding is difficult owing to the complexity levels of these traits. Genomic and phenomic approaches are gaining popularity as important tools that allow in-depth analyses of crops to increase our understanding of the complexity of the mechanisms underlying stress adaptation. Although both *cis*- and *trans*-genetic components, along with epigenetics, are involved directly in trait complexity, the role of *cis*-genetic modules appears to be more influential on the quantitative divergence in expression of genes controlling polygenic traits across dynamic environments. Therefore, interactions form the biggest challenge in the precise genetic determination of these traits under field conditions. This scenario demands an expression QTL analysis as a high-resolution genomics approach for the precise dissection of traits at morphological and physiological levels across varying environments. In addition, over the last decades, NGS and bioinformatics tools have been rapidly advancing, allowing the discovery of new genes and regulatory sequences controlling diverse complex traits.

## Conclusions

All things considered, high-throughput phenotyping and genotyping offices are not broad among maize raisers of helpless nations because of confined assets, noticeable by the sluggish pace of harvest improvement around there. This causes a gigantic contrast in the normal yield of maize among created and immature nations. For instance, the normal maize yield in the United States is 13.2 tons/ha, which is 340% more than the normal grain yield of 3 tons/ha in South Africa and 0.9 tons/ha in Mozambique. Another key restriction is deficient information on the atomic systems of complex attributes like warmth and cold resistance. Absence of proper foundation, insufficient functional help, restricted HR, and absence of empowering strategies and legal and administrative systems are the key factors that hamper the prosperous development of sub-atomic reproducing in agricultural nations.

A genuine exertion is important to address these critical difficulties among maize raisers across the world to guarantee feasible maize creation and food security. This could be accomplished through subsidized preparing of maize raisers from agricultural nations at worldwide exploration stations like CIMMYT, ICARDA, and so forth, to foster a fantastic human asset for mid-economy nations. Another key advance could be to give instruments to high-throughput phenotyping and genotyping just as seeds of further developed cultivars to these raisers, which can support their yield potential. Warm anxieties at basic development phases of maize diminish the grain yield, dietary benefit, and overall gain of ranchers. Hereditary variety exists among various cultivars for cold and warmth resilience, which shows the requirement for more precise plant reproducing projects to have site-explicit plant assets to further develop maize crop execution under restricting developing conditions. Exogenous utilization of manufactured and regular plant development controllers at low focuses additionally lessens usefulness misfortune under such conditions. New reproducing procedures, for example, marker-helped rearing and genome altering, especially the sans transgene CRISPR-Cas9 framework, offer incredible potential for the advancement of environment versatile cultivars in a nearly more limited time. Moreover, a solid foundation for assessment of maize germplasm dependent on high-throughput phenotyping in addition to genotyping is needed in agricultural nations.

## Authors' Contributions

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## Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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