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






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Advancements in QTL mapping and GWAS applications in plant improvement

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Abstract: In modern plant breeding, molecular markers have become indispensable tools, allowing the precise identification of genetic loci linked to key agronomic traits. These markers provide critical insight into the genetic architecture of crops, accelerating the selection of desirable traits for sustainable agriculture. This review focuses on the advancements in quantitative trait locus (QTL) mapping and genome-wide association studies (GWASs), highlighting their effective roles in identifying complex traits such as stress tolerance, yield, disease resistance, and nutrient efficiency. QTL mapping identifies the significant genetic regions linked to desired traits, while GWASs enhance precision using larger populations. The integration of high-throughput phenotyping has further improved the efficiency and accuracy of QTL research and GWASs, enabling precise trait analysis across diverse conditions. Additionally, next-generation sequencing, clustered regularly interspaced short palindromic repeats (CRISPR) technology, and transcriptomics have transformed these methods, offering profound insights into gene function and regulation. Single-cell RNA sequencing further enhances our understanding of plant responses at the cellular level, especially under environmental stress. Despite this progress, however, challenges persist in optimizing methods, refining training populations, and integrating these tools into breeding programs. Future studies must aim to enhance genetic prediction models, incorporate advanced molecular technologies, and refine functional markers to tackle the challenges of sustainable agriculture.

Key words: Molecular markers, QTL mapping, genome-wide association studies, plant breeding, next-generation sequencing, genomic selection

1. Introduction

The necessity of meeting the food demands of a rapidly growing global population expected to exceed 9 billion by 2050 presents critical challenges, intensified by climate change and the growing demand for biofuels (Kumar,

2020; Ali et al., 2022; Ahmed et al., 2023). To address these concerns, it is estimated that grain production will need to increase by up to 50% by 2025, necessitating the development of crop varieties with improved agronomic traits (Kumar et al., 2020). These traits, which include stress

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tolerance, yield optimization, and nutrient efficiency, are governed by complex interactions between multiple genes and environmental factors. Understanding these complex traits at the genetic level through quantitative trait locus (QTL) mapping and genome-wide association studies (GWASs) has become crucial for advancing plant breeding (Colasuonno et al., 2021; Zahid et al., 2022). These targeted approaches facilitate the integration of desirable traits through marker-assisted selection (MAS) and genomic prediction, driving the development of crop varieties that maintain high productivity under environmental stresses.

QTL mapping is a powerful tool in plant breeding, employed to explore the genetic architecture of complex traits and identify candidate genes (Andrade et al., 2020). Significant and stable QTLs identified across diverse genetic and environmental contexts are valuable resources for future gene cloning efforts and the development of molecular markers relevant to breeding programs. Traditional breeding techniques, such as mutation breeding and MAS using molecular markers, have broadened the genetic pool for crop improvement by facilitating the introgression of desirable traits (Ahmar et al., 2020). Advanced methods including GWASs, clustered regularly interspaced short palindromic repeats (CRISPR) technology, next-generation sequencing (NGS), and meta-analysis are poised to further enhance the precision and efficiency of modern plant breeding. Comparative studies have highlighted the distinct advantages of QTL mapping and GWASs in genetics (Mace et al., 2019; Alqudah et al., 2020). While QTL mapping is effective for pinpointing genomic regions associated with traits within specific populations (Khan et al., 2021), it has limitations including a dependence on allelic variation between parental lines and limited mapping resolution (Figure 1) (Sahito et al., 2024). GWASs overcome these limitations by assessing genetic associations across larger and more diverse populations.

GWASs are considered to be highly effective and promising for understanding complex traits (Uffelmann et al., 2021). In recent years, GWASs have been increasingly utilized in the study of various crop species, including sorghum (Wondimu et al., 2023), wheat (Hanif et al., 2021), soybean (Priyanatha et al., 2022), rice (Ma et al., 2016), pearl millet (Yadav et al., 2021b), and barley (Ogrodowicz et al., 2023), demonstrating its potential to enhance our understanding of genetics and trait improvement. The choice between QTL mapping and GWASs in breeding programs depends on the specific goals, trait complexity, and resources. QTL mapping is suitable for traits with major-effect loci in controlled crosses or with known parental lines, but lower resolution makes it less suitable for identifying minor-effect loci across diverse populations. GWASs are ideal for the study of polygenic traits influenced by multiple loci but they require large, well-characterized populations. This review aims to provide a comprehensive overview of recent advancements in QTL mapping and GWAS applications in plant improvement, with a specific focus on how these tools contribute to developing crop varieties resilient to environmental challenges with enhanced agronomic performance. By summarizing these innovations, this review seeks to underscore the transformative potential of QTL mapping and GWASs in addressing future food security and agricultural sustainability.

2. Advancements in sequencing technologies

2.1. Transcriptomics

The word “transcriptome” refers to all of the mRNA molecules produced by a cell or a group of cells (McGettigan, 2013). This concept was first introduced by Charles Auffray in 1996 (Piétu et al., 1999) and subsequently appeared in a scientific article in 1997 (Velculescu et al., 1997). Transcriptomics encompasses the methods used to study an organism’s transcriptome,

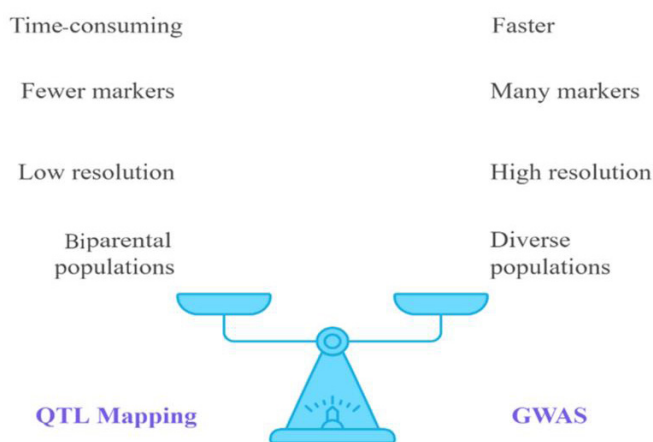


Figure 1. Comparison of QTL mapping and GWASs.

which includes all the RNA transcripts it generates. The genetic information of an organism is stored in its genomic DNA and expressed through a process called transcription. Understanding these transcripts, along with how genes are regulated and expressed, is crucial for addressing key issues in biology. Over the years, transcriptomics research has grown significantly due to rapid advancements in sequencing technologies (Abdel-Ghany et al., 2016).

In particular, short-read sequencing technologies (e.g., Illumina and NGS) have transformed the field, offering greater accuracy and higher data output than earlier methods like microarrays. The introduction of NGS from 2004 to 2006 marked a turning point, leading to a dramatic increase in the amount of sequencing data available for research (Mardis, 2013). Nanotechnology innovations have increased output by enabling parallel DNA molecule sequencing, allowing for higher throughput and improved accuracy via miniaturized platforms that facilitate the simultaneous processing of multiple samples and the sequencing of single DNA molecules (Hu et al., 2021b).

The dominance of RNA-Seq technology began in 2008 with the publication of significant studies that utilized newly developed short-read technology from Solexa, now known as Illumina (Mortazavi et al., 2008). Illumina's NGS technology utilizes sequencing by synthesis with fluorescently labeled reversible terminator technology (Mardis, 2013). Clonal amplification of DNA libraries is done through bridge amplification polymerase chain reaction (PCR), managed by the sequencing instrument. Sequencing involves optical detection of fluorescent nucleotides attached to a reversible terminator by DNA polymerase. Illumina NGS technologies assist in paired-end sequencing, allowing the development of high-quality data with deep coverage and numerous reads (Gandhi et al., 2017).

Third-generation sequencing platforms, such as Pacific Biosciences and Oxford Nanopore technologies, offer read lengths exceeding 10 kb, far surpassing those of Sanger and short-read sequencing methods. These "long-read" technologies address the challenges associated with short-read sequencing, such as the resolution of genome-wide repeats or detection of structural variants. Unlike second-generation methods, third-generation sequencing requires minimal library preparation and directly targets unfragmented DNA molecules in real time, with the primary limitation being the need for high-molecular-weight DNA. While early third-generation technologies had lower accuracy compared to second-generation methods, ongoing improvements, particularly in software analysis, have steadily enhanced their accuracy (Hu et al., 2021b).

PacBio sequencing employs SMRT technology, utilizing fluorescently labeled nucleotides to enable the sequencing of long DNA fragments extending to lengths of several tens of kilobases (Satam et al., 2023). At the heart of PacBio's DNA sequencing innovation lies zero-mode waveguide (ZMW) technology, initially detailed in a 2003 *Science* article co-authored by Webb and Craighead (Wang et al., 2023). This method employs PacBio's SMRT technology, which involves affixing the polymerase enzyme to the base of a ZMW well. By utilizing a single DNA strand as a template, the polymerase integrates fluorescently labeled nucleotides. Each nucleotide carries a distinct fluorescent dye that emits a signal when it traverses the ZMW. A detector captures this fluorescent signal, identifying the nucleotide by analyzing the color of the emitted light. The polymerase incorporates the nucleotide and then removes the fluorescent tag, allowing the sequencing to proceed.

Plant transcriptomic approaches are widely used to examine how plants respond to different stress factors. Analyses in this field have revealed significant changes in gene expression when plants face environmental challenges (Javed et al., 2020). The growing adoption of transcriptomics for gathering genetic data is attributed to its rapid, comprehensive, and efficient capabilities. This technology facilitates the identification of new functional genes, exploration of secondary metabolite pathways, and understanding of plant developmental processes, offering essential insights for plant breeding (Tyagi et al., 2022). Transcriptomic studies have been performed on many plant species including *Arabidopsis thaliana*, rice, oat, and maize, and they have been conducted in diverse research areas such as stress responses, developmental biology, and disease resistance (Kumar, 2020; Ahmed et al., 2022). The dominance of RNA-Seq technology began in 2008, revolutionizing transcriptomic analyses by enabling the high-throughput sequencing of RNA, thereby facilitating a deeper understanding of gene expression dynamics in these species.

2.2. Single-cell sequencing

Recent advancements in sequencing technologies have created new opportunities for obtaining valuable insights into diverse biological systems (Pazhamala et al., 2021; Sun et al., 2022). Notably, single-cell RNA sequencing (scRNA-Seq) enables the analysis of gene expression at the single-cell level (Sun et al., 2024). This approach provides higher resolution compared to traditional bulk sequencing, allowing for the detection of cellular heterogeneity within various biological tissues and systems that was inaccessible by bulk sequencing (Kolodziejczyk et al., 2015; Lim et al., 2024). Recently, reductions in cost and improvements in protocol efficiency have resulted in a significant rise in the number of scRNA-Seq datasets utilized in biological research (Svensson et al., 2020; Pullin and McCarthy,

2024). Concurrently, there has been a marked increase in the number of methods developed for analyzing scRNA-Seq data. As of July 2023, over 1500 tools were available to perform various steps in scRNA-Seq data analysis (Zappia et al., 2018; Zappia and Theis, 2021).

The isolation of single cells in scRNA-Seq necessitates the use of precise techniques (Giacomello, 2021). Serial dilution, micropipette aspiration, fluorescence-activated cell sorting (FACS), and microfluidic systems are some of the options that can be used depending on the needs of the experiment (Arsenio et al., 2020; Pensold and Zimmer-Bensch, 2020). FACS is efficient for sorting cells but may cause damage, whereas laser capture microdissection maintains spatial information but is technically challenging (Kamme et al., 2003; Hu et al., 2016). Microfluidic approaches offer high throughput and automation. The choice of method depends on the specific needs of the experiment, requiring a careful balance of precision, efficiency, and cost (Kolodziejczyk et al., 2015).

The capture of RNA and the synthesis of cDNA begin with reverse transcription. Most published protocols employ oligo(dT) priming, which selectively targets polyadenylated mRNAs and a subset of long noncoding RNAs (approximately 40%) (Yang et al., 2011). This method effectively avoids capturing ribosomal RNA (rRNA), which constitutes over 95% of the total RNA in mammalian cells (Slomovic, 2006). Unique molecular identifiers, or random sequences acting as barcodes to track individual transcripts, are incorporated into cDNA synthesis (Kivioja et al., 2011). Yang et al. (2024) added sequencing adapters to ensure compatibility with the sequencing platform. Several techniques can synthesize the second strand after converting RNA to first-strand cDNA. SMART technology is one way to do that. It uses the transferase and strand-switching abilities of M-MLV reverse transcriptase (i.e., Moloney murine leukemia virus reverse transcriptase) to add template-switching oligonucleotides as adaptors for further PCR amplification (Zhu et al., 2001). This approach forms the basis of protocols such as Smart-Seq2, Smart-Seq, and STRT-Seq. Alternatively, the 5' end of cDNA can be ligated with poly(A) or poly(C) to create universal adaptors for PCR amplification. PCR remains a popular method for amplifying cDNA from low amounts of starting material.

Single-cell sequencing in plants is an innovative technique that facilitates the in-depth analysis of gene expression and cellular heterogeneity at the individual cell level (Ali et al., 2024b). This method is particularly useful for elucidating the complexities of plant tissues and their responses to various environmental stimuli. Researchers have used single-cell sequencing to explore the diversity of cell types in various plant tissues (Yu et al., 2023). For instance, it can distinguish among various cell types in

leaves, roots, and flowers, thereby revealing specialized functions and regulatory mechanisms. This technique is also critical for understanding plant development, as it enables researchers to monitor changes in gene expression during key developmental phases, such as germination and flowering. Additionally, single-cell RNA sequencing has been utilized to examine how individual plant cells respond to environmental stresses, including drought, salinity, and pathogen attacks, thereby uncovering specific pathways activated in response to these stressors at the cellular level (Bawa et al., 2022).

3. Quantitative trait loci mapping

Identifying QTLs and associated genetic markers linked to key traits is crucial for enhancing genetic gains in breeding programs (Tables 1 and 2). QTL mapping serves as a fundamental method for pinpointing the genetic regions responsible for traits of interest, thereby accelerating the selection process and improving breeding efficiency (Kumar et al., 2017; Sharma et al., 2023; Altaf et al., 2024a). Mapping QTLs helps understand the contribution of QTLs to trait variation as well as their additive and dominant effects, genetic correlations, and interactions with environments (David et al., 2023). These investigations are related to quantitative genetics applications like MAS and marker-assisted gene introgression.

