

Review

Genomics-Assisted Breeding: A Powerful Breeding Approach for Improving Plant Growth and Stress Resilience

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Abstract: Climate change biotic and abiotic stressors lead to unpredictable crop yield losses, threatening global food and nutritional security. In the past, traditional breeding has been instrumental in fulfilling food demand; however, owing to its low efficiency, dependence on environmental conditions, labor intensity, and time consumption, it fails to maintain global food demand in the face of a rapidly changing environment and an expanding population. In this regard, plant breeders need to integrate multiple disciplines and technologies, such as genotyping, phenotyping, and envirotyping, in order to produce stress-resilient and high-yielding crops in a shorter time. With the technological revolution, plant breeding has undergone various reformations, for example, artificial selection breeding, hybrid breeding, molecular breeding, and precise breeding, which have been instrumental in developing high-yielding and stress-resilient crops in modern agriculture. Marker-assisted selection, also known as marker-assisted breeding, emerged as a game changer in modern breeding and has evolved over time into genomics-assisted breeding (GAB). It involves genomic information of crops to speed up plant breeding in order to develop stress-resilient and high-yielding crops. The combination of speed breeding with genomic and phenomic resources enabled the identification of quantitative trait loci (QTLs)/genes quickly, thereby accelerating crop improvement efforts. In this review, we provided an update on rapid advancement in molecular plant breeding, mainly GAB, for efficient crop improvements. We also highlighted the importance of GAB for improving biotic and abiotic stress tolerance as well as crop productivity in different crop systems. Finally, we discussed how the expansion of GAB to omics-assisted breeding (OAB) will contribute to the development of future resilient crops.

Keywords: plant stress; climate change; breeding; genomic-assisted breeding; omics; genome editing; markers



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1. Introduction

The increasing frequency and severity of biotic and abiotic stressors pose a major threat to crop productivity, global food security, and biodiversity [1]. Biotic stressors caused by fungi, bacteria, viruses, insects, nematodes, herbivores, or weeds leads to huge crop losses worldwide, and existing management approaches represent a severe threat to the environment and human health [1,2]. On the other hand, abiotic stressors, such as drought, floods, temperature, salt, heavy metals, UV radiation, and other factors, also affect crop yield [3]. These stressors can affect plant physiology and biochemical processes, causing unfavorable changes in plant growth and development processes. The occurrence of multiple stress combinations effect in crop plants leads to greater yieldlosses. Furthermore, climate change has worsened agricultural productivity in most developing countries by

intensifying environmental stressors [4]. The current issue of contemporary agriculture is to ensure a feasible growth in global food production to feed the world's expanding population under limited resources without harming the environment [5]. In addition, climatic anomalies, environmental cues, soil infertility, and malnutrition have pushed agricultural scientists and farmers to adopt new technologies to address these issues. To ensure food security, worldwide agricultural production needs to rise by 28% over the next ten years despite the limitations imposed by climate change [6]. Plant breeding has been a key driver in increasing agricultural productivity in a sustainable manner and will most likely play an even greater role in the future. Two approaches, traditional breeding and marker-assisted breeding (MAB), are commonly used in plant breeding. Plant breeding was one of the cornerstones of the green revolution, which significantly enhanced agricultural production. However, given the rate of climate change and the frequency of biotic and abiotic stressors, the primary goal of modern agricultural scientists will be to develop stress-resistant, nutrient-rich, and high-yielding crops, which may necessitate the use of new breeding technologies by integrating genotyping, phenotyping, and environmental data [4].

Earlier, improved crop selection was based on phenotypic features identified in crop germplasm under field conditions, which were utilized to produce new varieties via conventional breeding. It has several disadvantages since environmental influences affect phenotypic traits, resulting in the selection of inferior breeding materials. Furthermore, it may limit the germplasm gene pool, reducing crop development effectiveness. Traditional breeding has made significant contributions to the agricultural world over the last several decades; however, due to time consumption, labor intensity, reliance on environmental factors, and low efficiency, scientists are considering new alternatives for crop improvement in sustainable agriculture [7]. The advancements in breeding technology, particularly molecular marker-assisted selection (MAS), are extremely beneficial and boost breeding efficiency [8]. In contrast to phenotypic traits, molecular markers are unaffected by environmental influences and remain precise throughout selection, making MAS more appealing for breeding. It aids in the tracking of the genes responsible for tolerance within the crop genome and enhances precision breeding. Crop enhancement in modern agriculture is mostly accomplished by cross-breeding, mutation breeding, and transgenic breeding. Plant breeding has undergone various reformations, such as artificial selection breeding, hybrid breeding, molecular breeding, and precise breeding [8]. For instance, plant breeding began with the selection of exceptional plant phenotypes from early hybrids during plant domestication, followed by Mendel's discovery of genetic 'rules' and discovery of genetic structure, which enabled the assignment of genotypes to phenotypes, the formulation of a 'central dogma', mutation breeding, and hybrid varieties. One important revolution in plant breeding took place through the discovery of molecular technology that led to the development of 'molecular plant breeding', involving the marker-assisted selection of domesticated plants and their wild aliases. Over the last two decades, significant breakthroughs in next-generation sequencing technology have established genomics-assisted breeding as an alternative approach to conventional breeding for complex characteristics [8]. In recent years, genomics has made major contributions to selection intensity and precision, resulting in genetic gain in crop development while dramatically reducing breeding cycle time and manpower requirements during selection. Recently, the application of CRISPR/Cas genome editing in plant breeding has been one of the most promising approaches for improving diverse crop traits associated with yield, quality, and stress tolerance [9]. Plant breeders now have extensive control over the particular insertion of targeted sequence variation, providing a game-changing resource for quick agricultural crop improvement. Since then, continuing developments in CRISPR/Cas systems, such as CRISPR/Cpf1 and nucleotide substitution tools for base editing, have made genome editing a widely embraced, low-cost, easy-to-use targeted genetic modification tool that has been applied to numerous crops [10,11]. Further, we have shown a timeline of discovery in plant breeding from the pre-Mendel era to modern breeding (Figure 1).

