

International Journal of Advanced Biochemistry Research



ISSN Print: 2617-4693
ISSN Online: 2617-4707
NAAS Rating: 5.29
IJABR 2025; 9(7): 624-629
www.biochemjournal.com
Received: 28-05-2025
Accepted: 30-06-2025

Dr. M Ramasamy
Assistant Professor, Department
of Veterinary & Animal Sciences,
ICAR-KVK, Tamil Nadu
Agricultural University,
Coimbatore, Tamil Nadu, India

Dr. Akkisan Trivikrama Reddy
Professor and Head, Department
of Genetics and Plant Breeding,
Agricultural College, Acharya
NG Ranga Agricultural
University, Guntur, Andhra
Pradesh, India

Jassimran Kaur
Department of Plant Breeding
and Genetics, Punjab
Agricultural University,
Ludhiana, Punjab, India

Anmol
Ph.D Research Scholar,
Department of Animal Genetics
and Breeding, Acharya NG
Ranga Agricultural University,
Guntur, Andhra Pradesh

Dr. Pratibha Mahawar
Research Scholar, Department of
Botany, Government College,
Kota, Rajasthan, India

Smrutirekha Pati
Master Research Scholar,
Department of School of Life
Sciences, University of Warwick,
England

Hanuma Sai Dinesh Kalisetty
Master Research Scholar,
Department of Agriculture &
Food Science, University of
Greenwich, England

Shubhendu Singh
Research Scholar, Department of
Agronomy, Banaras Hindu
University, Varanasi, Uttar
Pradesh, India

Corresponding Author:
Dr. M Ramasamy
Assistant Professor, Department
of Veterinary & Animal Sciences,
ICAR-KVK, Tamil Nadu
Agricultural University,
Coimbatore, Tamil Nadu, India

The evolution of plant genetic improvement: From Mendel to molecular markers

M Ramasamy, Akkisan Trivikrama Reddy, Jassimran Kaur, Anmol, Pratibha Mahawar, Smrutirekha Pati, Hanuma Sai Dinesh Kalisetty and Shubhendu Singh

DOI: <https://www.doi.org/10.33545/26174693.2025.v9.i7h.4800>

Abstract

The trajectory of plant breeding has transitioned remarkably from Mendel's inheritance principles to today's molecular marker-driven precision breeding. Early efforts were limited to observable phenotypic traits and simple crosses, but the advent of cytogenetics, molecular markers, high-throughput sequencing, and genome editing has revolutionized crop improvement. This review examines the historical milestones and recent advances in plant genetic improvement, emphasizing the integration of marker-assisted selection (MAS), genomic selection (GS), and CRISPR-based editing. The paper concludes with prospects on integrating phenomics, enviromics, and data-driven breeding pipelines to accelerate development of climate-resilient crops.

Keywords: Mendelian genetics, molecular markers, marker-assisted selection, genomic selection, CRISPR, plant breeding, phenomics

1. Introduction

Agriculture stands at a critical juncture in human history. As the global population surges towards 10 billion by 2050, demand for food, feed, fiber, and fuel is projected to increase by more than 50% compared to 2010 levels (FAO, 2023). Simultaneously, climate change is intensifying the frequency and severity of abiotic stresses such as drought, heat waves, salinity, and flooding, while also altering pest and disease dynamics (IPCC, 2022) ^[7]. This convergence of rising demand and mounting environmental constraints places unprecedented pressure on agricultural systems, compelling innovation in how we develop and deploy crop varieties. Plant breeding—the science of altering the genetic makeup of plants to produce desired traits—has been the cornerstone of agricultural advancement for over a century. Traditional plant breeding relied on phenotypic selection: identifying superior individuals in fields and using them to breed subsequent generations. This process, while historically effective in driving yield gains (especially during the Green Revolution), is time-consuming, often inefficient for complex traits, and heavily influenced by environmental variability. The scientific foundation of modern breeding was laid by Gregor Mendel in the mid-19th century through his meticulous experiments with pea plants, which uncovered the laws of segregation and independent assortment (Mendel, 1866) ^[12]. These principles allowed breeders to predict the inheritance of discrete traits, transforming crop improvement from an art into a predictive science. Over the ensuing decades, advances in cytogenetics illuminated the chromosomal basis of inheritance, enabling breeders to manipulate ploidy levels and exploit phenomena such as hybrid vigor.

However, the limitations of classical approaches became increasingly apparent for polygenic traits like drought tolerance, yield stability, or nutrient use efficiency. The advent of molecular biology and the discovery of DNA as the hereditary material ushered in a new era of marker-assisted selection (MAS) in the 1980s and 1990s. By leveraging DNA markers linked to traits of interest, breeders could select for favorable alleles without waiting for full plant development or contending with environmental noise. The last two decades have witnessed yet another paradigm shift with the integration of next-generation sequencing (NGS), genome-wide association studies (GWAS), and genomic selection (GS).