3.1. Prerequisites for QTL mapping

Mapping QTLs in populations based on familial relationships consists of the following essential steps: 1) establishing a suitable mapping population and accurately phenotyping traits; 2) choosing appropriate molecular markers and collecting molecular data with a sufficient quantity of evenly distributed polymorphic markers; and 3) creating genetic linkage maps to pinpoint QTLs via statistical methods. The effectiveness of QTL mapping is determined by the size of the mapping population and the precision of both genotyping and phenotyping data (Snehi et al., 2024). The availability of comprehensive genomic resources, including molecular markers as well as genetic and physical maps, has enhanced the QTL and gene mapping processes (Vishwakarma et al., 2017).

3.2. QTL mapping strategies

Marker-based mapping experiments follow a fundamental strategy across different studies (Altaf et al., 2024b). Initially, the selection of parents that differ in terms of the target trait is crucial. The next step involves screening the two parents for marker loci to identify polymorphisms. Once this is achieved, mapping populations such as F₂ populations, backcrosses, recombinant inbred lines (RILs), or double haploid lines are developed. These populations are then subjected to phenotype screening. Subsequently, the means of homozygous dominant (MM) and homozygous recessive (mm) lines are compared at each marker locus.

Table 1. List of QTLs for abiotic stress among various crops.

Stress	Crop	Population	Traits	Marker	QTL/gene/ marker	Chromosome	Reference
Drought	Wheat	Cranbrook × Halberd	Osmotic stress spike	SNP	<i>IWB72377</i>	2A	Dolferus et al. (2019)
	Wheat		Stress tolerance trait	SNP	<i>VRN-A1</i>	5A	
	Wheat	Excalibur × Kukri	Yield	-	<i>QYld.aww-1B.2</i>	1B	Tura et al. (2020)
	Wheat	Chinese Spring × SQ1 (Highbury × TW269/9/3/4)	Yield	SSR	<i>Qyld.csdh.7AL</i>	7A	Gautam et al. (2021)
	Wheat	Reeder × Albany	Thousand-kernel weight	SNP	<i>QTW.ndsu.7B</i>	7B	Rabbi et al. (2021)
	Wheat		Yield	SNP	<i>QYL.ndsu.2B, QYL.ndsu.7B</i>	2B, 7B	
	Rice	MRQ74 and MR219	Grain yield	SSR	<i>qDTY12.1</i>	12	Mohd Ikmal et al. (2019)
		13 parents	Grain yield	RFLP, SSR	<i>qDTY1.1, qDTY3.1</i>	1,2, 3	Selamat and Nadarajh (2021)
		Cocodrie × N22	Grain number per panicle	SNP, SSR	<i>qGN3.1, qGN3.2, qGN5.1</i>	3, 5	Baisakh et al. (2020)
	Maize	Langhuang × TSI41	Ear height/plant height ratio	RFLP	<i>qEHPH-Ch.3-1</i>	3	Zhao et al. (2019)
		H082183 × Lv28	Ear weight	-	<i>qEW1s</i>	1	Abdelghany et al. (2019)
			Hundred-kernel weight	-	<i>qHKW7s</i>	7	
		RILs	-	SSR, SNP	<i>Pv01 and 08</i>	-	Diaz et al. (2018)
	Lentil	RILs	-	AFLP, SNP	<i>QRSVII: 21.94</i>	-	Idrissi et al. (2016)
	Chickpea	-	-	SSR	<i>CaLG01, CaLG02, CaLG06, and CaLG08</i>	-	Varshney et al. (2013)
		RILs	-	SSR	<i>Q1-1 and Q3-1</i>	-	Rehman et al. (2011)
Cold stress	Rice	Dongnong422 × Kongyu131	Percent seed set	SSR	<i>qPSST6</i>	6	Sun et al. (2018)
	Maize	B73 × Mo17 (IBM)	Plumule length	-	<i>qLTPL1-1</i>	1	Han et al. (2022)
			Seedling length	-	<i>qLTSL1-1</i>	3	
		80 inbred lines W72 × W10	Peroxidase activity at seedling stage	SNP	<i>qPOD3</i>	3	Jin et al. (2021)
	Wheat	-	Frost resistance	RFLP	<i>FR-2</i>	5A	Würschum et al. (2017)

Table 1. (Continued.)

	Norstar × Winter Manitou	Low-temperature tolerance	SNP	<i>QLT50.usw- 5A.1nm, QLT50. usw-5A.2nm</i>	5A		
	Capelle Desprez × Norstar	Low-temperature tolerance	SNP	<i>QLT50.usw- 5A.1nc</i>	5A	Fowler et al. (2016)	
	Norstar × Winter Manitou	Low-temperature tolerance	SNP	<i>QLT50.usw-5A.1</i>	5A		
	<i>Triticum spelta</i> 5A × Cheyenne 5A	Frost resistance	-	<i>FR2</i>	5D	Snape et al. (2001)	
Tomato	-	-	-	<i>qRGI-1-1, qRGI- 1-2, qRGI-12-1</i>	1, 4, 9, 12	Liu et al. (2016a)	
Heat stress	Tomato	Biparental F ₂	-	SNP	<i>qPV11, qPN7, qSP1, qSP3, qAL1, qIN1, qIN8</i>	1, 2, 3, 7, 8, 11	Xu et al. (2017)
		Diversity panel	-	SNP	15 markers	-	Ruggieri et al. (2019)
Potato		Diploid mapping population	-	SNP	3 QTLs	-	Trapero-Mozos et al. (2018)
	Bottle gourd	F ₂ population	-	SNP	<i>qHT1.1, qHT2.1, and qHT8.1</i>	1, 2, 5, 6, 7, 8	Song et al. (2020)
Salinity stress	Maize	Xianyu335 (PH6WC × PH4CV)	Root length	SNP	<i>qRLS1, qRLR1</i>	1	Luo et al. (2019)
			Shoot length	SNP	<i>qSLS1-2</i>	1	Luo et al. (2019)
			Full length	SNP	<i>qSLS1-2</i>	1	Luo et al. (2019)
			Root fresh weight	SNP	<i>qRFS1</i>	1	Luo et al. (2019)
			Full fresh weight	SNP	<i>qRFS1</i>	1	Luo et al. (2019)
		PH6WC × PH4CV	Plant height	SNP	<i>qSPH1</i>	1	Luo et al. (2017)
	Wheat	Kharacia65 × HD2009	Plant height	SSR	<i>QSph.iwbr-6A</i>	6A	Devi et al. (2019)
			Date of flowering	SSR	<i>QSdth.iwbr-2D</i>	2D	
		WTSD91 × WN- 64	Na ⁺ exclusion	SNP	<i>qSNAX.2A.1, qRNAX.7A.3</i>	2A, 7A	Hussain et al. (2017)
		Line 149 × Tamaroi	Leaf blade low Na ⁺ concentration	AFLP, RFLP	<i>NAX1</i>	2A	Lindsay et al. (2004)
	Rice	Pokkali × IR29	Na/K ⁺ absorption rate	RFLP	<i>Salto</i>	1	Karahara and Horie (2021)
	Pea	RILs	-	SNP	<i>LG3</i>	3, 7	Leonforte et al. (2013)

Table 1. (Continued.)

	Tomato	-	-	SSR	1 QTL	6	Liu et al. (2021)
	Cucumber	-	-	SSR	-	3	Kere et al. (2017)
	Chickpea	RILs	-	SSR	<i>CaLG05</i> and <i>07</i>	-	Pushpavalli et al. (2015)
		F ₂ Population	-	SSR	LG1	-	Chankaew et al. (2014)
		RILs	-	SSR	LG3, LG6, and LG4	-	Vadez et al. (2012)
	Cowpea	F2:5	-	RFLP, SSR	LGN	-	Lee et al. (2004)
Flooding stress	Rice	ID72 × Madabaru	Submergence tolerance	SSR	<i>qSub1.1</i> , <i>qSub2.1</i> , <i>qSub9.1</i> , <i>qSub12.1</i>	1, 2, 9, 12	Septiningsih et al. (2012)
		IR40931-26 × PI543851FR13A	Dry weight	-	<i>Sub1A</i>	9	Xu and Mackill (1996)
	Wheat	USG3209 × Jaypee	Chlorophyll content	-	<i>QSpad3.ua-1D.5</i>	1D	Ballesteros et al. (2015)
		W7984 × Opata85	Germination rate index	SSR	<i>Xfbb264</i>	7A	Yu et al. (2014)
Maize		Mo18W × B73	Submergence tolerance trait	-	<i>Subtol6</i>	6	Campbell et al. (2015)
		HZ32 × K12	Plant height	SSR	<i>ph1-1</i> , <i>ph1-3</i>	1, 3	Qiu et al. (2007)
			Shoot dry weight	SSR	<i>sdw9-1</i>	9	
			Total dry weight	SSR	<i>tdw9-1</i> , <i>tdw9-2</i> , <i>tdw9-3</i>	9	
Heavy metal stress	Wheat	UI Platinum × LCS Star	Cd content in grain	SNP	QCd.uia2-5B, QCd.uia2-7B, QCd.uia2-7D	5B, 7B, 7D	Qiao et al. (2021)
		D041735 × Divide	Cd absorption	SNP	<i>QCdu.ndsu-5B</i>	5B	Oladzad-Abbasabadi et al. (2018)
		Grenora × Haurani	Grain Cd content	SNP	<i>IWA1775</i>	5B	AbuHammad et al. (2016)
		Chinese spring × 'Synthetic 6x'	Al tolerance	SSR	<i>Xgdm125-Xgwm976</i> , <i>QaltCS.ipk-3B</i>	4D, 3B	Navakode et al. (2009)
Maize		B73 × Mo17	Root fresh weight (Pb and Cd tolerance coefficient)	-	<i>qRFLWLCTC2-1</i>	1	Hou et al. (2021)
		IBMSyn10 DH	Leaf Cd accumulation	SNP	<i>qLCd2</i>	2	Zhao et al. (2018)
		Zong3/87-1 × Yuyu22	Kernel As concentration	RFLP	<i>XAsK1a</i>	1	Fu et al. (2016)
Rice	Dhusura × Sebati	Fe toxicity tolerance	SSR	<i>qFeTox4.3</i> , <i>qFeTox6.1</i> , <i>qFeTox10.1</i>	4, 6, 10	Pawar et al. (2021)	

Table 1. (Continued.)

Soybean	RILs	Aluminum toxicity	SSR	<i>LG B1</i>	-	Korir et al. (2013)
	RILs	Aluminum toxicity	DNA markers	<i>LG F</i>	-	Sharma et al. (2011)
Soybean	RILs	Aluminum toxicity	SSR, RFLP, AFLP	<i>qAAC_04 and qRRE_04</i>	-	Wang et al. (2019a)

Table 2. List of QTLs for biotic stress among various crops.

Crop	Biotic stress	Mapping population	Gene/QTL	Markers	Chromosome	References
Common bean	Bean common mosaic virus	-	<i>bc-u, bc-1, bc-1², bc-2, bc-2², and bc-3</i>	-	-	Feng et al. (2018)
	Common bacterial blight	Rills population	2 QTLs	SSR, SNP, SCAR	<i>Pv08, Pv03</i>	Xie et al. (2017)
		DOR364 × G19833	<i>bc-1</i>	SCAR	-	Blair et al. (2007)
		-	<i>bc-u, bc-1, bc-2, and bc-3</i>	-	-	Feng et al. (2018)
		DOR364 × XAN 176, RIL DOR 476 × SEL 1309, RIL	<i>BGY4.1, BGY7.1, and BGY8.1; bgm-1</i> Candidate gene	SNP	Chr 03	Soler-Garzón et al. (2021)
Chickpea	<i>Fusarium</i> wilt and <i>Ascochyta</i> blight	Rills population	5 QTLs	SSR, SNP	<i>CaLG02, CaLG04, CaLG06</i>	Garg et al. (2018)
	<i>Botrytis</i> gray mold	Rills population	3 QTLs	SSR, RAPD, AFLP	-	Anuradha et al. (2011)
Cowpea	Cowpea severe mosaic virus	F ₁ , F ₂ , BC ₁ , BC ₂	Three genes	-	-	Umaharan et al. (1997)
Groundnut	Tomato spotted wilt virus	Tifrunner × GT-C20, RIL	11 QTLs	SSR	<i>A04, A01A09, B02, B04, B10</i>	Pandey et al. (2017)
		SunOleic 97R × NC94022, RIL(140)	3 QTLs	SNP	<i>A01</i>	Agarwal et al. (2019)
Mung bean	Mung bean yellow mosaic virus	<i>Vigna radiata</i> × <i>V. umbellata</i> Interspecific and RILs	<i>qMYMV4-1</i> <i>qYMIV5</i>	SNP	LG4	Mathivathana et al. (2019)
Pigeon pea	Pigeon pea sterility mosaic virus	ICPL 20096 × ICPL 332 (PRIL_B), ICPL 20097 × ICP 8863 (PRIL_C), and F ₂ (ICP 8863 × ICPL 87119)	<i>qSMD11.1, qSMD10.1, qSMD3.1, qSMD7.1, qSMD11.2, qSMD11.3, qSMD11.4, qSMD2.1, qSMD2.2, qSMD2.3, and qSMD10.1</i>	SNP	LG2, LG3, LG7 LG10, LG11	Saxena et al. (2017)
		BSMR 736 × ICP8863	<i>SV1</i> and <i>SV2</i>	-	-	Daspute et al. (2014)

Table 2. (Continued.)