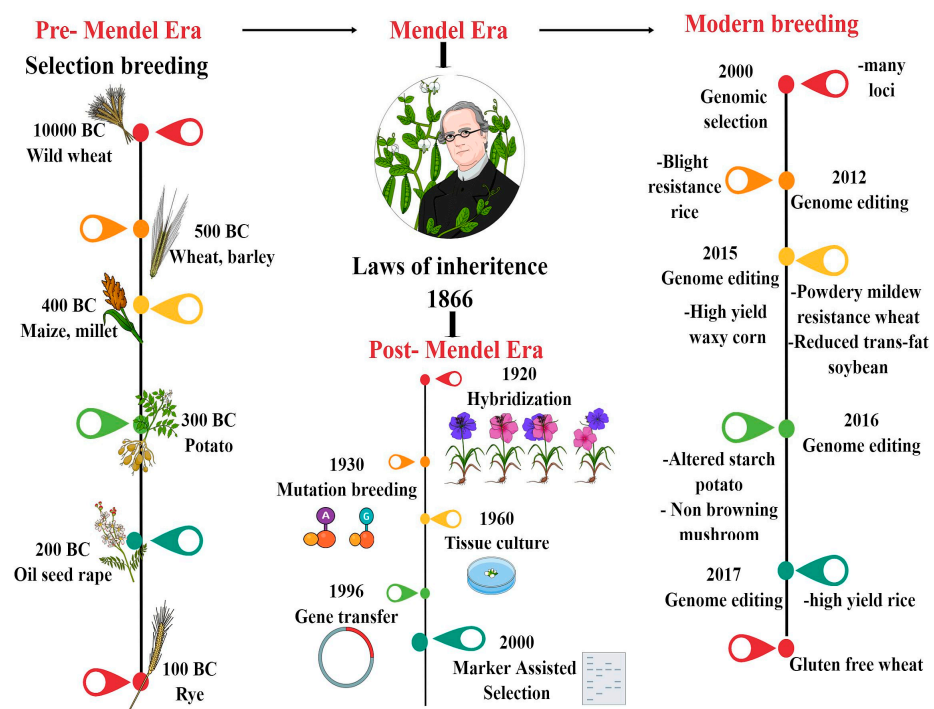


Figure 1. Shows crop domestication and plant breeding timeline reformation, for example, artificial selection breeding, hybrid breeding, molecular breeding, and precise breeding for crop improvement in traditional and modern agriculture.

Recent developments in high-throughput genotyping and phenotyping platforms have shifted plant breeding tactics from phenotype to genotype-based selection and made large-scale marker-trait association analysis, like GWAS (genome-wide association analysis), allowing researchers to precisely and robustly analyze the genetic and phenotypic architecture of crop traits. In addition, with the aid of high-throughput sequencing tools, genomic resources of many crops have been major drivers for identifying the target traits in desired plants and used for crop improvement using GAB (Figure 2).

Decoding of crop genomes led to the identification of molecular markers for trait dissection, selection, and enhancement in different crop systems [12]. Molecular markers such as restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), SSR-like expressed sequence tags (ESTs-SSRs), genome sequence (gSSRs), bacterial artificial chromosome (BAC)-end sequences (BES-SSRs), and single nucleotide polymorphisms (SNPs) have been instrumental in molecular breeding for improving not only genetic gain but also breeding cycles in different crop systems [13]. Furthermore, these incredible technologies, along with other tools, such as gene cloning and validation, mining of potential alleles/haplotypes, genomic selection (GS), and natural variation utilization, have transformed molecular breeding into GAB [14]. Different GAB approaches like marker-assisted backcrossing (MABC), marker-assisted recurrent selection (MARS), marker-assisted selection (MAS), advanced backcross quantitative trait loci (AB-QTL), allele addition and removal via genome editing (PAGE/RAGE), genomics selection (GS), and haplotype-based breeding (HBB) have been successfully used for designing tailored crops. Indeed, GAB-based approaches have the potential to be game changers not only for accelerating crop improvement but also for revolutionizing breeding science in sustainable agriculture in order to deal with future food security challenges. GAB enables the combination of genomic tools with other high-throughput phenotyping tools to aid breeding practices by identifying and utilizing genomic molecular markers linked to quantitative trait loci (QTLs), which will provide genotype-dependent phenotype prediction [15]. It also enables plant breeders to begin with a large population of only genotypically characterized offspring and then use only a subset

of that population for more expensive and arduous phenotypic evaluation [16]. Similarly, GAB has also aided in the identification and integration of allelic variation governing key agronomic traits for germplasm improvement and cultivar development practices [17]. Owing to its high rate accuracy, selection efficiency, and direct improvement, a short breeding cycle GAB has been used for the improvement of complex traits in various crop systems (Figure 2).

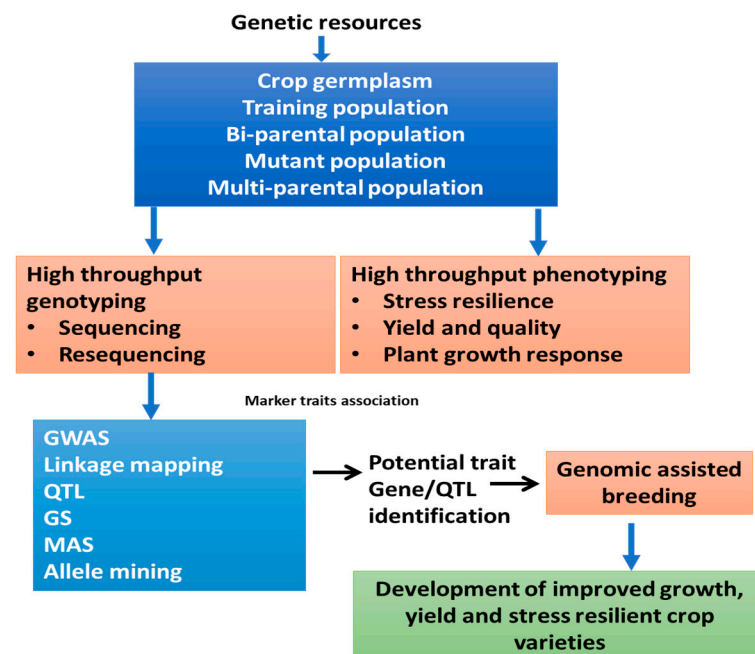


Figure 2. Genomic resources of different crops aid in the identification of complex traits in different crops using high-throughput genotyping and phenotyping that have aided in the full characterization of allelic variation underlying significant agronomic features, as well as their effective application into germplasm augmentation and cultivar development procedures using GAB.