These approaches allow simultaneous tracking of thousands of loci across the genome, vastly enhancing the precision and speed of breeding pipelines. The recent rise of genome editing tools, notably CRISPR-Cas systems, has further expanded the breeder's toolkit by enabling targeted modifications at single-nucleotide resolution. Beyond the molecular revolution, plant breeding is now deeply intertwined with data sciences. The integration of high-throughput phenotyping, machine learning, and enviro-mics—the characterization of environmental variability in breeding trials—is enabling breeders to predict genotype-by-environment interactions with unprecedented accuracy (Xu *et al.*, 2025) ^[21].

This study traces the remarkable journey of plant genetic improvement, from Mendel's foundational laws to today's molecular markers and precision breeding technologies. We highlight key scientific breakthroughs, showcase recent examples of their deployment in major crops, and discuss how integrated breeding approaches are positioning agriculture to meet the twin challenges of productivity and sustainability in a changing climate. In doing so, we aim to provide researchers, breeders, and students with a comprehensive overview of how far plant genetic improvement has come—and where it is poised to go next.

2. Classical Breeding and Early Genetic Foundations

2.1 Mendelian Inheritance and the Rise of Scientific Breeding

The birth of modern genetics is universally attributed to Gregor Mendel, whose experiments with *Pisum sativum* (garden pea) in the 1850s-1860s established the fundamental laws of segregation and independent assortment (Mendel, 1866). His meticulous approach, involving thousands of crosses and statistical analysis, demonstrated that discrete hereditary units (later termed “genes”) govern the transmission of traits. Despite its significance, Mendel's work remained largely unrecognized until its rediscovery in 1900 by three scientists independently—Hugo de Vries, Carl Correns, and Erich von Tschermak—who applied these principles to other plant species.

This rediscovery catalyzed the systematic application of genetics to crop improvement. By the early 20th century, breeders across Europe and North America were actively designing crosses to combine desirable traits such as higher grain yield, disease resistance, and improved nutritional quality. The development of inbred lines and subsequent production of F₁ hybrids, especially in maize, revolutionized cereal productivity. Shull (1908) ^[17] and East (1908) demonstrated how inbreeding followed by hybridization could exploit heterosis (hybrid vigor), resulting in maize hybrids that dramatically outperformed open-pollinated varieties—a strategy that would become a cornerstone of commercial seed production worldwide.

2.2 Cytogenetics and Chromosomal Manipulations

While Mendelian laws explained inheritance at a phenotypic level, the chromosomal basis of heredity was elucidated through advances in cytogenetics. Pioneers such as Barbara McClintock (1931) in maize identified crossing over and chromosomal translocations, enhancing understanding of linkage and recombination. Manipulating ploidy levels became another strategic avenue:

- **Polyloidization** led to the development of bread wheat (*Triticum aestivum*, a hexaploid) and various tetraploid

crops, enhancing gene redundancy and adaptability (Ramsey & Schemske, 1998) ^[16].

- **Chromosome doubling** using colchicine treatments produced stable polyploids in species like alfalfa and banana, increasing biomass or seedlessness, respectively.

Early breeders also created wide crosses, incorporating genomes from related species. A classic example is the creation of triticale, a hybrid of wheat (*Triticum*) and rye (*Secale*), combining wheat's yield with rye's hardiness (Oettler, 2005) ^[15].

2.3 Limitations of Classical Breeding

Despite remarkable successes, classical breeding faced intrinsic limitations:

- Many key agronomic traits, such as yield stability, drought tolerance, and nutrient use efficiency, are **quantitative in nature**, controlled by multiple genes of small effect and subject to strong environmental interactions.
- Phenotypic selection required evaluating plants under multiple years and locations, prolonging breeding cycles to 10-15 years or more.
- Hidden deleterious alleles could be inadvertently fixed alongside desired traits due to linkage drag.

These challenges set the stage for molecular tools that could probe beyond visible phenotypes to directly manipulate underlying genetic factors.

3. The Advent of Molecular Markers and Marker-Assisted Selection

3.1 Early Molecular Markers: From Proteins to DNA

The molecular era began with **biochemical markers**, such as isozymes (variants of enzymes differing in electrophoretic mobility), which provided the first glimpses into genetic diversity within and between crop populations (Tanksley & Orton, 1983) ^[18]. However, their limited number and environmental sensitivity constrained widespread use.