		ICP 8863 × ICPL 20097, TTB	Six QTLs including <i>qSMD4</i>	SSR	LG7	Gnanesh et al. (2011)
		7 × ICP 7035, F ₂				
		ICP 7035 × ICP 8863 and ICP 7349 × ICP 8863	Single gene with three alleles	-	-	Srinivas et al. (1997a)
		ICP 7035 × BDN1 and ICP 7349 × BDN1, ICP7349 × LRG30 and ICP8850 × LRG30	Two genes	-	-	Srinivas et al. (1997b)
		ICPL 20096 × ICPL 332, RIL	<i>C. cajan_01839</i> , <i>C. cajan_07067</i> , <i>C. cajan_15535</i> , and <i>C. cajan_01839</i>	SNP	LG2, LG8 LG11	Singh et al. (2016)
Soybean	Soybean mosaic virus	Raiden × Williams 82, F ₂	<i>Glyma.13g184800</i>	SSR and SNP	Chr 13	Wu et al. (2019)
Urdbean	Mung bean yellow mosaic virus	MDU 1 × TU 68	<i>qMYMVD_60</i>		LG10	Subramaniyan et al. (2022)
Tomato	YLC virus		<i>Ty-3</i>	ACY (indel)	-	Nevame et al. (2018)
	Bacterial wilt		<i>Bwr-6</i> , <i>Bwr-12</i>	SNP	6, 12	Kim et al. (2018)
	<i>Fusarium</i> wilt (<i>Fusarium oxysporum</i>)		<i>I-3</i>	CAPS/SCAR	7	Catanzariti et al. (2015); Zhang and Panthee (2021)
			<i>Frl</i>	TG101 (RFLP)	9	Devran et al. (2018)
	<i>Meloidogyne javanica</i>		<i>Mi3</i>	RAPD	-	Yaghoobi et al. (1995)
	Late blight		QTL	SNP	9, 12	Panthee et al. (2017)
Cucumber	Powdery mildew		<i>Pm-s</i>	pmsSR27, pmSSR17s	5	Liu et al. (2017)
	CMV		<i>cmv6.1</i>	SSR11	6	Shi et al. (2018)
	ALS		<i>Psl5.1</i> , <i>psl5.2</i>	IS_163253001, SSR	5	Slomnicka et al. (2018)
Pepper (<i>Capsicum</i> spp.)	Powdery mildew	Double haploid	5 QTLs	AFLP, RAPD, RFLP	5, 6, 9, 10, 12	Lefebvre et al. (2003)
		F2:3	96 QTLs	SNP	4	Jo et al. (2017)
	Phytophthora root rot	Two BC1; one F ₂	<i>PhR10</i>	SLAF-Seq	10	Xu (2016)
	Anthracnose disease	BC1	12 QTLs	CAPS, INDEL, SSR	3, 5, 7, 10, 12	Sun et al. (2015)
Pea	<i>Fusarium oxysporum</i> f. sp. <i>melonis</i>		<i>Fo</i>	SSP		Wechter et al. (1998)

Table 2. (Continued.)

	Pea common mosaic virus		<i>Mo</i>	RFLP	-	Dirlewanger et al. (1998)
	<i>Erysiphe polygoni</i>		<i>Er</i>	RAPD	-	
Rice	Sheath blight resistance	F ₂ population	9 QTLs	SSR	1, 6, 7, 8, 9	Yadav et al. (2015)
		RILs	10 QTLs	SSR	1, 2, 3, 5, 6, 9	Liu et al. (2009)
	Brown planthopper resistance	F ₂ population	2 QTLs	SSR	12	Tamura et al. (2014)
Wheat	Powdery mildew resistance	BC2DH population	2 QTLs	SNP	1BL, 2BL	Mohler and Stadlmeier (2019)
	Spot blotch	RILs	6 QTLs	SNP	-	Ayana (2017)
	Crown rot resistance	RILs	2 QTLs	SSR, DArT	3B, 4B	Ma et al. (2010)
	Strip rust	RILs	19 QTLs	SNP	1B, 1D, 2A, 2B, 2D, 4B, 4D, 5A, 5B, 6A, 6B, 7B	Cheng et al. (2022)
	<i>Septoria tritici</i> blotch resistance	DH population	4 QTLs	SNP	4B, 5A, 7B	Karlstedt et al. (2019)
	Black point disease resistance	RILs	5 QTLs	SSR	4B, 5A, 5B, 5D	Gao et al. (2023)
		RILs	9 QTLs	SNP	2AL, 2BL, 3AL, 3BL, 5AS, 6A, 7AL, 7BS	Liu et al. (2016a)
	Cyst nematode resistance	DH population	1 QTL (Cre8)	SNP	6B	Jayatilake et al. (2015)
	Root lesion nematode	DH population	8 QTLs	SSR, SNP	2A, 2B, 2D, 5D, 6D	Linsell et al. (2014)
	Bacterial leaf streak resistance	RILs	5 QTLs	SNP	1AL, 1BS, 3AL, 4AL, 7AS.	Ramakrishnan et al. (2019)
		RILs	4 QTLs	SNP	2B, 6D, 7A, 7B	Ayana (2017)
	Hessian fly resistance	RILs	11 QTLs	-	1A, 2A, 3D, 6A, 6D	Hao et al. (2013)
		RILs	2 QTLs	SNP	1A, 6B	Li et al. (2013)
	Orange wheat blossom midge resistance	RILs	7 QTLs	SNP	2D, 4A, 4D, 7D	Zhang et al. (2020a)
	Russian wheat aphid resistance	RILs	27 QTLs	SSR	1A, 1B, 1D, 2D, 3A, 4A, 5A, 5B, 6A, 6B, 6D, 7A	Kisten et al. (2020)

A greater difference in means between MM and mm lines suggests a higher likelihood of detecting a QTL. The QTL is declared at the locus where the difference (MM – mm) is the greatest, with larger differences indicating a stronger QTL effect.

3.3. Mapping a population's development

3.3.1. Biparental populations

The development of mapping populations is a critical step in the process of QTL mapping. These populations are designed to reveal the genetic architecture of traits by linking phenotypic variation to specific genetic loci.

The traditional method for QTL mapping primarily utilizes biparental populations, such as F₂ populations, backcrosses, doubled haploids, RILs, and near-isogenic lines, each with distinct advantages and limitations, as illustrated in Figure 2. The standard biparental QTL mapping process involves the following steps: 1) selecting parental lines that differ in the traits of interest; 2) choosing molecular markers such as SSRs, RFLPs, or SNPs that can differentiate the parent lines; 3) developing the mapping population; 4) conducting genotyping and phenotyping of the population; and 5) applying statistical analyses to

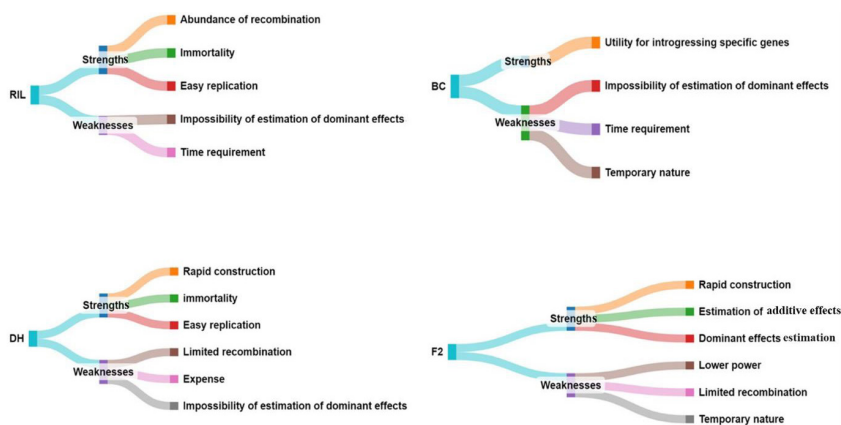


Figure 2. Commonly used biparental populations along with their strengths and weaknesses.

detect QTLs. While biparental mapping has been valuable in crop breeding, it also has limitations (Morrell et al., 2012; Hasan et al., 2021). Due to limited recombination events, these populations usually demonstrate QTL localization within intervals of 10–20 cM. However, they may only show a small part of the genetic diversity in the species. For instance, in *Arabidopsis* and maize, a 10-cM interval can encompass approximately 440 and 310 genes, respectively (Salvi and Tuberosa, 2005). Many genes contribute to the identification of QTLs for a target trait, necessitating further fine mapping to pinpoint closely linked markers within 1 cM. This process helps in identifying functional QTLs and candidate genes. Various crops have mapped and functionally characterized several QTLs for agronomically important traits (Kumar et al., 2009; Mohan et al., 2009; Xu, 2016). Recently, Liu et al. (2022b) identified 43 QTLs from 209 RILs and 537 multiparent advanced generation intercross (MAGIC) lines, with three major QTLs (i.e., qPH13-3, qPH17-1, and qLW20-1) consistently found across environments. qLW20-1 was validated for the improvement of leaf width in tobacco, useful for MAS. Mazumder et al. (2020) identified 23 additive QTLs across 10 traits in 68 RILs, with 1895 genes mapped, including some in the region of 22.09–38.29 Mb, potentially improving rice stress tolerance. Recent advances such as QTL-Seq have addressed these limitations by providing high-resolution genome-wide mapping, as demonstrated in chickpea with the identification of a major genomic region for seed weight (Das et al., 2015) and in *Sorghum bicolor* for anthracnose resistance. These advancements, combined with classical methods, have enhanced the precision of QTL detection and are facilitating the identification of candidate genes for targeted traits.

3.3.2. Multiparent mapping populations

Multiparent mapping populations such as nested association mapping (NAM) and MAGIC have been developed to

address the limitations of biparental populations (Li et al., 2024b). These populations leverage the genetic diversity of multiple parents, leading to great phenotypic diversity and enabling high-resolution QTL mapping. NAM, proposed by Yu et al. (2008), involves crossing multiple inbred lines with a common reference line, such as the B73 inbred in maize, resulting in a large population suitable for detecting QTLs with high resolution. In maize, a NAM population has been extensively utilized for large-scale genetic mapping of key traits such as disease resistance and leaf structure (Kump et al., 2011; Poland et al., 2011; Tian et al., 2011). Similarly, another maize NAM population consisting of 5000 individuals was developed to identify QTLs for traits such as time to flowering, disease resistance, plant architecture, and a set of 12 metabolites (Buckler et al., 2009; McMullen et al., 2009; Peiffer et al., 2013; Zhang et al., 2015). Moreover, NAM populations have played a critical role in enhancing QTL analysis, as exemplified by Nice et al. (2016), who employed an advanced backcross NAM population in barley to identify QTLs associated with seed protein content and qualitative attributes. Saade et al. (2016) leveraged NAM populations in barley to clarify flowering time under saline conditions, identifying beneficial alleles for improved yield. The NAM population in sorghum developed by Bouchet et al. (2017) further illustrates the broad application of these populations in mapping complex traits.

The use of MAGIC populations for QTL mapping was first introduced by Threadgill et al. (2002) in mice. Kover et al. (2009) developed the first MAGIC population in *Arabidopsis thaliana*, with 527 lines from 19 founder strains. Since then, MAGIC populations have been used for QTL identification in various crops such as wheat for traits like plant height and hectoliter weight (Huang et al., 2012) and rice for both QTL mapping and varietal improvement using indica and japonica parents (Bandillo

et al., 2013). Unlike other multiparent populations, MAGIC populations involve the intermating of several inbred founders over multiple generations before inbred lines are developed. This process enhances QTL detection accuracy by increasing genetic diversity and recombination events, which allows for a more comprehensive exploration of the genetic landscape. The greater genetic variability captured in MAGIC populations facilitates the identification of favorable alleles and their interactions, providing insights into complex traits that are often obscured in traditional breeding methods. Additionally, statistical methods for QTL mapping in MAGIC populations, such as the general linear model used in biparental populations (Zeng, 1994), have been specifically tailored to account for this complexity, further improving the precision of trait mapping and accelerating the breeding of improved varieties. Although QTL mapping has a significant role in crop improvement, it also entails challenges due to the complexity of traits, which often involve multiple QTLs with small effects that are difficult to detect and map accurately. Additionally, environmental interactions can obscure these effects, complicating the reproducibility and limiting the application of QTL findings across diverse environments.

4. Genome-wide association studies (GWASs)

QTL mapping and GWASs are complementary methods in plant breeding for analyzing the genetic architecture of complex traits. QTL mapping, used in controlled populations, identifies major-effect loci, while GWASs use natural variation across diverse populations to locate minor-effect loci. Both methods offer comprehensive insights for gene discovery. The GWAS approach represents an advancement in association mapping, employed to identify genetic markers in close proximity to genes of interest. Initially introduced for human genetic research by Klein et al. (2014), GWASs involve scanning the entire genome using a high density of markers to detect genetic variations associated with specific traits. Over time, GWASs have become a widely adopted method for identifying genotype–phenotype associations in plants, with certain methodological adaptations to suit plant genomics (Susmitha et al., 2023). GWASs are a highly effective approach in plant genetics for identifying the genes associated with specific traits (Tables 3–5). Table 3 summarizes the significant loci related to stress tolerance identified in recent studies, while Table 4 presents findings on yield-related traits. Table 5 highlights candidate genes associated with nutrient efficiency, illustrating the breadth of GWAS applications in pinpointing genetic markers essential for crop improvement. This method enables the precise mapping of genomic regions where genotypic and phenotypic variations show significant correlation. Unlike approaches based on traditional biparental populations,

GWASs provide superior mapping resolution, facilitating the detection of interactions between molecular markers and desirable traits across diverse crop species (Liu et al., 2016b). Its foundation on the mixed linear model (MLM) framework together with advancements in computational speed and statistical power have made the GWAS approach indispensable in modern agricultural genetics (Alamin et al., 2022). The general procedure for conducting a GWAS is given in Figure 3.

4.1. Prerequisites for GWASs

Before conducting a GWAS, several prerequisites need to be considered to ensure the validity and reliability of the results:

- **Well-defined phenotype:** The accurate and consistent measurement of the phenotype of interest is crucial. This could include clinical traits, physiological measures, or other quantifiable characteristics.
- **Large sample size:** GWASs require many samples to detect small genetic effects and achieve sufficient statistical power. Larger sample sizes increase the ability to identify true associations and reduce the likelihood of false positives.
- **High-quality genotype data:** Genotyping should be performed using reliable methods to ensure accurate and comprehensive coverage of the genome. High-density single-nucleotide polymorphism (SNP) arrays and NGS are commonly used.
- **Population structure control:** It is essential to account for population stratification, which can lead to spurious associations if not properly controlled. This can be done using statistical methods or by carefully matching case and control groups.
- **Statistical methods:** Appropriate statistical models and methods should be employed to analyze the data, including correction for multiple testing, which is a significant concern given the large number of SNPs tested in GWASs. The factors affecting GWAS accuracy and resolution power are summarized in Figure 4.