GAB has been successfully used in diverse crop improvement programs, including MABC and MARS, to improve carotene content in maize and crown rot in bread wheat, respectively [18]. Additionally, GAB has proved important in boosting not just stress resilience but also quality attributes in agronomically significant crops, including wheat, rice, barley, and others. For example, the important rice cultivars developed using GAB include Pusa Basmati 1, Pusa Basmati 1121 and improved Samba Mahsuri (ISM), and ‘Pusa Basmati 6’, which are resistant to blast and blight, respectively [19,20]. Similarly, recent releases of enhanced rice cultivars with QTL regulating salt tolerance (Saltol), submergence tolerance (sub1), and drought tolerance provide an indication of the immense potential of GAB for boosting the abiotic stress response of agricultural genotypes [17]. Owing to its incredible success in sustainable agriculture, GAB has drawn increasing attention to the enhancement of quality traits, for example, the development of ‘Manawthukha’, a superior rice cultivar with intermediate amylose content and better fragrance [21]. Recently, GAB-developed groundnut cultivars with improved disease (rust and leaf spot) resistance and high oil content have been made available for commercial production [22,23]. Remarkably, the development of high grain protein content (GPC) wheat cultivars is one of the greatest successes in quality enhancement in agricultural plants utilizing GAB [24]. In recent times, the expanded usage of GS in GAB has enabled fast crop improvement employing genome-wide high-throughput SNP markers [25]. GS has already demonstrated tremendous promise in forecasting genotype performance and selecting complex traits in maize and rice drought and blast resistance, respectively [26,27]. Further, we have highlighted the role of GAB in improving biotic and abiotic stress resilience as well as crop yield in different crop plants (Table 1).

Table 1. List of some important food crops developed by GAB 1.0 for biotic and abiotic stress tolerance and improving quality traits.

Crop Species	Trait	Genes/Locus	Approach Used	Improved Variety Developed	References
Cereals and multiple (biotic/or abiotic) stress tolerance with quality traits					
<i>Oryza sativa</i> (Rice)	Bacterial blight disease resistance	<i>Xa21</i> , <i>Xa13</i> , and <i>Xa5</i>	MAS	Improved ‘Samba Mahsuri’ (ISM)	[28]
	Blast disease resistance	Blast resistance genes (<i>Pi-2</i> and <i>Pi-54</i>); <i>BB</i> (<i>Xa38</i>)	Gene stacking	Improved ‘Samba Mahsuri’ (ISM)	[20,29]
	Blast disease resistance	<i>Pi2</i> , <i>Pi5</i> , <i>Pi54</i> , <i>Pi1</i> , <i>Pita</i>	Gene stacking	Pusa Basmati 1	[30]
	Blast and bacterial blight diseases	<i>Pi2</i> and <i>Pi54</i>	MABC	Pusa Basmati 1121	[31]
		<i>Xa13</i> and <i>Xa21</i>	MABC	Pusa Basmati 6	[31]
	Submergence tolerance	<i>Sub1</i>	MAS	Swarna, ‘Samba Mahsuri’ (BPT 5204), ‘CR 1009’, ‘Thadokkham 1’ (TDK1) OM1490/IR64-Sub1cross (in Vietnam); ‘BR 11’	[32–34]
	Salt tolerance	<i>Saltol</i>	MAS	‘Pusa Basmati 1121’, ‘Pusa Basmati 6’, BRRI-Dhan 49’ ‘AS 996’, ‘BT 7’, ‘Q5DB ‘Bachthom 7’	[35]
	Drought tolerance and high yield		MAS	‘Sabitri’	[36]
	Blast and gall midge disease resistance submergence and salinity stress tolerance	<i>Pi2</i> , <i>Pi9</i> , <i>Gm1</i> , <i>Gm4</i> , <i>Xa4</i> , <i>Xa5</i> , <i>Xa13</i> , <i>Xa2</i>	Gene pyramiding	Improved Tapaswini	[37]
<i>Triticum aestivum</i> (Wheat)	Improved fragrance and intermediate amylose content	<i>badh2</i> and <i>Wx</i>	Transfer of variant allele from basmati into ‘Manawthukha’	Improved ‘Manawthukha’ (from Myanmar)	[21]
	Stress response and quality traits	<i>Yr40/Lr57</i> and <i>Lr58</i>	MAS	‘Jagger’ and ‘Overley’ (hard red winter wheat (HRWW)) cultivars	[38]
	Stress response and quality traits	<i>Lr34</i>	MAS	Spring wheat cultivar ‘HUW510’	[39]
	Improving protein content	<i>Gpc-B1</i>	MAS	High GPC wheat cultivars Farnum’, ‘Lassik’, ‘Westmore’, and ‘Desert King-High Protein’, ‘Lillian ‘Somerset’, ‘Burnside’, ‘VR 1128’ Wyalkatchem’, ‘Gladus’	[24]
<i>(Pennisetum glaucum</i> (L.) R. Br.) (Pearl millet)	Downy mildew resistance, drought tolerance, and fodder quality	Downy mildew-resistant genes/locus (QRsg.icp-4.1/4.2; Qgydt.icp-2.1/6.1; 863B)	MAS	HHB 67-improved	[40]
<i>Hordeum vulgare</i> (Barley)	Eyespot (<i>Rhizoctonia cerealis</i>) resistance	resistance gene <i>Pch1</i>	MAS	DD 248/12, KBP 15.2, and STH 4431	[41]
	Barley yellow mosaic viruses’ resistance	<i>rym4/rym5</i>	MAS	Improved winter barley	[42]
	Barley powdery mildew disease resistance	<i>mlo</i>	Gene silencing	Improved resistance in barley	[43]

Table 1. Cont.