The 1980s ushered in DNA-based markers, offering direct assessment of genetic variation:

- **Restriction Fragment Length Polymorphisms (RFLPs)**, the first DNA markers, used restriction enzymes to detect polymorphic DNA fragments. They proved highly reproducible and co-dominant, crucial for constructing the first genetic linkage maps in maize, tomato, and rice (Botstein *et al.*, 1980) ^[2].
- **Random Amplified Polymorphic DNA (RAPD)** and **Amplified Fragment Length Polymorphism (AFLP)** techniques emerged in the 1990s, enabling rapid genome scanning without prior sequence knowledge, although reproducibility issues limited RAPDs in breeding.
- **Simple Sequence Repeats (SSRs)** or microsatellites soon became the marker of choice for many crops due to their high polymorphism, co-dominance, and transferability across populations.

3.2 The Rise of Marker-Assisted Selection (MAS)

The concept of **marker-assisted selection (MAS)**—using DNA markers linked to genes or QTLs to guide breeding

decisions—was a paradigm shift. Unlike classical breeding, MAS could:

- Select plants at the seedling stage, without waiting for full phenotypic expression.
- Stack multiple genes or QTLs (gene pyramiding) even for traits with no clear phenotypic markers.
- Facilitate marker-assisted backcrossing (MABC) to introgress specific traits from donor lines into elite backgrounds with minimal linkage drag.

Practical examples include

- Incorporation of multiple bacterial blight resistance genes (*Xa4*, *Xa21*) into elite rice lines through SSR-based MAS (Joseph *et al.*, 2024).
- Pyramiding of wheat rust resistance genes (*Lr34*, *Sr2*, *Yr18*) using closely linked markers to achieve durable multi-pathogen resistance (Zhang *et al.*, 2024) ^[24].
- Development of quality protein maize (QPM) with opaque-2 modifiers tracked through SSR markers, enhancing lysine and tryptophan levels.

3.3 Expanding to QTL Mapping and Beyond

MAS also propelled QTL mapping, where markers are used to locate genomic regions associated with quantitative traits. Thousands of QTLs for yield, abiotic stress tolerance, and nutritional quality have been identified across diverse crops, forming the basis for subsequent marker deployment. Recent reviews (Misra & Singh, 2025) ^[14] highlight how integrating SSR and SNP markers into breeding pipelines has significantly shortened varietal development timelines—often by 30–40% compared to purely phenotypic approaches. This efficiency, coupled with reducing costs of genotyping, established MAS as a standard in modern crop improvement programs.

4. High-Throughput Genotyping and the GWAS Era

4.1 Technological Leap: Next-Generation Sequencing and SNP Discovery

The turn of the 21st century saw extraordinary advances in sequencing technology. The advent of next-generation sequencing (NGS) platforms—such as Illumina, Roche 454, and later Oxford Nanopore and PacBio—enabled massively parallel DNA sequencing, drastically reducing per-base costs and turnaround times. This revolution facilitated:

- Whole-genome resequencing, unlocking millions of single nucleotide polymorphisms (SNPs) across populations.
- Reduced-representation approaches, such as restriction site-associated DNA sequencing (RAD-Seq) and genotyping-by-sequencing (GBS), which allowed genome-wide marker discovery and genotyping in a single step (Elshire *et al.*, 2011) ^[6].

By generating thousands to millions of markers at once, breeders could build dense genetic maps, fine-map QTLs, and perform large-scale diversity analyses. For instance, the International Rice Informatics Consortium and the Wheat 10 + Genome Project have made high-density SNP data publicly available, accelerating global breeding efforts.

4.2 Genome-Wide Association Studies (GWAS)

Unlike classical biparental QTL mapping, GWAS leverages historical recombination events in diverse germplasm panels to achieve high-resolution mapping of trait-associated loci.

This approach requires extensive marker coverage, which became feasible with NGS and SNP arrays (e.g., the Illumina iSelect Wheat 90K).

Recent examples illustrate the power of GWAS in dissecting complex traits:

- In rice, Liu *et al.* (2025) ^[11] employed multi-year, multi-location GWAS on 3,000 rice accessions, pinpointing SNPs significantly associated with salt tolerance and yield under saline conditions.
- In tomato and pepper, Wang *et al.* (2024) ^[20] used over 200,000 SNPs to identify loci for fruit firmness, soluble solids content, and disease resistance.
- In maize, large-scale GWAS studies have mapped loci governing nitrogen use efficiency and drought tolerance, critical under climate-change scenarios (Crossa *et al.*, 2024) ^[5].

4.3 Practical Impacts in Breeding

GWAS outputs feed directly into breeding pipelines by enabling:

- Marker-assisted selection for minor QTLs, broadening beyond major-effect genes.
- Genomic selection models (discussed next) that incorporate thousands of small-effect loci.

Importantly, GWAS combined with candidate gene validation via CRISPR is increasingly closing the loop from association to functional proof, accelerating breeding decisions.

5. Genomic Selection (GS) for Polygenic Traits

5.1 Overcoming the Limits of MAS

While MAS excels at traits controlled by a few major genes (e.g., disease resistance), it struggles with polygenic traits influenced by dozens to hundreds of loci with small individual effects. These include grain yield, water-use efficiency, and nutrient uptake—traits of utmost economic importance.