4.2. Single-locus versus multiple-locus GWASs

GWASs have become a key method for investigating yield-related traits and genetic variation in crops. Initially, single-locus models like the MLM (Zhang et al., 2005; Yu et al., 2006) were widely used. More recently, MLM-based models have advanced with the integration of novel traits and omics data due to developments in bioinformatics and sequencing (He et al., 2024a). However, single-locus models such as the generalized linear model are prone to high false-positive rates. Bonferroni corrections in MLMs reduce the false-positive rate but may also lead to important loci being missed. To address this, multiple-locus GWAS models including mrMLM, ISIS EM-BLASSO, and pLARM EB have been introduced (Cui et al., 2018; Peng et al., 2018; Zhong et al., 2021). These methods,

Table 3. List of genome-wide association studies of biotic stress among various crops.

Stress (disease/pathogens)	Crops	Markers	Traits	p-values	Chromosomes	Reference
<i>Xanthomonas vasicola</i>	Maize (<i>Zea mays</i> L.)	SNP	Leaf streak resistance	$-\log_{10}(\text{p-value}) > 3.5$ (p-value < 0.0003165)	1, 2, 5, 7, 8, 9	Ruiz et al. (2023)
Late blight and potato cyst nematodes (PCN)	Potato (<i>Solanum tuberosum</i> L.)	SNP	Late blight and potato cyst nematode resistance	≥ 0.053	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12	Sood and Chauhan (2023)
Tobacco rattle virus (TRV) and potato mop-top virus (PMTV)	Potato (<i>Solanum tuberosum</i> L.)	SNP	TRV and PMTV resistance	–	1, 2, 3, 5, 11	Anglin et al. (2024)
Root knot nematode (<i>Meloidogyne graminicola</i>)	Rice (<i>Oryza sativa</i> L.)	SNP/QTL	Number of galls, eggs/egg mass, and multiplication factor/plant	< 0.01	1, 2, 3, 4, 6, 10, 11	Hada et al. (2020)
Bacterial leaf streak (<i>Xanthomonas oryzae</i>)	Rice (<i>Oryza sativa</i> L.)	QTN	Lesion length	< 0.001	1, 2, 3, 4, 5, 6, 8, 9, 11, 12	Xie et al. (2021)
Tan spot (<i>Pyrenophora tritici-repentis</i>)	Wheat (<i>Triticum aestivum</i> L.)	SNP	Tan spot resistance	< 0.05	3AS, 3AL, 3BS, 6AL	Kokhmetova et al. (2021)
Leaf rust (<i>Puccinia triticina</i>)	Wheat (<i>Triticum aestivum</i> L.)	SNP	Leaf rust resistance	1.06×10^{-5}	6D, 6A, 6B, 5A, 1B, 2A, 2B, 7A	Leonova et al. (2020)
<i>Septoria tritici</i> blotch and powdery mildew	Wheat (<i>Triticum aestivum</i> L.)	SNP/QTL	<i>Septoria tritici</i> blotch and powdery mildew resistance	–	1A, 1B, 1D, and 7B for PM	Alemu et al. (2021)
Stripe or yellow rust (<i>Puccinia striiformis</i>)	Wheat (<i>Triticum aestivum</i> L.)	SNP	Stripe rust resistance	$< 5\%$	1A, 2A, 2B, 3A, 3B, 4B, 4B, 7D (2BS and 6AL)	Shahinnia et al. (2022)
Bacterial wilt of common bean (<i>Curtobacterium flaccumfaciens</i>)	Common bean (<i>Phaseolus vulgaris</i>)	SNP	Bacterial wilt resistance	–	Pv02, Pv04, Pv07, Pv08, Pv09	Zia et al. (2022)
<i>Fusarium</i> wilt (<i>Fusarium oxysporum</i>)	Common bean (<i>Phaseolus vulgaris</i>)	SNP	<i>Fusarium</i> wilt resistance	1.50×10^{-5} to 5.81×10^{-6}	Pv01, Pv03, Pv11	Paulino et al. (2021)
Yellow mosaic disease (YMD)/heat stress	Mung bean (<i>Vigna radiata</i> L.)	SNP	Flowering time, YMD resistance, trichome density, and leaf area	$p = 0.0001$ [$-\log(p) = 3.0$]	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11	Kohli et al. (2024)
<i>Phoma medicaginis</i> infection	Alfalfa (<i>Medicago sativa</i> L.)	SNP	Number of healthy leaves, number of ramifications, and length of main stem	–	1, 2, 3, 4, 6, 7 and 8	Mnafgui et al. (2024)
<i>Cercospora</i> leaf blight infection	Soybean (<i>Glycine max</i> L.)	SNP	<i>Cercospora</i> leaf blight resistance	$-\log_{10}(\text{p-value}) = 3.5$	1 to 20	Patel et al. (2024)
<i>Pythium sylvaticum</i>	Soybean	SNP/QTL	<i>Pythium sylvaticum</i> resistance	–	10, 18, 20	Lin et al. (2020)
<i>Xanthomonas citri</i> pv. Glycines	Soybean	SNP	<i>Xanthomonas citri</i> pv. Glycines resistance	–	3, 5, 8, 10, 13	Capobiango et al. (2022)
<i>Fusarium oxysporum</i>	Soybean	SNP	<i>Fusarium oxysporum</i> resistance	$p \leq 1/30,602$ or $-\log_{10}(p) \geq 4.49$	6	Sang et al. (2023)

Table 3. (Continued.)

<i>Phytophthora sojae</i>	Soybean	SNP	<i>Phytophthora sojae</i> resistance	–	1	Niu et al. (2018)
<i>Coniothyrium glycinis</i>	Soybean	SNP	Red leaf blotch disease resistance	–	1, 5, 20	Lukanda et al. (2023)
<i>Phytophthora sojae</i>	Soybean	SNP	<i>Phytophthora sojae</i> resistance	<0.001	3, 4, 5, 7, 10, 13, 14, 18	Qin et al. (2017)
<i>Corynespora cassiicola</i> infection	Soybean	SNP	<i>Corynespora cassiicola</i> resistance	$-\log_{10}(p) \geq 3.5$	3, 4, 5, 6, 10, 12, 13, 20	Patel et al. (2023)
<i>Ascochyta rabiei</i>	Chickpea (<i>Cicer arietinum</i> L.)	QTL	<i>Ascochyta</i> blight (<i>Ascochyta rabiei</i>) resistance	–	Ca1, Ca2, Ca6, Ca7	Farahani et al. (2022)
<i>Pythium ultimum</i>	Chickpea	SNP/QTL	<i>Pythium ultimum</i> resistance	–	2, 4, 6, 7, 8	Agarwal et al. (2022)
<i>F. oxysporum</i>	Chickpea	SNP	<i>Fusarium</i> wilt resistance	$-\log_{10} p\text{-value} \geq 2.3$ ($p \leq 0.005$)	2, 4, 5, 6, 7, 8	Alsamman et al. (2024)
<i>Ascochyta</i> blight (<i>Ascochyta rabiei</i>)	Chickpea	SNP	<i>Ascochyta</i> blight resistance	–	1, 4	Raman et al. (2022)
<i>Ascochyta</i> blight (<i>Ascochyta rabiei</i>)	Chickpea	SNP	<i>Ascochyta</i> blight resistance	–	1, 2, 3, 4, 7, 8	Şahin et al. (2023)
<i>Verticillium dahliae</i>	Cotton (<i>Gossypium hirsutum</i> L.)	SNP	<i>Verticillium dahliae</i> resistance	$p = 1/n$ ($n = 198,736$)	A10	Zhang et al. (2023)
<i>Fusarium oxysporum</i> f. sp. <i>vasinfectum</i>	Cotton (<i>Gossypium hirsutum</i> L.)	SNP/QTL	<i>Fusarium</i> wilt resistance	–	A04, A06, A11	Abdelraheem et al. (2024)
Pest - <i>Aphis gossypii</i>	Cotton (<i>Gossypium hirsutum</i> L.)	SNP	<i>Aphis gossypii</i> resistance	–	A08	Yang et al. (2023)
<i>Fusarium oxysporum</i> f. sp. <i>vasinfectum</i>	Cotton (<i>Gossypium hirsutum</i> L.)	SNP/QTL	<i>Fusarium</i> wilt resistance	–	D02	Zhu et al. (2022)
<i>Verticillium dahliae</i>	Cotton (<i>Gossypium hirsutum</i> L.)	KASP markers	<i>Verticillium</i> wilt resistance	–	Ghir_A01, Ghir_A05, Ghir_D13	Zhao et al. (2021)
<i>Verticillium dahliae</i>	Cotton (<i>Gossypium hirsutum</i> L.)	SNP	<i>Verticillium</i> wilt resistance	–	A03	Gong et al. (2018)
<i>Verticillium dahliae</i>	Cotton (<i>Gossypium hirsutum</i> L.)	SNP/QTL	<i>Verticillium</i> wilt resistance	–	A01, D02, D08, A13, D01	Zhang et al. (2020b)

Table 4. List of genome-wide association studies of different traits among various crops.

Crops	Markers	Traits	p-values	Chromosomes	Reference
Maize	SNP	Ear traits (ear length, diameter, kernel length and width, cob diameter)	–	1, 2, 3, 4, 5, 6, 7, 8, 9, 10	Zhu et al. (2018)
Maize	SNP	Leaf angle and leaf orientation	–	1, 3, 4, 5, 6, 7, 9	Lu et al. (2018)
Rice	SSR	Seedling vigor index, root- and yield-related traits	<0.05	2, 3, 12	Padmashree et al. (2023)

Table 4. (Continued.)

Wheat (<i>Triticum aestivum</i> L.)	SNP	Winter survival rate; days to heading and maturity; stem, spike, and awn length; liter- and thousand-kernel weight; number of seeds per spike	0.001 (log ₁₀ (p) = 3)	2, 3, 4, 5, 6, 7	Jung et al. (2021)
Wheat	SNP/QTL	Grain weight	-log ₁₀ (p) = 3	1B, 5B, 7B, 5A, 6A	Wang et al. (2021a)
Mung bean	SNP	Agronomic traits (flowering time, plant height, pod characteristics, nitrogen status, seed traits, and yield)	>0.0001	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11	Manjunatha et al. (2024)
Mung bean	SNP	Phenological (days to heading and days to maturity) and agronomic traits (leaf nitrogen status using SPAD, plant height, number of primary branches, pod length, number of pods per plant, seeds per pod, 100-seed weight, and yield per plant)	<0.00001	1, 2, 8	Manjunatha et al. (2023)
Mung bean	SNP	Grain micronutrients (grain iron and zinc concentration) and antinutritional factors (grain phytic acid and tannin content)	–	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11	Sinha et al. (2023b)
Mung bean	SNP/QTN	Seed size-related traits (seed width and seed length)	<0.05	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12	Liu et al. (2022a)
Alfalfa	SNP	Forage quality	–	1, 2, 3, 4, 5, 6, 7, 8	Lin et al. (2021)
Alfalfa	SNP	Leaf length and width	<0.001	1, 3, 4, 5, 6, 7, 8	Xu et al. (2023a)
Soybean (<i>Glycine max</i> L.)	SNP	Shoot length, shoot dry weight, root dry weight, root dry weight per shoot dry weight, total plant biomass, total root length, surface area, average diameter, root volume, and branching number	–	2, 6, 8, 9, 13, 16, 18	Mandozai et al. (2021)
Chickpea (<i>Cicer arietinum</i> L.)	SNP/QTL	Four seed micronutrients (Zn, Cu, Fe, and Mn)	≤0.05	1 to 8	Fayaz et al. (2022)
Chickpea (<i>Cicer arietinum</i> L.)	SNP/QTL	Vigor and vigor-related traits	–	1, 3, 4	Nguyen et al. (2022)
Chickpea (<i>Cicer arietinum</i> L. and <i>C. reticulatum</i>)	SNP	Seed molybdenum (Mo) and selenium (Se) concentrations	–	1, 2, 5, 6	Agarwal et al. (2022)
Chickpea (<i>Cicer arietinum</i> L.)	SNP	Iron and zinc concentrations	–	1, 4, 6, 7	Diapari et al. (2014)
Chickpea (<i>Cicer arietinum</i> L.)	SNP	Protein, fiber, and fat concentrations; 100-seed weight	–	1 to 8	Sari et al. (2024)
Sorghum (<i>Sorghum bicolor</i>)	SNP	Fe and Zn concentration in grains	–	1, 3, 5	Thakur et al. (2024)
Sorghum (<i>Sorghum bicolor</i>)	SNP/QTN	Number of nodal roots, nodal root angle, nodal root length, root dry weight	–	SBI-05, SBI-01, SBI-02	Elias et al. (2024)
Cotton (<i>Gossypium hirsutum</i> L.)	SNP	Yield and fiber traits, boll weight, seed index, lint percentage, fiber length, fiber elongation, micronaire, fiber strength, and flowering data	-log ₁₀ (p) > 5.27	A06, A07, D11	Wang et al. (2021b)
Cotton (<i>G. arboreum</i> L.)	SNP	Root color		A02, A04, A08, A09, A13	Zhao et al. (2021)

Table 4. (Continued.)

Cotton (<i>Gossypium hirsutum</i> L.)	QTL	Weight and lint percentage in 13 field environments, and boll number per plant and seed index	0.0001	A08	Zhu et al. (2021)
<i>Gossypium hirsutum</i> L.	SNP	Fiber traits (lint percentage)	–	D05	Song et al. (2019)
Cotton (<i>Gossypium hirsutum</i> L.)	QTL	5 fiber traits (myristic acid, palmitic acid, stearic acid, oleic acid, and linoleic acid)	–	A2, A6, A7, A9, A10, A13, D1, D5, D6, D7, D8, D10, D11, D12	Yuan et al. (2019)
Cotton (<i>Gossypium hirsutum</i> L.)	SNP	13 fiber traits (fiber length, fiber strength, micronaire value, elongation ratio, length uniformity, maturity, spinning consistency index, boll weight, lint percentage, seed index, lint index, fiber weight per boll, and flowering date)	–	A10, A07, A08, D11	Ma et al. (2018)
Cotton (<i>Gossypium hirsutum</i> L.)	SNP/QTL	Oil content	–	D12	Yuan et al. (2018)
Cotton (<i>Gossypium hirsutum</i> L.)	SNP	Early maturation	–	A6, A7, A8, D01, D02, D09	Li et al. (2018a)
Cotton (<i>Gossypium hirsutum</i> L.)	QTL	Fiber quality traits (fiber length, fiber strength, fiber micronaire, fiber uniformity, and fiber elongation)	–	Dt11, At07	Sun et al. (2017)

Table 5. List of genome-wide association studies of abiotic stress among various crops.