Crop Species	Trait	Genes/Locus	Approach Used	Improved Variety Developed	References
<i>Zea mays</i> (Maize)	Nutritional traits (QPM, pro-vitamin A)	opaque2	Transferred in elite hybrids (MAS)	Pusa Vivek QPM-9, Pusa Vivek Hybrid-27, Pusa HQPM5, Pusa HQPM7,	[44,45]
Legumes and multiple (biotic/or abiotic) stress tolerance with quality traits					
<i>Glycine max</i> (Soybean)	Multiple soybean cyst nematode (<i>Heterodera glycines</i>) races (2, 3, 5, and 14)	Multiple disease resistance and high-yielding genes	Gene stacking/ pyramiding	'JTN 5503', 'JTN 5303', 'DS 880', and 'JTN 5109'	[46–48]
<i>Arachis hypogaea</i> (Groundnut)	Rust (<i>Puccinia arachidis</i>) resistance	Increased yield and rust resistance genes	MAS	'ICGV 91114', 'JL 24', and 'TAG 24' (introgression lines)	[49]
	Abiotic/biotic stress	Rust and late leaf spot resistance, stress adaptation- related traits	MAS	Resistant peanut	[22,23,50–53]
	Improved oil quality	Oil quality	MAS	Improved quality peanut	[54]
	High oleic acid content and nematode resistance	Tifguard high O/L'	MAS/gene pyramiding	Reducing breeding cycle	[55]
<i>Cicer arietinum</i> (Chickpea)	Wilt and blight disease resistance	foc1 locus, ABQTL-I, and ABQTL-II	MABC	C 214	[56]
	Biotic stresses	Ascochyta blight resistance and botrytis gray mold resistance genes	MAS	Biotic stress- resistant chickpea	[57,58]
	Drought tolerance traits	Introgression into Pusa 372	QTL hotspot by MAS	'Pusa 10216'	[59]
	Abiotic stresses	Terminal drought stress	QTL	Improved grain yield in <i>Cicer arietinum</i>	[60]
		Salt stress	QTL	Improved seed yield and their components in ICCV 2 × JG 62 Progenies	[61]
	Quality traits	Seed weight- regulating gene	CNMS, genome mapping, and transcript profiling	Improved seed weight in chickpea	[60,62–67]

2. How to Use Genomic Information to Maximize Genetic Gain in Plant Breeding Program?

Genomic selection (GS) is complementary to MAS and is an association breeding that does not necessitate the knowledge of the underlying genetic control or biological function. The gist of this popular breeding methodology is to enable more material or accurate estimates of breeding values of complex traits from different locations that cost the same, as well as to shorten the time required for both two-parent selection and product development to maximize genetic gain per year [28]. Integrating environmental covariance and crop modeling with the GS framework to forecast G×E can increase prediction accuracy and provide insight into the genetic architecture controlling G×E. This could be performed using a training population (TP) design with a subset collection of smaller yet more informative populations to develop a more advanced breeding population (BP) with high genomic breeding value (GEBV). The optimization algorithms for selecting the target training population set, viz., maximize diversity and minimize prediction error variance, can help prediction ability in breeding programs. Genomic revolution by whole-genome sequencing, resequencing, and genotype by resequencing (GBS) (e.g., 6K array, SNP chips) has been used to identify the huge number of genes (mostly SNPs, InDELs, CNVs) of variation in the genome level associated with different important traits, which could be used both as

genomic resources databases for genomic prediction and gene pyramiding for developing more superior varieties. Capturing all this SNP information affecting a particular trait from genomic selection and multiple loci gives a suitable proportion of variance to track all chromosome segments as compared to the limited response of individual SNP from MAS. Further, these genomic data could be combined with phenotypic data of any complex trait (biotic or abiotic stress) to enable predictions and selection by getting an idea of true genetic value using a statistical model.

3. GxE in Genomic Predictions

A genome-wide approach (correlation between the prediction and actual observed phenotype) typically provides better accurate predictions of multiple combinations of populations and traits (with GxE effects) than the MAS approach. There are different over fit genomic prediction models, which are used to create multi-collinearity with small number marker (p) and population size (n) having enough degrees of freedom (f). The infinitesimal model (linear fixed models) is the foundation of animal breeding; however, it is spectacularly successful in plant breeding value prediction in many cases. The complex features are dictated by an endless number of unlinked and additive loci, each having a negligible influence. Among them, genomic best linear unbiased prediction (G-BLUP), Bayesian models, machine learning models, and ridge-regression (RR-BLUP) are examples of specialized models that are adapted and developed for this problem, which capture the variations (frequency of pairs) in the bi-parental pedigree using marker similarity. They differ by types of assumptions and characterize polygenic traits in individuals that are more related to each other than other individuals having Mendelian sampling that causes deviations from expected resemblance. However, there are different factors affecting genomic prediction accuracy, viz., size of reference population (N_p), heritability of trait (h^2), number of independent chromosome segments or loci for trait (M_e), relationship between TP and BP, and linkage disequilibrium (LD) [68,69]. This pedigree relationship can be captured by an ideal and estimate matrix (genomic relationship matrix or G-matrix) using casual polymorphism and markers, respectively. In addition, these models could be helpful in predicting GxE effects with all the genomic and environment data targeting its performance in future target environments (kinship models) as well as crop growth models. The framework of crop growth models could also integrate into the GS model for making predictions in future environments. Breeding communities need to build G+P+E databases using a multi-trait GBLUP approach to bring the accuracy of genomic prediction to function. Interestingly, the decreasing cost of NGS technology has generated a whole-genome sequence of different crops with high-density SNP genotyping chips that are now available in the public domain, potentially improving the prediction capacity of a GS model. Even after more than a decade of research into genetic selection, there is still much room for improvement. Also, methodological improvements, including imputation of missing genotypic values, epigenetic regulation, implementation of GxE interactions, haplotypes, and the incorporation of multi-trait information into prediction models, will undoubtedly aid in the successful utilization of GS in plant breeding programs.

4. GAB for Improving Stress Resilience and Quality Traits in Food Crops

GAB in crop science aims to identify the best allele combinations (or haplotypes), gene networks, and specific genomic regions to aid in the development of future stress-resilient crops [70]. To feed the world's growing population, agricultural scientists are developing superior varieties by carefully selecting parents that are not only disease- and climate-resistant but also have improved nutrition and productivity while maintaining environmental sustainability. As a result, breeders are gradually making progress on genetic gain by selecting highly improved varieties with high prediction accuracy and, in time, sequencing the genomes of various crops, both wild and cultivated, to improve truly complex traits.

4.1. GAB for Improving Disease Resistance in Crops

Due to their sessile nature, crops are exposed to a wide range of biotic stressors, such as fungi, bacteria, oomycetes, nematodes, and insects, which not only affect their growth but also result in significant economic losses. The use of pesticides and incorporation of resistant gene(s)/QTLs into crops have significantly contributed to safeguarding crops against economic losses. However, the continuous evolution of pests and pathogens into novel types demands a constant need to find new and effective genomic areas that confer resistance to counterbalance these variants. The basic understanding of biotic and abiotic stress tolerance has substantially improved due to the rapid advancement in functional genomics. Interestingly, genomic tools can improve the accuracy and efficacy of modern breeding programs by improving phenotypic prediction on an available genotype through GAB [71].