Stress	Crops	Markers	Traits	p-values	Chromosome	Reference
	Maize	SNP	Drought resistance	$<1.02 \times 10^{-5}$	1, 3, 4, 5, 6, 8, 9	Chen et al. (2023)
	Maize	SNP	Days to 50% anthesis, days to 50% silking, anthesis silking interval, stalk lodging, husk cover, plant aspect, leaf death, plant height, root lodging, ear height, ear rot, ear aspect, ears per plant, tassel blasting, leaf firing, and grain yield	$-\log_{10}(p) \geq 3.89$	1, 2, 3, 4, 5, 6, 7	Osuman et al. (2022)
	Maize	SNP	Ear leaf structure (leaf size of the first leaf above the first ear, first ear leaf size, leaf size of the first leaf below the first ear, leaf angle of the first leaf above the first ear, first ear leaf angle, leaf angle of the first leaf below the first ear, leaf orientation value of the first leaf above the first ear, first ear leaf orientation value)	1.00E-04 to 2.71E-06	2, 5, 8, 9, 10	Li et al. (2024a)
	Potato (<i>Solanum tuberosum</i> L.)	SNP	Drought tolerance, yield, tuber fresh weight, tuber number, starch content, dry matter, reducing sugars, chlorophyll content and fluorescence, stomatal conductance, NDVI, and leaf area and circumference	$<7.05 \times 10^{-6}$	4, 11	Alvarez-Morezuelas et al. (2023)

Table 5. (Continued.)

Drought	Potato	SNP/QTL	Drought tolerance, proline concentration, water consumption, and yield	$-\log_{10}(p) \geq 4.35$	1, 4, 10	Tagliotti et al. (2021)
	Potato	SNP	Drought tolerance	<0.05	1, 2, 4, 5, 6, 8	Fofana et al. (2024)
	Rice	SNP/QTL	Drought tolerance, days to 50% flowering, plant height, panicle length, flag leaf area, number of effective panicles, biomass at maturity, grain yield, 1000-grain weight, harvest index, and spikelet fertility	1e-6 and 1e-4	1, 2, 5, 6, 9, 11, 12	Bhandari et al. (2020)
	Common bean	SNP	Drought tolerance	–	6, 7, 10, 11	Valdisser et al. (2020)
	Common bean	SNP	Drought tolerance, relative germination vigor, and relative germination rate	$<1 \times 6^{-10}$ ($-\log_{10}(p) = 6$)	6	Wu et al. (2021)
	Common bean	SNP	Drought tolerance, root morphology	<0.01	11/PvXIP1;2	Wu et al. (2022)
	Common bean	SNP	Drought tolerance agronomic (genetic architecture of yield component) and photosynthetic traits	<0.05	Pv02, Pv03, Pv04, Pv06, Pv09, Pv10, Pv11	Dramadri et al. (2021)
	Mung bean	SNP	Seed mineral concentrations (calcium, iron, potassium, manganese, phosphorous, sulfur, zinc)	$-\log_{10}(7.7 \times 10^{-6}) = 5.11$ or = 0.05	Vr01, Vr05, Vr06, Vr07, Vr08, Vr09	Wu et al. (2020b)
	Mung bean	SNP	Drought tolerance-related agronomic traits (seed weight, plant height, number of branches, node number of main stem, number of pods per plant, pod length, number of seeds per pod, number of seeds per plant, yield per plant, biomass per plant, plot yield)	7.62×10^{-7} to 2.23×10^{-5} / 7.32×10^{-6} to 3.16×10^{-5}	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11	Chang et al. (2023)
	Soybean	SNP	Yield-related traits including pod number per plant, biomass per plant, and seed weight per plant	<7.36E-07	1, 3, 4, 8, 15, 17, 18, 19, 20	Li et al. (2023)
	Soybean	SNP/QTL	Drought tolerance, canopy architecture, and seed hardness	<0.01	4, 5, 6, 7, 9, 11, 12, 13, 14, 17, 18, 19, 20	Liu et al. (2020)
	Chickpea (<i>Cicer arietinum</i> L.)	SNP	Drought tolerance, grain yield per hectare, hundred-seed weight, seed number per plant, empty pod ratio, harvest index, biomass dry weight, flowering time score, podding time score, maturity score, emergence score, early vigor score, and plant height	–	1 to 8	Li et al. (2018c)
	Chickpea (<i>Cicer arietinum</i> L.)	SNP/QTL	100-seed weight, harvest index, biomass, days to 50% flowering, days to maturity, plant height	9.18×10^{-8}	1 to 8	Thudi et al. (2024)

Table 5. (Continued.)

Chickpea (<i>Cicer arietinum</i> L.)	SNP	Drought tolerance, nodule dry weight, nodule biomass, nodule fresh weight, plant height, height index, days to maturity, days to 50% flowering, grain yield, biological yield, 100-seed weight	-log ₁₀ p-value ≥ 2.5, 1, 4, 7 p ≤ 0.003		Istanbuli et al. (2024)
Chickpea (<i>Cicer arietinum</i> L.)	SNP	Ten morphological traits, including days to 50% flowering, plant height, number of primary branches, number of secondary branches, number of pods per plant, biological yield, harvest index, 100-seed weight, seed yield, and drought susceptible index, and three physiological traits, including relative water content, membrane stability index, and canopy temperature depression	–	1 to 8	Harish et al. (2024)
Chickpea (<i>Cicer arietinum</i> L.)	SNP	Grain nutrients (protein, Fe, and Zn)	≤0.05	1, 4	Samineni et al. (2022)
Cotton (<i>Gossypium hirsutum</i> L.)	SNP	Yield-related traits and agronomic traits (seed cotton, single boll weight, lint cotton, plant height, fruit branch number, effective fruit branch number, boll number, and effective boll number)	–	D04, D08	Sun et al. (2023)
Sorghum	SNP	Flowering time, plant height, grain weight, forage biomass, drought tolerance, and water use	–	6, 7	Maina et al. (2022)
Sorghum	SNP	Leaf senescence, drought tolerance, and plant height	–	1	Wang et al. (2020)
Sorghum	SNP	Grain weight, flowering time, plant height, and drought tolerance	–	6	Faye et al. (2022)

as shown by Li et al. (2017), effectively identify quantitative trait nucleotides (QTNs) in crops such as *Brassica napus*.

The mrMLM method improves the detection of loci by more than 55% across the examined genomic regions. Misra et al. (2017) utilized both ML-GWAS and SL-GWAS to identify key rice variants associated with grain traits. This combined approach successfully revealed genetic loci such as GWi7.1 and GWi7.2, in addition to identifying new genes. Similarly, Xu et al. (2018) employed both ML-GWAS and SL-GWAS to assess the importance of newly identified QTNs related to starch pasting attributes in maize. The ML-GWAS method, referred to as FASTmrEMMA, detected 29 new QTNs, while the SL-GWAS method, referred to as GEMMA, identified only 7 (Xu et al., 2018). Peng et al. (2018) applied six ML-GWAS techniques to explore the genetic basis of 20 amino acid concentrations in wheat, highlighting the robustness and versatility of ML-GWAS models. Xu et al. (2018)

further corroborated those findings, showing that most QTNs were detected with the ISIS EM-BLASSO method in multiple-locus GWASs. Su et al. (2018) also identified 70 QTNs in upland cotton, concluding that ML-GWAS methods outperformed SL-GWAS methods (MLM) while using TASSEL v5.0 in terms of power and accuracy. These studies collectively confirm the superiority of ML-GWAS approaches over SL-GWAS methods, although recent evidence suggests that combining both strategies significantly improves the reliability and robustness of GWAS outcomes (Xu et al., 2018; Zhang et al., 2019).

5. Development of functional markers

Functional markers (FMs) are located within genic regions and are directly linked to phenotypic traits, making them highly efficient for evaluating germplasm diversity and stabilizing advantageous alleles in breeding populations (Andersen and Lubberstedt, 2003; Salgotra and Stewart,

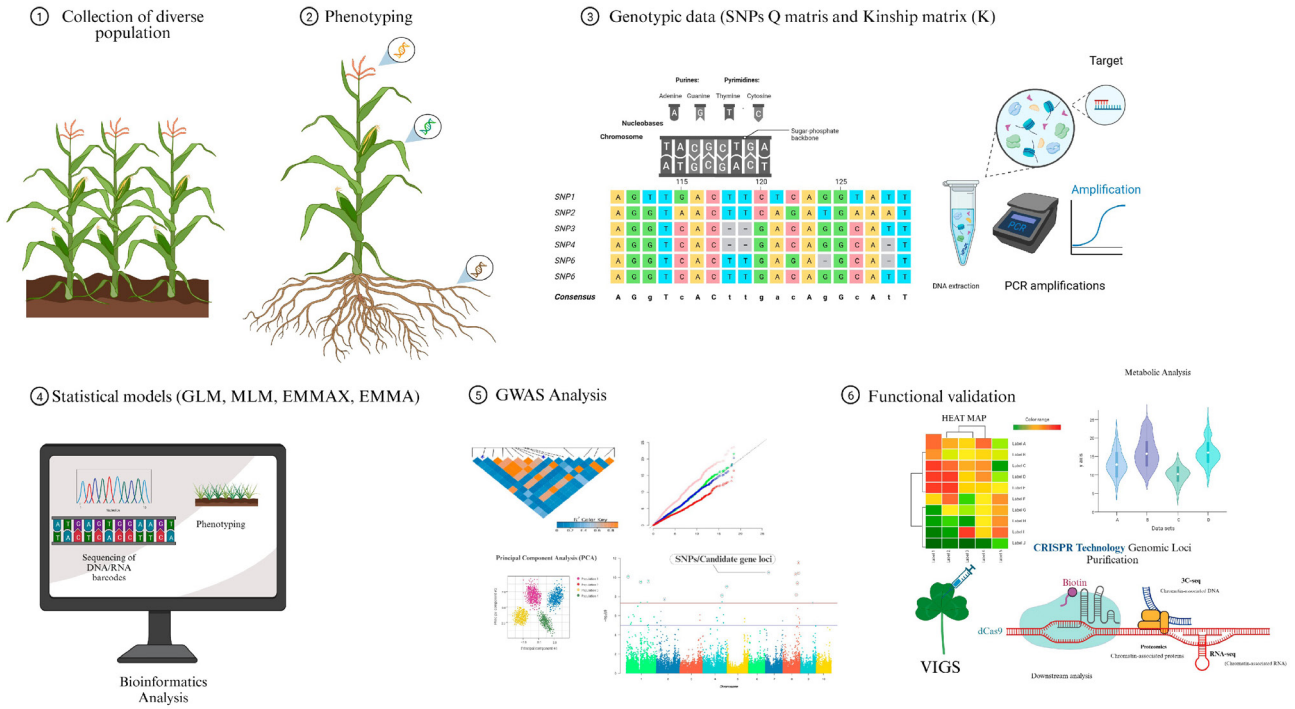


Figure 3. The basic steps involved in a GWAS (Sahito et al., 2024).

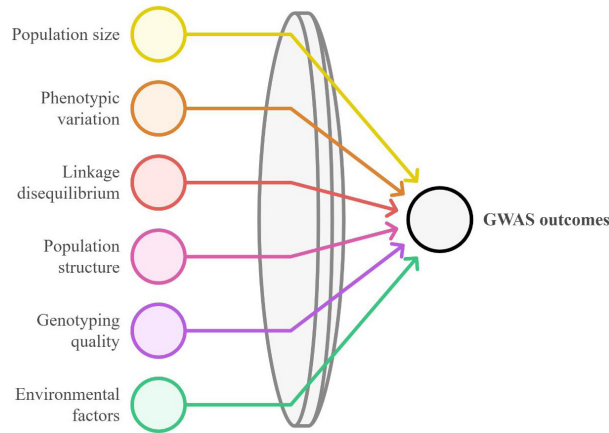


Figure 4. Factors that affect GWAS accuracy and resolution.

2020). FMs are especially useful for selecting complex traits due to their associations with target genes (Bagge et al., 2007). The development of FMs begins with the identification of a gene affecting a specific trait, followed by functional characterization and sequencing to find allelic variations that cause phenotypic differences (Thornsberry et al., 2001; Amom and Nongdam, 2017). Advances in NGS have accelerated the identification of QTLs through mapping populations like RILs, DHs, and association mapping (Soto-Cerda and Cloutier, 2012). This technique detects genetic polymorphisms and facilitates MAS (Breshegello and Sorrels, 2006). GWASs have identified

SNPs linked to traits in crops including rice, wheat, finger millet, and peaches (Forcada et al., 2019; Puranik et al., 2020). Genotyping by sequencing (GBS) further supports breeding efforts by generating SNPs across the genome, aiding in genomic selection.

RNA-Seq provides insights into gene expression and facilitates the development of FMs, even in nonmodel species without sequenced genomes (Chen et al., 2013). Additionally, functional genomics techniques such as RNA interference and CRISPR-Cas9 have enhanced our understanding of gene function, with CRISPR offering significant advantages in gene editing for crop

improvement (Schaeffer and Nakata, 2015; Romay and Bragard, 2017). When integrated with the GWAS method, CRISPR can target specific genetic variations identified through GWASs, allowing for precise editing of alleles associated with desirable traits. This synergistic approach not only accelerates the development of improved crop varieties but also deepens our understanding of the genetic basis of complex traits, paving the way for more holistic crop improvement strategies. These advancements are critical for modern molecular breeding strategies aimed at improving agricultural traits.

TILLING is a rapid, cost-effective method for detecting induced point mutations in mutagenized populations. It enables the analysis of multiple alleles at specific loci, offering an advantage over functional genomics. Using ethyl methane sulfonate as a mutagen causes A/T to G/C transitions, leading to a high frequency of random point mutations across the genome. Endonucleases effectively cut DNA duplexes containing multiple mismatches, and the resulting heteroduplex DNA can be compared to known sequences to identify polymorphic sites. As a result, TILLING is proficient at identifying nucleotide alterations as well as minor insertions or deletions, all at a lower expense compared to comprehensive sequencing techniques typically employed for SNP identification. Additionally, numerous crops have established and validated TILLING protocols, such as lotus (Perry et al., 2003); common bean, barley, maize, and field mustard (Till et al., 2004); pea, oat, potato, rice, and peanut (McCallum et al., 2000); and sorghum, rapeseed, soybean, wheat, and tomato (Slade et al., 2005). In summary, TILLING is a compelling approach for a wide range of applications from essential functional genomic investigations to practical crop breeding initiatives (Mohapatra et al., 2023). Regardless of the DNA source, once FMs are established, the next phase involves validating these markers functionally in relation to a specific target gene of interest (Kage et al., 2016). The functionality of newly created FMs can be assessed through gene expression analyses, which encompass methods such as virus-induced gene silencing (VIGS) and gene knockdown or knockout experiments (Tadege et al., 2005; Rodenburg, 2018; Ali et al., 2024a). Notably, the VIGS technique offers significant advantages over other methods, particularly in its ability to silence multiple genes within gene families, thereby providing enhanced analytical capabilities for polyploid species (Gupta, 2019).

5.1. Kompetitive allele-specific PCR (KASP) genotyping

KASP is a refined PCR-based homogeneous fluorescent genotyping technology that facilitates the swift and accurate identification of codominant alleles linked to SNPs and indels at a designated locus in both parent and offspring populations, utilizing fluorescence resonance

energy transfer (Rahman et al., 2023). Relative to alternative technologies, KASP's primary advantages are its robustness and cost-effectiveness (Semagn et al., 2014). KASP is a customizable high-throughput genotyping platform suitable for various experimental designs incorporating diverse target loci and sample sizes.

6. Marker-assisted selection (MAS)

MAS entails the targeted modification of genomic regions associated with a specific desirable trait by utilizing DNA markers (Ribaut and Hoisington, 1998). This approach represents a new era in molecular breeding for crop enhancement (Baloch et al., 2023). MAS offers advantages over traditional phenotypic selection based solely on visual traits, as the desired trait is directly associated with a molecular marker, thereby enhancing the efficiency of selecting for the targeted characteristic (Jiang, 2013).

The primary objective of any crop enhancement initiative is to identify plants that exhibit desirable traits of interest. In traditional plant breeding methods, there is an increased risk of overlooking traits that are crucial, which consequently prolongs the timeline for developing new cultivars with preferred characteristics. In contrast, MAS has demonstrated its effectiveness in enhancing various traits in crop plants by mitigating environmental influences and improving selection efficiency for traits of interest (Simko et al., 2021). Nevertheless, the effectiveness of MAS in selection may be hindered by the genetic background as well as the reliability and precision of QTLs (Melchinger et al., 1998). Additionally, inadequate linkages between the gene of interest and the corresponding markers can pose challenges (Sharp et al., 2001). Other considerations include relatively high input costs, a limited number of molecular markers with narrow polymorphic ranges, and the existing knowledge gap between plant breeders and molecular biologists (Collard and Mackill, 2008).

Various markers, including morphological, isoenzymatic, chromosome-specific, and DNA markers, have been used in plant improvements. However, these markers are most widely employed in MAS for different traits in pivotal crops (Madina et al., 2013). Recent molecular breeding advancements, such as PCR-based techniques (e.g., SSRs and indels), SNPs, genomic sequencing, and GBS, have been extensively applied in crop improvement programs globally (Platten et al., 2019). Figure 5 presents the steps involved in MAS.

7. Genomic selection and genomic prediction

Genomic selection (GS), which involves using genomic prediction (GP) models to choose potential individuals, has made substantial progress in the last 20 years, dramatically speeding up improvements in plant breeding (Crossa et al., 2017). GS has become a powerful technique in plant

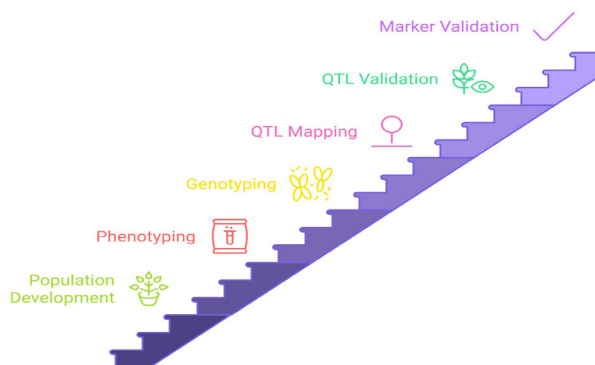


Figure 5. Steps involved in marker-assisted selection.

breeding, especially with the availability of genome-wide SNPs (Figure 6). It involves the application of developed GP models in practical selection (Haley and Visscher, 1998; Krishnappa et al., 2021). Meuwissen et al. (2001) were the first to extensively develop the concept of GS. In their innovative study, they introduced a new approach to plant breeding, proposing that by predicting genetic values using marker profiles, significant improvements could be made in genetic gain in both plant and animal breeding. This approach can be further enhanced by combining it with reproductive techniques to reduce the time between generations. Traditional MAS methods often prioritize a narrow range of markers associated with extensively studied large QTLs while disregarding most minor-effect QTLs. In contrast to those methods, GS is a crucial approach in breeding efforts due to its ability to accurately measure the genetic value of individual plants using a large number of genome-wide SNPs (Alemu et al., 2024). It reduces breeding costs, increases selection intensity and accuracy, and shortens the time needed to establish a cultivar compared to traditional methods (Crossa et al., 2017; Edwards et al., 2019). GP is a recently developed data-driven approach that has gained widespread acceptance and is being extensively utilized as a beneficial tool to enhance the rate of genetic improvement in plant-breeding programs (Farooq et al., 2021). Genetic programming leverages advanced statistical machine learning algorithms to pinpoint specific individuals within a breeding population. This selection process is grounded in breeding values derived from genome-wide markers. The approach relies on data collected from a training population, which encompasses both phenotypic and genotypic information. Following a comprehensive training phase, these models forecast breeding or phenotypic values for traits in a given population based solely on genotypic data. Prior to implementing selection, it is essential to assess the performance of prediction models through cross-validation. Evaluating the efficacy

of predictive models and contrasting various statistical machine learning frameworks is an essential phase in GP. This assessment entails examining diverse situations, including the integration of numerous traits, established key genes, marker-trait associations (QTLs), genotype-environment interactions, and other omics data such as transcriptomics, metabolomics, and proteomics. Factors like training population composition and machine learning models can affect the accuracy of GP for wheat, tomato, rice, maize, lentils, and potato traits. Pearson's correlation coefficient is used to evaluate the accuracy of GP, indicating the correlation between predicted and actual genetic values. This measurement allows an assessment of selection accuracy (Merrick et al., 2022). The precision of selection is strongly correlated with the selection response (R), also known as genetic gain. GP considers the breeding values of parental averages and the deviations of Mendelian sampling to ascertain the genomic estimated breeding values (GEBVs) of the progeny. This method serves two functions: it efficiently identifies favorable traits in early generations by forecasting additive effects, as seen in a biparental cross at the F_2 stage, and it selects lines in advanced breeding stages by estimating the genotypic values of individuals, accounting for both additive and nonadditive effects (Dreisigacker et al., 2023).

7.1. Prerequisites for genomic selection (GS)

GS is an advanced method in plant improvement that uses high-density genomic data and complex statistical models to speed up breeding processes and increase trait development (Alemu et al., 2024; Veerendrakumar et al., 2024). To conduct GS efficiently, it is crucial to have numerous advanced prerequisites. The utilization of modern genotyping technologies, including high-throughput sequencing and SNP genotyping, is necessary to obtain high-quality genomic data. Additionally, the availability of complete reference genomes and genetic maps is vital. Utilizing strong statistical and computational methods, such as Bayesian models and machine learning

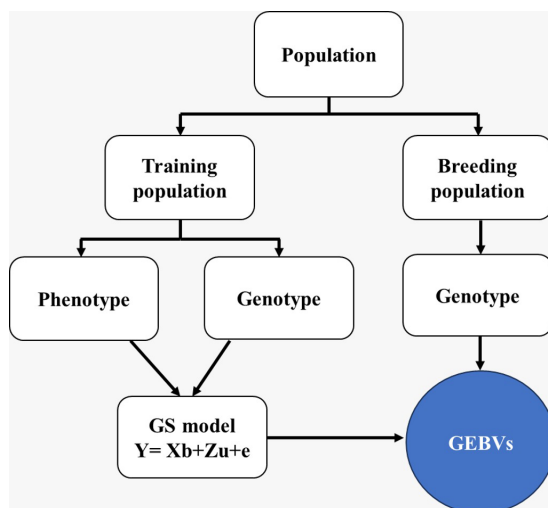


Figure 6. Basic scheme of the genomic selection process.

algorithms, is essential for the precise prediction of genetic values from genomic data (Lourenço et al., 2024; Zeng et al., 2024). Furthermore, there is a requirement for advanced phenotyping technologies that can handle large amounts of data and provide accurate and thorough evaluations of traits. The successful integration of phenotypic and genomic data also necessitates the use of complex data management systems. A strong understanding of genetics, statistics, and plant breeding, together with training programs and interdisciplinary collaboration, is essential for effectively implementing GS (Gerullis et al., 2023; Blue et al., 2024). To ensure appropriate procedures, it is vital to examine ethical and regulatory aspects, such as compliance with legislation on genetic alterations and data protection. Public participation and stakeholder communication are important in promoting acceptance of GS developments. Securing sufficient funds and establishing specialized infrastructure, like laboratories and data centers, are crucial for enabling the implementation and advancement of GS projects. Meeting these requirements allows for the successful implementation of GS to improve plant breeding programs, resulting in the creation of crops with exceptional characteristics and enhanced ability to withstand challenges (Chaudhary et al., 2024).

7.2. Genomic versus phenotypic selection

Classical breeding has made significant advancements, particularly in enhancing crop quality. It was instrumental in the development of high-yielding, nutrient-responsive semidwarf cereals during the Green Revolution and hybrid rice in the 1970s. Since the mid-20th century, these strategies have improved nearly all major crops, boosting both production and productivity. Despite this, however, the annual genetic gain of 1% in potential grain production is insufficient to meet the demands of a population growing

at 2% per year, which heavily depends on crop products for food (Fischer et al., 2014). Traditional breeding, based on phenotypic selection (PS), is less effective for complex traits like yield and stress resistance, which are influenced by the environment and gene-environment interactions ($G \times E$). Moreover, it faces challenges such as being time-consuming, labor-intensive, and imprecise (Jeon et al., 2023). In response, GS, which relies on reduced phenotyping and marker-based selection, was proposed by Meuwissen et al. (2001). GS uses a model combining genetic and physical data to calculate the GEBVs of individuals, predicting their potential as breeding parents (Poland et al., 2012). This approach accelerates breeding cycles by skipping late filial generations and increases genetic gains per year compared to PS, particularly for traits like insect resistance and quality, which are harder to assess (Zhong et al., 2009; Heffner et al., 2011). GS enhances selection accuracy, intensity, and efficiency while reducing time and costs, making it a more reliable and environmentally independent method (Budhlakoti et al., 2022). To integrate GS into breeding programs, cost-effective high-density molecular markers are essential (Sinha et al., 2023a).

7.3. Training populations versus breeding populations

Advanced training populations and breeding populations have unique but complementary functions in the process of plant improvement. For training prediction models to evaluate the performance of new genotypes, advanced training populations are utilized in GS (Lamichhane and Thapa, 2022). These populations comprise a wide variety of plant genotypes, encompassing a comprehensive set of phenotypic and genotypic data. By using high-density molecular markers and powerful statistical methodologies, these populations improve the accuracy of their predictions

and speed up the breeding cycle. Breeding populations, on the other hand, are directly involved in the process of generating new plant varieties (Salgotra and Stewart, 2020; Swarup et al., 2021). These populations include segregating populations such as F_2 or RILs, as well as more advanced forms such as MAGIC populations (Arrones et al., 2020; Scott et al., 2020). Field trials are conducted to select for characteristics such as yield, quality, and resistance, which ultimately results in the development of superior plant types. These populations are assessed through rigorous field experiments. Breeding populations concentrate on the more practical aspects of variety generation in contrast to advanced training populations, which enhance selection efficiency through data-driven approaches. In contemporary plant breeding, both are essential, with sophisticated training populations improving selection precision and breeding populations driving the creation of new varieties, hence accelerating progress towards sustainable agricultural goals (Werner et al., 2020).

7.4. Genomic selection models

A straightforward linear model commonly referred to as least-squares regression or ordinary least-squares regression, serves as a starting point for selecting appropriate individuals in GS. The starting point for the process of picking the appropriate individuals in GS is based on $Y = 1n\mu + X\beta + \epsilon$, where Y is the vector of observations; μ is the mean; β is the vector of marker effects; ϵ is the vector of random residual effects; X is the design matrix of order $n \times p$, where each row represents the genotype/individuals/lines (n) and each column corresponds to the marker (p); and ϵ is the vector of random residual effects. One significant issue with linear models when using genome-wide markers is that the number of markers (p) exceeds the number of observations (n), leading to the “big p , small n ” problem, which can be addressed by selecting a subset of significant markers. Ridge regression assumes equal marker contributions, which may not reflect the genetic architecture of traits. To address this, various Bayesian models (e.g., Bayes A, B, C π , and D π ; Bayesian LASSO; and BRR) incorporate the prior distributions of marker effects using posterior distributions to estimate parameters (Habier et al., 2011). Additionally, BLUP and its derivatives, GBLUP, ssGBLUP, RRBLUP, and rrGBLUP, are widely used in GS, with GBLUP leveraging genomic relationships estimated via markers instead of pedigrees (Meuwissen et al., 2001). While these models work well for additive genetic traits, nonparametric and semiparametric methods (e.g., NW estimator, RKHS, SVM, ANN, and RF) better account for complex epistatic architectures (Gianola et al., 2006; Holliday et al., 2012). STGS methods, which predict single traits, may lose vital information in cases of pleiotropy, where one gene affects multiple traits. Multitrait genomic selection (MTGS) approaches, such as

multivariate mixed models (Klápště et al., 2020), Bayesian multitrait models (Cheng et al., 2018), MRCE (Rothman et al., 2010), and cGGM (Chiquet et al., 2017), offer higher accuracy by considering multiple traits simultaneously. Studies comparing STGS and MTGS methods have confirmed improved prediction accuracy for traits with low heritability when leveraging related traits (Budhlakoti et al., 2019).