The marker-assisted backcrossing (MABC) strategy, among the other GAB approaches, has been successfully employed in transferring the target genomic areas into the best cultivars [72]. MABC for gene pyramiding, in conjunction with selection for the recurrent parent's genetic background and recombination at the target region (s), resulted in quicker and more effective development of improved cultivars, boosting production and enhancing smallholder farmers' lives. Despite years of intensive research focused on understanding the complex host–pathogen interplay and developing more effective control strategies, biotic stress remains a substantial threat to agricultural yield [73,74]. Even when insecticides and biotic stress-tolerant varieties are deployed in the target area, production losses due to pests and pathogens are predicted to be between 20 and 30 percent [19]. This decrement can be linked to the rapidly evolving virulence characteristics of pathogens/pests, along with subsequent dissemination to different locations as a result of climate change and the integration of new agricultural techniques. In rice, diseases including bacterial blight and blast, as well as rust in wheat, are common. Although rice productivity and quality are threatened by various factors, including biotic stresses, among which prevalent *Xanthomonas oryzae*-caused bacterial blight and *Magnaporthe oryzae*-caused rice blast diseases are the two serious limitations, with global yield losses of up to 50–90% observed [31]. Several genes and QTLs for diverse virulent strains have recently been discovered. In a backcross-breeding effort, three key bacterial blight resistance genes (xa21, xa13, and xa5) were introgressed into the popular indica rice variety Samba Mahsuri from a homozygous donor line (SS1113). However, the expansion of this bacterial blight-resistant released 'Samba Mahsuri' variety was limited by its high susceptibility to blast disease [19]. Madhavi et al. [75] reported MABC-derived eight pyramided rice lines homozygous for both bacterial blight resistance genes (Xa21 and xa13) and blast resistance genes (Pi-2 and Pi-54), thereby incorporating multi-resistance into the 'Samba Mahsuri' variety. In addition, another bacterial blight resistance gene, Xa38, was further incorporated into the improved 'Samba Mahsuri' rice variety to widen the resistivity against pathotypes, considering the highly evolving nature of the bacterial blight [29]. Near-isogenic lines (NILs) of Basmati rice variety 'Pusa Basmati 1' pyramided with two (Pi2+Pi5) and three (Pi54+Pi1+Pita) blast resistance genes against *Magnaporthe oryzae* were developed through MABC exhibiting higher yield and cooking quality, respectively [31].

In wheat, rust resistance genes (Yr40 and Lr57) were introgressed into the genetic background of hard red winter wheat cultivars, viz., Jagger and Overlay [38]. Indian wheat cultivar HUW510 was genetically improved by the introduction of a spot blotch resistance gene from Picaflor#1 line of CIMMYT using MABC [39]. In 2005, MABC-based downy mildew disease-resistant HHB 67 hybrid pearl millet was released for cultivation. In barley, GAB was used for the transfer of the eyespot resistance gene (Pch1), two barley yellow mosaic virus resistance genes Rym4/Rym5, and the powdery mildew resistance gene (MLO) [76]. Soybean, an industrially and nutritionally valuable legume crop, is prone to many biotic stressors. The principal pests of soybeans include cyst, root-knot, and reniform nematode, which cause significantly high yield losses [77]. Efforts to identify genomic markers associated with the cyst nematode have resulted in the production and marketing

of JTN-5503, JTN-5303, and JTN-51Q9 soybean cultivars in the United States, which are basically gene pyramids of Rhg1, Rhg4, and Rhg5 [46,47]. In chickpea, introgression of Fusarium wilt resistance from WR 315 in Annigeri-1 led to the development of the Super Annigeri 1 chickpea variety. Varshney et al. [49] also introgressed Fusarium wilt (*foc1* locus) and Ascochyta blight (ABQTL-I and ABQTL-II) resistance in chickpea C 214 for improving disease resistance.

4.2. Utilizing GAB for Improving Abiotic Stress Tolerance in Plants

Abiotic stress, which includes extreme temperature, drought, radiation, salinity, heavy metal toxicity, etc., affects crop development and productivity. In reality, abiotic stressors are the leading factor of yield loss globally, with agricultural output for key crop plants falling by over half. Abiotic stressors, in comparison to biotic stresses, represent a greater threat to agricultural productivity, especially in light of increasing climatic circumstances. GAB has been used to improve abiotic stress tolerance in different crop systems. For instance, in rice, Sub1 QTL conferring submergence-tolerant was transferred using MABC from the FR13A landrace into the elite cultivars that led to development of improved varieties like Swarna-Sub1, Samba Mahsuri-Sub1, BR11-Sub1, CR1009-Sub1, Ciherang-Sub1, TDK1-Sub1, PSB Rc18-Sub1, and IR64-Sub1, respectively [78,79]. Similarly, for improving submergence tolerance in rice susceptible cultivar, a *Sub1* gene from IR64-Sub1 was successfully introgressed into OM1490 (submergence susceptible variety), which showed high tolerance to waterlogging Vietnam [33]. Thomson et al. [80] mapped Saltol QTL in an FL47 line derived from Pokkali and IR29 for incorporation of salinity tolerance in rice. Using GAB approaches, Saltol QTL has been successfully transferred through marker-based breeding into popular rice cultivars like Pusa Basmati 1121 [81], Pusa Basmati 6 [81], AS 996 [82], BT 7 [83], Bacthorm 7 [84], Q5DB [85], BRRI-Dhan 49 [86], and Novator [87] for improving salt tolerance. Das et al. [37] successfully assembled a combination of biotic-resistant and abiotic-tolerant genes, namely submergence (*Sub1*) from FR13A, salinity (Saltol) from FL478, blast (*Pi2* and *Pi9*) from C101A51 and WHD-1S-75-1-127, respectively. Similarly, gall midge (*Gm1* and *Gm4*) from Kavaya and Abhaya, introgressed into the improved Tapaswini rice cultivar, previously pyramided with bacterial blight resistance genes (*Xa4*, *Xa5*, *Xa13*, *Xa21*). This work showed the huge potential of GAB in developing crop varieties conferring a broader range of resistance/tolerant against prevailing stresses originating from wide-scale biotic and abiotic sources. In addition to submergence and salinity, drought-tolerant QTLs *qDTY3.2* and *qDTY12.1* were pyramided to develop NILs of drought-susceptible rice variety Sabitri [36]. Similarly, the Pusa Chickpea 10216 variety has been developed through genomics-assisted introgression of ‘QTL-hotspot’ carrying drought tolerance genes identified in ICC 4958 chickpea genotype into the Pusa—372.