7.5. Genome estimated breeding values (GEBVs)

GEBVs constitute a revolutionary method in the field of plant breeding. This method makes use of genomic data to forecast the genetic potential of plants to exhibit desirable characteristics. This idea incorporates cutting-edge genetic technologies and statistical models in order to improve the effectiveness and precision of breeding programs, which in turn speeds up the process of developing new crop varieties (Grattapaglia, 2017; Sood and Chauhan, 2023; Ranjan et al., 2024). GEBVs are determined by evaluating genetic markers that are spread out across the genome of a plant. These markers, which include SNPs, offer a comprehensive map of the genetic variation that exists in the plant. Through the process of connecting these markers with trait data from breeding populations, breeders are able to assess the genetic potential of new individuals for specific qualities (Singh et al., 2022; Joshi et al., 2024). These traits include yield, disease resistance, and stress tolerance. To complete the process, phenotypic data must be collected, traits of interest must be measured, and genetic data must be gathered using high-throughput sequencing or genotyping technologies. Following this, statistical models such as GBLUP or Bayesian approaches are utilized to establish a connection between genotypic data and phenotypic observations (Yin et al., 2023; Strandén and Jenko, 2024). This allows for the estimation of breeding values based on the contribution of each genetic marker to the trait of interest. Compared to traditional breeding values, which are simply based on phenotypic data, GEBVs offer several benefits, one of which is higher accuracy. This is because they predict genetic potential with greater precision than traditional breeding values. For traits that are influenced by environmental variables, they also enable shorter breeding cycles by allowing early and informed selection decisions. This leads to increased genetic gain and more precise identification of superior genotypes, particularly for traits that are influenced by environmental factors. In several different crop species, including cereals, legumes, and vegetables, GEBVs have been effectively implemented, which has contributed to the development of variants that have better yield, resilience to disease, and tolerance to stress (Chawla et al., 2023). As genomic technologies continue to improve, it is anticipated that the precision and utility of GEBVs will further alter the process of plant breeding. In summary, GEBVs are a huge

step forward in the field of plant improvement. They make use of genomics to increase the accuracy, efficiency, and efficacy of breeding programs, which in turn drives the development of crops that are more adapted to the issues that modern agriculture faces.

7.6. Factors affecting genomic prediction (GP)

A higher density of markers typically improves the accuracy of predictions when employing various genomic selection models such as LASSO, BLUP, and machine learning-based approaches. However, it is possible that approaches such as Bayesian methods (Bayes A, Bayes B, Bayes C π , and Bayes D π) may experience sluggish convergence, particularly considering the required Markov chain Monte Carlo iterations (Arruda et al., 2016; Norman et al., 2018; Zhang et al., 2022). In certain cases, small numbers of low-density markers, ranging from a few hundred to a few thousand, can still yield accurate predictions for breeding populations as long as there is a significant level of linkage disequilibrium among the markers. However, it is important to note that this accuracy may depend on the specific trait being studied, as well as the genetic architecture and heritability of the traits under investigation (Werner et al., 2020). Incorporating economic restrictions into the evaluation of GS methods is crucial for ensuring profitability and efficiency, as maintaining a very high density of markers might be economically challenging. Establishing a definitive standard for genomic markers is challenging, but maintaining a moderate density of at least 2000 SNPs is recommended for accurate predictions (Abed et al., 2018). Nevertheless, the expense of genotyping can be substantially decreased by increasing the level of multiplexing without compromising the accuracy of genomic prediction. Intergenic regions contain crucial regulatory sequences, making the genomic positioning of SNPs more effective in capturing haplotype diversity compared to genes (Contreras-Soto et al., 2017). High-quality SNP genotyping data with minor allele frequencies greater than 0.1 are recommended for high prediction accuracy, with population size influencing accuracy in conventional MAS and genomic selection. Small population sizes or training populations lead to a decrease in accuracy due to the inadequate estimation of marker effects in the model. If the size of the training population is reduced to 1NeL, the prediction accuracy drops to 0.7. Nevertheless, in the majority of circumstances, there is a correlation between the training population and the breeding population. As a result, a smaller training population size can still yield a high level of accuracy in genomic prediction, contrary to the previously mentioned need (Meuwissen, 2009). In addition to these parameters, the accuracy of predictions can also be influenced by the heritability of traits, particularly when the heritability is low ($h^2 < 0.4$) (Hayes et al., 2009). Recent studies have

consistently demonstrated that the precision of genomic selection is significantly impacted by the heritability of the trait being studied. Heritability signifies the proportion of the total variation in a characteristic that can be attributed to genetic factors. Typically, it is assumed that a trait with high heritability is likely to have accurate predictions, and the opposite is also true. Nevertheless, the presence of low to moderate heritability in most agricultural variables presents a significant obstacle for genomic selection studies, particularly in the context of plants. Traits with low heredity necessitate a larger training population to achieve prediction accuracy comparable to that of traits with moderate to high heritability. In efforts to accomplish this objective, the cost may occasionally serve as a constraining element, particularly in developing countries. Furthermore, the literature to date suggests that even for traits with low heritability and complexity, methods such as BLUP and its derivatives, Bayesian methods, and RKHS appear to be more robust compared to their counterparts. These findings have been reported in various studies (Spindel et al., 2015; Juliana et al., 2019; Michel et al., 2019; Crossa et al., 2022). Additionally, the majority of models do well with features that have a significant degree of heritability, but the most appropriate approach typically depends on the specific scenario. Estimating the GEBVs might be challenging when there are missing observations. Simultaneously addressing the problem of lowly heritable traits and missing observations is possible if data on many characteristics are available. When dealing with many characteristics, if we have a few traits that reflect low inbreeding but are strongly correlated with other qualities that have high heritability, we can utilize a suitable MTGS model to leverage knowledge from those other characters. By employing MTGS, we can obtain a more exact and accurate estimation of the GEBVs in such situations.

8. Genomic selection: implications in crop improvement

Breeding programs are typically designed to have fewer repetitions in the initial generations, when the offspring are being separated, and more repetitions with larger experimental plots and testing in many locations in later generations (Bernardo, 2022). Efforts to integrate GS should consider the important system characteristics of the breeding program, which affect both genetic gain and costs. In early generations, GS can significantly reduce breeding cycles by skipping one or two selfing cycles. Selecting individuals with high GEBVs shortens the breeding process, while using GS in later generations improves selection precision without shortening the cycle. The reduced cost of genotyping later generations makes GS appealing, although it shows only minor advantages over PS (Endelman et al., 2014). To optimize genetic improvement, various GS strategies must be employed

while balancing cycle length and selection precision. Bassi et al. (2016) found that applying GS to the F_2 generation in wheat breeding provided a significant annual genetic gain of 0.47, but the high genotyping costs in early generations made the F_3 and F_4 generations more cost-effective. High prediction accuracies can be obtained with multiple GS cycles, and when the prediction accuracy is low, GS can eliminate poorly performing individuals (Longin et al., 2015). To balance the benefits and costs, one or two GS cycles followed by PS are recommended. Empirical studies across crops such as wheat, maize, pearl millet, and rice show the growing role of GS in enhancing genetic improvement (Guo et al., 2012; Srivastava et al., 2020). For example, an assessment of 206 wheat landraces for rust resistance using the GBLUP and Bayes R techniques yielded promising prediction accuracies (Cui et al., 2020).

A lentil GS study using single-trait and multiple-trait models showed higher prediction accuracies when considering genotype \times environment interactions for low-heritability traits, with within-population predictions being more accurate than those across populations (Haile et al., 2020). A soybean GS study obtained higher prediction accuracies for traits like protein and

oil compared to yield, with a larger training population proving more impactful than increased marker density (Stewart-Brown et al., 2019). Similarly, chickpea breeding research conducted with 320 lines and multiple GS models showed that GS within environments performed better than GS across environments, especially for traits like seed yield and days to maturity (Roorkiwal et al., 2018). Groundnut studies also confirmed the advantages of integrating genotypic information and genotype \times environment interactions in improving prediction accuracies for traits like oleic acid and rust resistance (Pandey et al., 2020). Other examples include sorghum, for which GS outperformed PS in terms of genetic gain and cost efficiency, particularly for polygenic traits and large populations (Muleta et al., 2019). Similarly, pearl millet GS studies found tGBS to be more efficient than RAD-Seq for genotyping, improving the accuracy for traits like flowering time and plant height. Therefore, the choice of suitable genomic selection models and genotyping platforms is crucial for enhancing prediction accuracy and expediting the progress of crop improvement initiatives. Other examples of the successful application of GS are presented in Table 6.

Table 6. Genomic selection studies on crop plant improvements.

Crop	Population	Model	Markers	Traits	Reference
Soybean	1284 lines	G-BLUP and Bayesian models	4141 markers (SNPs)	Enhanced biological yield and protein contents	Duhnén et al. (2017)
Soybean	483 elite lines	RR-BLUP	5403 markers (SNPs)	Enhanced biological yield and protein contents	Rajsic et al. (2016)
Chickpea	320 elite lines	RR-BLUP, kinship GAUSS, Bayes C π , Bayes B, BL, RF	3000 DArT-Seq	Enhanced biological yield and protein contents	Roorkiwal et al. (2016)
Wheat	659 inbred lines	RR-BLUP	-	Enhanced biological yield and protein contents	Michel et al. (2016)
Wheat	1127 lines	G-BLUP	38,894 markers (SNPs)	Enhanced biological yield and protein contents	Isidro et al. (2015)
Wheat	156 RILs, 239 lines, 100 DHs	RR-BLUP	5665, 1187, and 2780 markers (SNPs)	Enhanced biological yield and protein contents	Lozada et al. (2019)
Wheat	365 and 503	G-BLUP	17,178 GBS	Resistance to fungal pathogen	Rutkoski et al. (2015)
Wheat	1100 lines	G-BLUP	27,000 markers (SNPs)	Enhanced biological yield	Belamkar et al. (2018)
Wheat	8416 and 2403	G-BLUP	40,000 DArTs	Abiotic stress	Crossa et al. (2016)
Wheat	324 lines	G-BLUP, RR-BLUP, Bayes A, RKHS B, BL	9752 markers (SNPs)	Enhanced biological yield, protein contents, and gluten index	Haile et al. (2018)
Wheat	470 soft winter	RR-BLUP, BL, RF	4858 markers (SNPs)	Enhanced biological yield and protein contents	Hoffstetter et al. (2016)
Maize	255 inbreds, 150 hybrids	RR-BLUP	37,404 and 18,795 markers (SNPs)	Enhanced biological yield and protein contents	Juliana et al. (2018)
Maize	788 from 4 inbreds	RR-BLUP	857 markers (SNPs)	Enhanced biological yield and protein contents	Zhao et al. (2012)

Table 6. (Continued.)

Maize	257 inbreds	G-BLUP	48,814 markers (SNPs)	Enhanced biological yield and protein contents	Guo et al. (2014b)
Wheat	365 lines	G-BLUP, BL, Bayes $C\pi$	4040 markers (SNPs)	Adult plant stem rust resistance	Rutkoski et al. (2014)
Wheat	374 lines	G-BLUP and BRR	18,653 GBS	Resistance to stem rust	Rutkoski et al. (2015)
Wheat	1739 genotypes	RR-BLUP, Bayes $C\pi$, W-BLUP	1280 SNPs markers	Enhanced heading time and plant height	Zhao et al. (2014)
Maize	240 subtropical lines	RR, RF, Bayes B and A	29,610 markers (SNPs)	Enhanced biological yield and protein contents	Shikha et al. (2017)
Maize	300 inbreds	BL, RKHS	1150 markers (SNPs)	Fungal pathogen resistance	Crossa et al. (2011)
Maize	100 dent and 97 flint	G-BLUP	37,908 markers (SNPs)	Fungal pathogen resistance	Technow et al. (2013)
Maize	1073 and 857 DH lines	G-BLUP	15,732 and 16,846 SNPs	Enhanced biological yield and protein contents	Albrecht et al. (2011)
Maize	238 lines	RR-BLUP	23,155 DArTs	<i>Fusarium</i> resistance	dos Santos et al. (2016)
Maize	4699 from 25 crosses	RR-BLUP, Bayes A and B	1107 markers (SNPs)	Days to silking, anthesis, anthesis-silking interval	Guo et al. (2014b)
Rice	343 lines	LASSO, RR-BLUP, BRR, BL, G-BLUP	8337 markers (SNPs)	Enhanced biological yield and protein contents	Grenier et al. (2015)
Rice	280 rainfed accessions	G-BLUP, RKHS	2858 markers (SNPs)	Enhanced biological yield and protein contents	Bhandari et al. (2019)
Maize	294 RILs and 441 hybrids	BLUP, RR-BLUP	261 SSRs	10 agromorphological traits	Guo et al. (2015)
Maize	31 parents, 1380 DHs	G-BLUP	588 SNPs, 734 markers (SNPs)	Enhanced biological yield and protein contents	Albrecht et al. (2011)
Maize	300 inbred lines	BL, RBFNN, RKHS	55,000 markers (SNPs)	Enhanced biological yield and protein contents	González-Camacho et al. (2012)
Maize	413 inbreds	G-BLUP	36,901 markers (SNPs)	Enhanced biological yield and protein contents	Guo et al. (2014b)
Rice	309 and 327, japonica and indica	G-BLUP, GK	Indica: 92,430 and japonica: 44,598 markers (SNPs)	Enhanced biological yield and protein contents	Monteverde et al. (2018)
Rye	201 and 219 lines	Multitrait RR-BLUP	584 and 394 DArTs	Enhanced biological yield and protein contents	Schulthess et al. (2016)
Rye	2 sets, each 220	RR-BLUP	1048 DArTs	Enhanced biological yield and protein contents	Wang et al. (2014)
Rice	210 RILs	LASSO	270,820 markers (SNPs)	Enhanced biological yield and protein contents	Xu et al. (2013a)
Rice	369 elite lines	RR-BLUP	73,147 markers (SNPs)	Enhanced biological yield and protein contents	Spindel et al. (2015)
Barley	2 datasets, DH lines (160 and 140)	G-BLUP, Bayes A and B	224 RFLP, 108 AFLP/RFLP	Enhanced biological yield and protein contents	Lorenzana et al. (2009)
Barley	647 lines	RR-BLUP, GAUSS, EXP, Bayes $C\pi$	1536 markers (SNPs)	<i>Fusarium</i> head blight resistance, yield, plant height	Sallam et al. (2015)
Barley	691 lines	RR-BLUP, Bayes $C\pi$	3072 markers (SNPs)	<i>Fusarium</i> head blight resistance	Lorenz et al. (2012)
Sorghum	114 genotypes	GBLUP, Bayesian RR, BL, Bayes B	61,976 markers (SNPs)	Polyphenols, enhanced biological yield, protein contents	Habier et al. (2011)
Wheat	816 breeding lines	RR-BLUP	21,643 markers (SNPs)	Enhanced biological yield and protein contents	Xu et al. (2013b)

Table 6. (Continued.)