4.3. Application of GAB for Improving Growth and Quality Traits

Another significant category of targeted attributes that plant breeders look for to enhance crop yield and nutritive value is quality traits. Among the end-use quality, grain protein concentration is considered to be of high priority for wheat breeders [88]. Several commercial varieties of wheat, viz. Farnum, Lassik, Westmore, and Desert King-High Protein in the USA, Lillian, Somerset, Burnside in Canada, and Wyalkatchem, Gladius, VR 1128 in Australia have been developed by introducing *Gpc-B1* from *Triticum turgidum* ssp. *dicoccoides* into the tetra and hexaploid wheat. Brevis and Dubcovsky [89] also reported introgression of *Gpc-B1* into hexaploid and tetraploid wheat genotypes for their qualitative improvement. In rice, *badh2* and *Wx* genes controlling fragrance and intermediate amylose content were transferred from Basmati370 into an elite non-fragrant Myanmar cultivar, Manawthukha, by MABC [21]. In order to improve the oleic and linoleic acid ratio in the seeds of nematode-resistant peanut cultivar Tifguard. Chu et al. [55] generated ‘Tifguard High O/L’ through backcrossing with cultivars Georgia-02C and Florida-07. Janila et al. [22] reported groundnut introgression lines with improved oil quality developed by transferring *FAD2* mutant alleles from SunOleic 95R into the genetic background

of ICGV 06110, ICGV 06142, and ICGV 06420. Recently, Shasidhar et al. [23] generated an improved three elite Indian groundnut varieties (GJG 9, GG 20, and GJGHPS 1) for foliar disease resistance and high oleic acid content using MABC.

GAB has been successfully used for crop improvement programs in many economically important cereal crops, such as wheat, rice, barley, and maize; however, its use needs to be translated to other important horticulture crops to increase their economic viability and crop productivity. With the advent of modern techniques for sequencing, next-generation sequencing (NGS), GWAS, nested association mapping (NAM), and selection like marker-assisted recurrent selection (MARS) and genomic selection (GS) and also tools such as an integrated system for marker-assisted breeding (ISMAB), OptiMAS, GS modules, and platforms like Integrated Breeding Platform (IBP), GAB is expected to advance revolutionarily for utilization in a broader range of crops/traits in crop breeding. Despite GAB's enormous potential, several impediments continue to stymie its immediate application. Thus, it is anticipated that GAB 2.0 will be crucial to breeding research in the future in order to produce resilient and climate-smart crop cultivars with more nutritional value in a timely and cost-effective manner [17]. Further, we have highlighted the importance of various approaches associated with GAB2.0 for sustainable crop improvement in various agriculturally important crops (Table 2). In the upcoming years, we anticipate that widespread application of MAS and GS, either separately or in combination, utilizing cutting-edge sequencing technology, will contribute to improving genomic plant breeding. Furthermore, combined genome analysis of different cultivars of the same species or several different species, known as pangenomes and super-pangenomes, respectively, are milestones in GAB for crop improvement.

Table 2. Shows the importance of various approaches associated with GAB2.0 for crop improvement in different crops.

Crop Species	Trait Improvement	Gene Targeted	Approach Used	References
<i>Oryza sativa</i> (Rice)	Grain yield and quality	Genetic gain-related genes	Large-scale whole-genome resequencing (WGRS) + haplo-pheno analysis	[90]
	Yield component	Grain yield	High-throughput phenotyping	[91]
	Disease resistance	OsMPK5	Gene editing	[92]
<i>Solanum lycopersicum</i> (Tomato)	Disease resistance	Plant disease and pest recognition traits	Deep learning-based detectors	[93]
<i>Vitis vinifera</i> (Grapevine)	Yield component	Berry number/cluster	High-throughput phenotyping	[94]
<i>Cajanus cajan</i> (Pigeon pea)	Drought tolerance	Plant weight and relative water content	Haplotype breeding	[95]
<i>Triticum aestivum</i> (Wheat)	Yield-related traits	<i>TaGW2-A</i>	Haplotype breeding	[96]
	Physiological and morphological traits	Nitrogen per unit leaf area, leaf dry mass per area, Rubisco activity, and electron transport rate	High-throughput phenotyping	[97]
	Yield component	Grain yield	High-throughput phenotyping	[98]
	Yield component	Yield and sowing date	Microsatellite data	[99]
	Powdery mildew diseases	TaMLO-A1	Gene editing	[100]
	Australian high-protein milling variety (DS Faraday)	Tolerance to preharvest sprouting and leaf, stem rust, stripe	SB	[101]

Table 2. Cont.

Crop Species	Trait Improvement	Gene Targeted	Approach Used	References
<i>Zea mays</i> (Maize)	All plant phenotypic traits (morphological, physiological), biotic and abiotic stress-related traits	Plant/canopy height, plant density, fruit size, grain number and size, diseases, senescence, chlorophyll content	High-throughput phenotyping	[102]
	Qualitative/quantitative traits	Ear, cob, kernel	High-throughput phenotyping	[103]
	Fertilization	Nitrogen fertilization	High-throughput phenotyping	[104]
	Fertilization and abiotic stress	Nitrogen fertilization and heat stress	High-throughput phenotyping	[105]
	Physiological and biochemical traits in leaf	Chlorophyll content, nitrogen content, sucrose content, leaf area, photosynthesis rate, leaf oxygen radical, rate of phosphoenolpyruvate carboxylation	High-throughput phenotyping	[106]
	Stress resilience	Leaf/canopy reflectance for low-N stress	High-throughput phenotyping	[107]
	Yield component	Plant height	High-throughput phenotyping	[108]
	Yield component	Kernel trait	High-throughput phenotyping	[109]
	Drought tolerance	Drought tolerance-related genes	Big data	[110]
	Grain Yield trait under drought stress	AGROS8	Gene editing	[111]
<i>Solanum tuberosum</i> (Potato)	Tuber quality traits (phenotypic, physiological, biochemical, and molecular)	Tuber flesh color, DSC onset, tuber shape, and enzymatic discoloration	Integration of the multi-omics (transcriptomics, metabolomics, proteomics) data with the genetic mapping	[112]
<i>Anthonomus grandis</i> (Cotton)	Stress resilience	Stress-responsive traits	High-throughput phenotyping	[113]
<i>Solanum pimpinellifolium</i> (Wild tomato)	Quality and nutritional traits (self-pruning, fruit weight, lycopene beta cyclase)	SP, SP5G, SICLV3, SI SIWUS,	Genome editing for de novo domestication	[114–116]
<i>Physalis pruinosa</i> (Groundcherry)	Quality and nutritional traits SELF-PRUNING, SELF-PRUNING 5G, CLAVATA WUSCHEL	SP, SP5G, and CLV	Genome editing	[117]
<i>Arabidopsis thaliana</i> , <i>Nicotiana tabacum</i> , <i>Sorghum</i> <i>bicolor</i> , <i>Oryza sativa</i> (Arabidopsis, Tobacco, Sorghum, and Rice)	Bacterial blight	OsSWEET14 and OsSWEET11	Gene editing	[118]
<i>Populus tremula x alba</i>	Lignin and flavonoid biosynthesis	4-coumarate: CoA ligase (4CL) genes, 4CL1, 4CL2, and 4CL5	Gene editing	[119]
<i>Brassica napus</i> (Rapeseed)	High oleic acid	FAD2	Gene editing	[120,121]
<i>Camelina sativa</i> (Camelina/false flax)	High oleic acid	FAD2, FAE1	Gene editing	[122–124]
<i>Glycine max</i> (Soybean)	10 h photoperiod + blue light	Improve generation turnover.	Speed breeding	[125]
	Kuntiz-trypsin inhibitor (KTI) free	NRC21, UEL175	Molecular breeding and gene editing	[126,127]
	Light quality/intensity	Photo-morphogenic response	Speed breeding	[128]
<i>Oryza sativa</i> and <i>Amaranthus</i> spp. (Rice and Amaranth)	Light quality/intensity	Improve generation turnover	Speed breeding	[125]

5. Omics-Assisted Breeding (OAB): Toward More Efficient Food Production

The adoption of omics technologies has received a tremendous boost in recent decades as a result of breakthroughs in next-generation sequencing (NGS) technology, sophisticated bioinformatics tools, and an abundance of accessible biological data. In the last two decades, modern breeding has undergone a dramatic transformation with advances in ‘Omics’, which includes genomics, transcriptomics, proteomics, and metabolomics. ‘Genomics’, as an ever-evolving applied field of research, deciphers the genome present in the cells of a species, creating opportunities for understanding the genetic makeup and behavior of plant genomes, including characterization of all the genes to explore their expressions, interactions, and functions [129]. The information generated through genomic approaches is now being routinely used in plant breeding programs, which improved both accuracy and duration of selection, referred to as GAB. In addition, with the advent of bioinformatics tools and genomics databases, the processing and analysis of vast data generated from genome-wide studies have now become easier for researchers.

With the advent of next-generation sequencing (NGS) technologies, a large amount of high-throughput data was generated in both model and crop plants, providing breeders with numerous opportunities to develop elite crops. However, owing to the complexity of the data, there is a further need to integrate next-generation computational tools and artificial and machine learning, which will further improve our mechanistic understanding of complex traits with different phenotypes. Multiomics-based tools have proven to be useful for investigating the genetic and molecular basis of crop improvement via changes in DNA, RNA levels, metabolites, proteins, and mineral nutrients in the context of physiological and environmental stress responses [130]. These high-throughput techniques have been critical in understanding a number of traits, such as growth, yield, senescence, and responses to abiotic and biotic stress in a variety of crops. For instance, multi-omics studies have been used in many crops, viz., *Oryza sativa* L., *Glycine max*, *Triticum aestivum* L., *Zea mays* L., *Solanum lycopersicum*, *Gossypium hirsutum* L., *Hordeum vulgare* L., *Setaria italica* L., and *Medicago truncatula*, for decoding the complexity of important agronomic traits [131]. Interestingly, at present, there is a huge amount of data available on different crops that aided in improving crop breeding in sustainable agriculture. Among various high-throughput sequencing approaches, transcriptomics is widely used in crop breeding to evaluate gene expression under diverse growth stages or environmental conditions. For instance, in rapeseed, the differential expression of mRNAs during developmental stages was identified to uncover the potential genes regulating seed size, which can provide an important path for improving seed quality using GAB [132]. Identifying essential genes and understanding gene expression is thus a powerful method for breeding crops with improved features. A substantial quantity of data has been deposited to public repositories, making it feasible to combine them for co-expression analysis under various biotic and abiotic stressors and perform meta-analyses of transcriptome responses. These days, crop breeding programs can benefit greatly from all the data produced by proteomics studies since they make proteome-driven marker identification easier. Similarly, metabolite profiling using metabolomics is an important approach for investigating crop interactions with environmental stressors. Various methods used to analyze agricultural metabolites, including liquid chromatography-mass spectrometry (LC-MS), gas chromatography-mass spectrometry (GC-MS), and nuclear magnetic resonance (NMR), have been instrumental in identifying target metabolites in crops under stress conditions. For instance, comparative metabolic profiling in soybean cultivars during floodings led to the identification of key metabolites in susceptible and resistant cultivars and, thereby, provided a novel avenue for omics-based breeding crop improvement using metabolic traits [133]. With advances in omics, metabolic profiling can be utilized as a phenotypic input for genetic association studies such as QTL, enabling crop development. The metabolome study of 81 barley accessions grown under heat and drought stress identified 57 metabolite QTLs, the majority of which were related to antioxidant defense responses [134]. Interestingly, metabolite-based GWAS is another effective approach for linking genetic variables to pri-

mary and secondary metabolites. It opens up the possibility of discovering candidate genes by combining genomic and metabolite data. This technique was employed successfully in tomatoes, and 44 loci were discovered to be linked with fruit metabolites [135]. Ionomics gives molecular dynamics of the ionome, which, when combined with GWAS and QTL, may predict distinct genomic areas associated with different ions or elements, allowing for the manipulation and interrogation of complex traits. Moreover, combining the data for omics such as genomics, transcriptomic, metabolomics, and proteomics provides in-depth information on different traits associated with the environment and genome to phenotypic interactions [136]. Furthermore, it has been demonstrated that combining GWAS with omics techniques is a useful way to analyze the genetic and biochemical mechanisms in a number of model crop species, such as tomato, rice, and maize [137,138]. Many mutants with precise variations in stress tolerance, growth, and development have been identified using functional genomics and mutagenomics in a number of crop systems, like barley, maize, rice, and wheat [139]. GWAS, pangenomes, super-pangenomes, and large-scale genome resequencing are helping to identify and analyze species-level genome variations; on the other hand, transcriptomics has provided transcript-level information for decoding the cell-specific stress response. High-throughput phenomics has been focusing on new study areas recently, like the analysis of root architecture and the investigation of microbiota linked with plant roots for better crop health and climate resistance. On the other hand, metagenomic prediction can be used to improve the predictions of future phenotypes using information from the microbiome. This can be performed by microbiome profiling with respect to the relative abundance of symbiotic micro-organisms associated with traits of interest. In plants, nitrogen emission and microbiome profiling surrounding the agriculture soil by sequencing to improve future predictions. Also, the development of novel genetic resources for commercially significant and stress-resistant crop development for sustainable agriculture will be facilitated by the present advancements in ‘omics’ methods and integration tactics. Finally, the incorporation of omics into current breeding programs may result in a shift in future studies from GAB to OAB, which can provide novel avenues for crop improvement in a more precise, accurate, and timely manner.