Wheat	329 genotypes	G-BLUP	7748 markers (SNPs)	Enhanced biological yield and protein contents	Ward et al. (2019)
Pearl millet	320 hybrids, 37 inbreds	RR-BLUP	14,306 and 33,463 markers (SNPs)	Enhanced biological yield and protein contents	Liang et al. (2018)
Chickpea	324 genotypes	RR-BLUP, BL, BRR	4947 markers (SNPs)	Enhanced biological yield and protein contents	Matei et al. (2022)
Oat	446 lines	RR-BLUP, Bayes C π	1005 DArTs	Enhanced biological yield, beta-glucan, protein contents	Asoro et al. (2011)
Sorghum	453 diverse sets	G-BLUP	59,264 markers (SNPs)	Biomass, moisture, height	Fernandes et al. (2018)
Wheat	247 landraces	G-BLUP, Bayes R	5568 markers (SNPs)	Enhanced resistance to leaf, stem, and stripe rust	Daetwyler et al. (2014)

8.1. High-throughput phenotyping: boosting QTL mapping and GWAS precision for crop improvement

High-throughput phenotyping (HTP) has emerged as a transformative tool for modern crop improvement, offering advanced capabilities to capture complex plant traits under diverse environmental conditions quickly and accurately (Jangra et al., 2021). HTP uses advanced imaging and sensor technologies for the noninvasive assessment of plant traits, including spectral imaging, LIDAR, RGB, and multispectral imaging, which provide three-dimensional measurements of plant architecture and growth stages (He et al., 2024b). By enhancing the precision and throughput of phenotypic data collection, HTP significantly boosts the effectiveness of QTL mapping and GWASs, both of which are essential for identifying the genetic basis of traits related to yield, disease resistance, and environmental resilience (Sahito et al., 2024). This integration has streamlined the development of high-yield climate-resilient crop varieties, accelerating the pace of agricultural innovation.

8.2. Precision in QTL mapping through HTP

QTL mapping aims to pinpoint genome regions linked with specific traits, traditionally depending on manual phenotyping methods that are labor-intensive and susceptible to inconsistency. HTP significantly enhances QTL mapping by providing higher precision and repeatability, enabling researchers to gather detailed, high-resolution data on essential traits like leaf area index, chlorophyll content, and water-use efficiency (Kumari et al., 2024). This accuracy fosters more precise QTL identification and facilitates the capture of dynamic traits over time, such as growth rates and stress responses, which are crucial for understanding traits with temporal variability (Jamann et al., 2015).

A total of 89 QTLs were identified for root structure in rice using a specialized 3D root imaging and analysis platform, which captures detailed images of root systems for in-depth trait analysis (Topp et al., 2013). This platform enables the precise measurement of root characteristics like length, branching, and architecture, which are critical

for improving water and nutrient uptake efficiency in rice. SmartGrain, an automated imaging system, was used to identify 13 QTLs associated with rice seed shape. This platform allows for high-precision analysis of seed dimensions, including length, width, and roundness, making it a powerful tool for selecting desired seed traits in rice (Tanabata et al., 2012). The Rice Automatic Phenotyping Platform (RAP) was utilized to map 141 QTLs linked to traits related to plant morphology, biomass, and yield. The RAP automates the measurement of these traits, reducing the need for manual labor and improving accuracy in identifying yield-related markers (Yang et al., 2014). A specialized agar-based high-throughput root phenotyping system identified 38 QTLs associated with root architecture and biomass in *Brassica napus*. This setup supported root trait mapping under controlled conditions, allowing the researchers to focus on genetic factors influencing root structure and resource allocation, which are crucial for breeding resilient plants (Shi et al., 2013). With the RAP adapted for maize, researchers identified 988 QTLs across three QTL hotspots related to plant growth traits. This approach allowed for the simultaneous measurement of 106 distinct traits, providing an extensive phenotypic dataset to improve maize breeding for growth-related traits (Zhang et al., 2017).

In maize, 12 marker-trait associations related to plant size and biomass accumulation were mapped using an automated noninvasive phenotyping platform. This setup measures biomass accumulation without destructive sampling, enabling precise quantification of growth dynamics and aiding in the selection of high-yielding maize varieties (Muraya et al., 2017). This precision facilitates a better understanding of complex traits by accurately linking genotype to phenotype, ultimately accelerating the development of improved crop varieties with enhanced yield, stress tolerance, and resource use efficiency.

8.3. Precision in GWASs through HTP

GWASs are crucial for linking genetic markers to trait variations across diverse populations, and HTP enhances

their precision and scope. By providing high-resolution trait data, HTP allows researchers to detect subtle phenotypic differences across many genotypes, thereby increasing the statistical power of GWASs. HTP also enables multitrait analysis by capturing a range of traits simultaneously, such as canopy temperature, plant height, and greenness, facilitating the discovery of genomic regions tied to complex trait interactions. Studies on the integration of HTP in GWASs are presented below.

Yang et al. (2014) developed an automated phenotyping system for greenhouse-grown rice, combining X-ray computed tomography with visible light imaging to measure 15 agronomic traits including plant height, tiller count, and shoot fresh weight. This integration enabled the identification of 141 loci, with 25 loci positioned near known genes such as *SD1*, *Hd1*, and *OsGH3-2*. Similarly, Crowell et al. (2016) made advancements in field-based inflorescence phenotyping by introducing an image skeletonization technique that allowed the capture of 49 panicle traits and led to the discovery of 10 candidate genes in proximity to significant GWAS peaks among 242 rice accessions. Wang et al. (2019b) revealed that plant height-related QTLs vary at different growth stages. In that study, plant growth rates were recorded by aerial imaging and used in a GWAS. Multiple candidate genes involved in plant height regulation, including *SAUR61*, which encodes an auxin response protein, were identified. Similarly, growth rates were measured in a GWAS of biomass, which accumulates gradually during plant growth (Muraya et al., 2017). A microscopic RGB imaging-assisted GWAS effectively identified candidate genes linked to bulliform cell characteristics, including cell column number and width, with the analysis of tens of thousands of leaf epidermal glue-impression images using convolutional neural networks (Qiao et al., 2019). Similarly, microcomputed tomography imaging has been applied to explore the genetic architecture of maize stem vascular bundles, offering insights into traits critical to structural integrity (Zhang et al., 2020c). In maize, the integration of HTP with GWASs has proven successful for the analysis of complex traits, such as cell and root architecture, and the identification of genetic markers associated with male inflorescence transformation. This approach reflects the potential for uncovering evolutionary shifts in genetic information (Gage et al., 2018), advancing our understanding of trait selection and adaptation.

A GWAS of 231 synthetic hexaploid wheat accessions (*Triticum aestivum* L.) employed visible light/RGB imaging to measure 29 traits associated with grain morphology, successfully identifying QTLs linked to these traits (Rasheed et al., 2014). Notable candidate genes such as *TaCwi-2A*, *TaSUS-6B*, *TaCKX-6D*, and *TaGW2-2B*, which influence grain size and weight, were discovered, together

with key favorable allele associations with specific grain phenotypes (Rasheed et al., 2014). Using a semiautomated system with spectrometers, the canopy reflectance of wheat under both optimal nitrogen-sufficient and nitrogen-deficient conditions was measured, yielding three vegetation indices for the GWAS, which identified loci associated with canopy traits and photoperiod regulator PPD-D1 (Jiang et al., 2019). Another GWAS utilizing unmanned aerial systems identified significant genetic markers on chromosome 2A associated with lodging traits (Singh et al., 2019). Similarly, unmanned aerial vehicles combined with multispectral imaging facilitated NDVI measurements, identifying 46 QTLs linked to NDVI-related traits (Condorelli et al., 2018). Furthermore, LiDAR technology was instrumental in a wheat GWAS in assessing genetic responses to temperature changes during stem elongation (Kronenberg et al., 2021). Aerial systems are anticipated to greatly enhance phenotyping capabilities for traits such as canopy coverage and lodging, potentially enabling the discovery of new loci. Additionally, RGB imaging combined with the GWAS approach was used to explore genetic resistance to diseases, with flatbed scanning revealing 26 chromosome intervals linked to *Septoria tritici* blotch resistance traits (Yates et al., 2019). For root trait genetics, Beyer et al. (2019) utilized a scanner and WinRHIZO software to evaluate five root traits, identifying 63 marker-trait associations for root morphology through a GWAS of 20,881 polymorphic sites.

Herritt et al. (2016) pinpointed genetic loci linked to a photosynthetic trait in soybean using photochemical reflectance index (PRI) data derived from canopy spectral reflectance measured in the field via visible/near-infrared spectroscopy. They identified 15 loci with significant associations to PRI, several of which mapped near genes involved in photosynthesis, nonphotochemical quenching, and sugar transport. Dhanapal et al. (2016) also employed visible/near-infrared spectroscopy and the GWAS method to investigate chlorophyll content traits, finding 27 loci associated with total chlorophyll, with four confirmed across both extract-based and canopy spectral reflectance methods. Furthermore, ground-based and aerial RGB imaging was used to assess canopy coverage, revealing a QTL on chromosome 19 with a notable positive impact on yield (Xavier et al., 2017). The dark green color index (DGCI), analyzed through aerial imagery and a GWAS, identified 43 loci associated with greenness, 21 of which overlapped with previously identified nitrogen and ureide concentration loci (Kaler et al., 2020). Similarly, Wang et al. (2021a) explored the genetic underpinnings of growth and yield traits in a Chinese soybean population using hyperspectral imaging to assess NDVI and the chlorophyll index (CHL). Collectively, GWASs combined with HTP have revealed key genetic regions linked to

spectral traits such as NDVI, CHL, and DGCI, which are often correlated with growth and yield (Kaler et al., 2020; Wang et al., 2021a). Wang et al. (2021a) also noted that investigating upstream traits such as NDVI and CHL can yield further insights into the control of key agricultural traits, underscoring the utility of HTP for advancing crop functional genomics and breeding potential.

In spinach, aerial RGB imaging has been effectively utilized for time-course analysis of growth traits across the crop cycle. A GWAS identified 99 SNPs, some located in genes associated with transcription factors and stress responses, suggesting potential roles in developmental regulation (Awika et al., 2019). Similarly, in cotton, combining RGB imaging with the GWAS method enabled the identification of 390 loci related to drought resistance using 119 image-based traits. Notably, some previously known loci and genes potentially negatively affecting drought response were also highlighted (Li et al., 2020). In sorghum, near-infrared spectroscopy was applied to quantify total phenolic content, procyanidins, and 3-deoxyanthocyanins in grain samples from 381 accessions. That study identified novel QTLs linked to polyphenol synthesis, with some homologous to flavonoid genes in *Zea mays* and *Arabidopsis* (*Pr1* in maize and *TT16* in *Arabidopsis*) (Rhodes et al., 2014). Visible light and fluorescence imaging have further facilitated genetic variation analyses of growth traits for crops like canola (Knoch et al., 2020) and *Arabidopsis thaliana*, for which GWASs identified 23 genes implicated in pathogen responses, including resistance to *Botrytis* infection and immunity to *P. syringae* effectors (Martel et al., 2020; Fordyce et al., 2018). Additional applications include visible light/RGB imaging, near-infrared reflectance spectroscopy, and NMR-based GWASs of seed traits, such as germination and vigor, as well as biochemical traits like glucosinolate and oil content (Hatzig et al., 2015; Wang et al., 2018). These studies underscore the potential of HTP techniques integrated with GWASs to enhance our understanding of complex traits across diverse species.

9. Conclusion and future perspectives

Over the past two decades, GS has demonstrated considerable promise in plant and animal breeding research, driven by the advent of affordable NGS technologies. This progress has facilitated the completion

of numerous genomes and the development of high-density SNP genotyping chips. However, further advancements are necessary, including methodological refinements, the updating of training sets, and assessments of training populations under controlled conditions. Looking ahead, the integration of emerging technologies such as gene editing, and particularly CRISPR, alongside HTP and AI-based predictive modeling could significantly enhance current genomic approaches. These innovations promise to improve crop resilience and productivity by enabling precise modifications of genetic material and the prediction of trait performance with greater accuracy. A structured program for GS, encompassing human resource development and enhanced data collection practices, is essential for successfully harnessing these technologies and achieving effective outcomes in breeding programs.

Author Contributions

All authors substantially contributed to the conception and design of this review article, interpreted the relevant literature, and were involved in writing the article. M.T.A., M.T., A.A., W.L., and P.M.: Writing - original draft. F.Ö., M.A.N., and J.J.: Formal analysis. G.J.Y., M.L.W., S.M., U.U.D.U., and K.K.: Initial review and editing, visualization. C.K., A.A., N.Ç., H.Y.D., M.Y., S.M., and F.S.B.: Supervision, critical review, English editing, and final validation.

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Declarations

Conflict of interest

The authors declare that they have no conflicts of interest related to the content of this article.

Authors' consent to publish

All authors have reviewed and approved the article and confirmed their willingness to publish this study.

Data availability

All data needed to conduct this study are provided within the manuscript.

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