In order to enhance crop genetics, growth, yield, and stress tolerance, integration of multi-omics based on genotype to phenotype would, therefore, offer insights into the functional mechanisms of genes and their networks. Importantly, combining omics data with systems biology has been instrumental in increasing our mechanistic understanding of molecular regulator networks and their signatures for crop improvement. From this standpoint, we propose integrating multi-omics with plant systems biology with a focus on both phenotypes to genotype and genotype to phenotype model, which will aid in the development of valuable agronomic traits, such as nutritional augmentation, stress resilience, and crop production in sustainable agriculture. Recently, a new platform that integrates complex omics, called panomics, was proposed by Weckwerth et al. [140]. The primary goal of this versatile platform is to combine inductive multi-omic data sets and build models that can be used to predict complex traits in crop plants [136]. The use of panomics datasets for genotype–phenotype prediction may also reduce the number of false positives generated by single data sets [141]. Further, integration of panomics with other systems biology tools, functional genomics environmental platforms, artificial intelligence (AI), and machine learning (ML) can be used to identify potential target genes, markers, and QTLs to improve crop varieties’ tolerance to abiotic and biotic stress and also to develop to elite lines to improve germplasm. Many tools, including PAINTOMICS, COVAIN, and KaPPA-view, have been used to combine multi-omics data before interpretation. Integration of panomics with GWAS has also been employed not only to elucidate and comprehend crop phenotypic variation but also for the identification of novel potential genes and their functional pathways underlying complex traits. Similarly, a joint metabolome-based GWAS was used (mGWAS with eQTL) to discover metabolite features linked to kernel weight in maize crops. Furthermore, the combination of panomics and genome-editing tools (for example, TALENs and CRISPR/Cas9) has been proposed as a model for precision

breeding advancement. There is a need to expand the role of multi-omics orphan crops as well as least studied crops that can further provide an alternative for future global food security. Further, we have highlighted the importance of integrating multi-omics approaches with other next-generation technologies that could provide a foundation for improving plant breeding science, nutrition, genetic development, crop yields, and crop tolerance to environmental stressors in Figure 3.

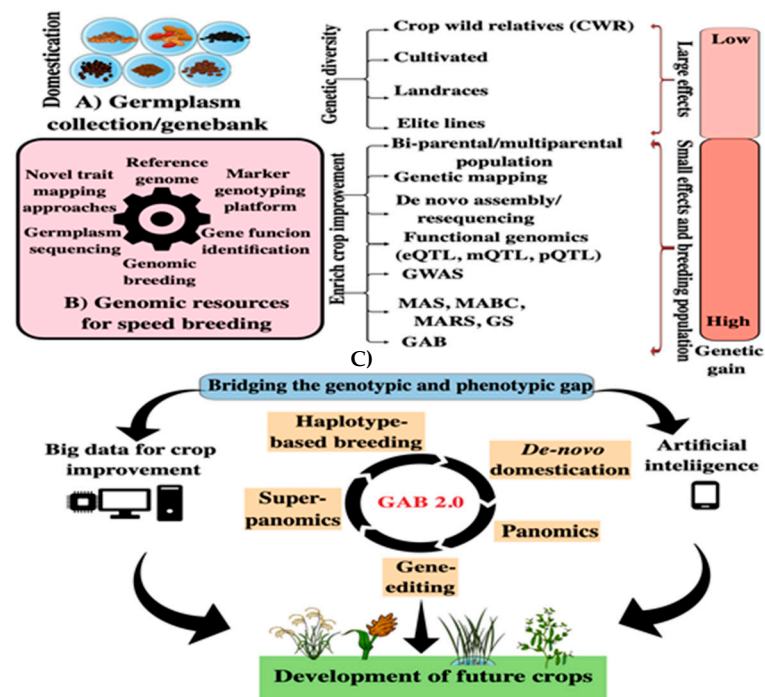


Figure 3. Illustration showing the abundant genomic resources available from a wide range of crops that have improved the accuracy of selection and accelerated the breeding process for new cultivars. The different steps of integrating (A) germplasm collection, (B) development of genomic resources for speed breeding for crop improvement using genetic diversity analysis and high genetic gain tools such as marker-assisted selection (MAS), genomic selection (GS), genomic-assisted breeding (GAB), genome-wide association analysis (GWAS), and other next-generation technologies (multi-omics) to enrich crop improvement, and (C) bridging the genotypic and phenotypic gap (GAB2.0) using big data and artificial intelligence (AI) are the foundation for developing future smart crops.

6. Conclusions

Given the fast advancement of molecular breeding and GS techniques in breeding programs, there is enormous promise for using GS for yield and stress improvement in a variety of crop systems. The large-scale mapping of agronomically significant quantitative trait loci, elite allele/haplotype mining, natural variation exploitation, gene cloning and characterization, and genomic selection have been instrumental in the development of GAB. In the context of crop trait improvement, GAB (MAS, QTL mapping, and GWAS) has been widely applied in breeding programs and is promising but faces challenges for its wide implementation, like the need for high-throughput phenotyping platforms. At present, current phenome initiatives fall short of reaching GAB's full potential due to restricted phenotyping capabilities and prices. Secondly, there has been much genomic data generated from different crop systems in the past, but analyzing target genome structure and function remains difficult due to the complexity of traits. Therefore, future studies are required to address the above challenges in order to harness the potential of GAB for crop improvement in the wake of climatic change and food demand. Harnessing the potential of multi-omics, pangenomics, systemic biology, and high-throughput phenotyping tools will provide high-quality genetic and phenotypic information on complex traits,

making it more viable to minimize the gap between theories and breeding practices. In modern agriculture, targeted and precise breeding procedures are necessary for speedy and successful cultivar development. In this regard, the introduction of genome editing in plant breeding technology has been the most recent achievement for targeted and precise trait improvement. Genome editing technologies have developed as potent tools for accurately modifying crop genomes at specific places within the genome, which has long been an aim of plant breeders.

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