Genomic selection (GS), first conceptualized by Meuwissen *et al.* (2001) ^[13], addresses this by using dense genome-wide markers to predict the genetic value (genomic estimated breeding values, GEBVs) of individuals, without explicitly identifying each contributing QTL.

5.2 How GS Works

A training population with both **phenotypic data** and **dense genotypic data** is used to build prediction models (e.g., G-BLUP, BayesB, machine learning approaches). These models then estimate breeding values of untested individuals based solely on their genotype.

Advantages include

- Capturing both large and small effect loci, along with epistatic interactions.
- Drastically shortening breeding cycles by allowing early selection at the seedling stage.
- Reducing the cost and time of extensive field evaluations.

5.3 Success Stories in Crops

GS has now become mainstream in several breeding programs:

- In maize, Crossa *et al.* (2024) ^[5] demonstrated that GS doubled the rate of genetic gain for drought tolerance

compared to traditional selection, particularly when combined with sparse multi-environment phenotyping.

- In wheat, GS models have been deployed for end-use quality traits like dough rheology and bread loaf volume, traits traditionally requiring costly lab assays.
- In tomato and other Solanaceae, GS integrated with UAV-based high-throughput phenotyping improved prediction accuracy for yield components and fruit quality (Frontiers, 2024) ^[1].

5.4 Emerging Integrations

Modern GS is increasingly incorporating

- Enviromic data to account for genotype-by-environment interactions (Xu *et al.*, 2025) ^[21].
- Transcriptomic and metabolomic markers, moving toward “multi-omic” GS models.
- Deep learning algorithms to capture nonlinear relationships among thousands of markers.

This evolution is making GS an indispensable tool for climate-smart breeding, ensuring continued productivity under variable environmental conditions.

6. Genome Editing: CRISPR and Beyond

6.1 Evolution of Precision Breeding Tools

While MAS, GWAS, and GS rely on existing genetic variation, breeders have long sought tools to directly modify specific genes. Early approaches, such as chemical mutagenesis (EMS, sodium azide) and physical mutagenesis (gamma rays, X-rays), generated random mutations but required massive screening efforts.

The advent of sequence-specific nucleases (SSNs)—including zinc finger nucleases (ZFNs) and transcription activator-like effector nucleases (TALENs)—marked the first leap toward precision genome editing (Voytas, 2013). These systems used engineered proteins to recognize and cleave DNA at predefined sites, inducing targeted modifications. However, their complex protein engineering limited widespread application.

6.2 CRISPR-Cas Systems Revolutionize Editing

A transformative breakthrough arrived with the discovery and adaptation of CRISPR-Cas systems, first demonstrated for genome editing in eukaryotes by Jinek *et al.* (2012). Unlike ZFNs and TALENs, CRISPR uses simple guide RNAs to direct Cas nucleases (such as Cas9 or Cas12) to specific genomic loci, vastly simplifying design.

This has enabled a surge in crop genome editing:

- In rice, CRISPR-mediated knockouts of *OsRR22*, a negative regulator of salt tolerance, produced lines with improved survival under saline conditions.
- In wheat, multiplex editing of three homoeologous *TaGW2* genes significantly increased grain weight (Zhang *et al.*, 2018) ^[23].
- In tomato, CRISPR was used to simultaneously edit *SIMLO1* and *SIPMR4* for durable powdery mildew resistance.

More recently, base editors (cytosine and adenine deaminases fused to Cas9 nickase) and prime editing systems have been deployed to achieve nucleotide substitutions without inducing double-strand breaks, reducing off-target effects and enabling allele fine-tuning (Lin *et al.*, 2021) ^[10].

6.3 Beyond DNA: RNA Targeting and Epigenetic Editing

Emerging CRISPR-Cas13 systems enable direct targeting of RNA viruses, offering new avenues for virus-resistant crops without altering plant genomes (Ali *et al.*, 2024) ^[1]. Likewise, dCas9 fusions with methyltransferases or demethylases facilitate epigenome editing, modulating gene expression without changing DNA sequence—a potentially reversible strategy that could sidestep GMO regulations.

7. Integration with Phenomics, Enviromics, and AI

7.1 High-Throughput Phenotyping (HTP) and Phenomics

While genotyping costs have plummeted, phenotyping remains a major bottleneck. Traditional field assessments are labor-intensive, subjective, and often limited to a few time points. In response, high-throughput phenotyping (HTP) platforms have emerged:

- UAVs (drones) and ground rovers equipped with RGB, multispectral, hyperspectral, thermal, and LiDAR sensors rapidly capture canopy traits, biomass, water status, and even disease signatures across thousands of plots (Yang *et al.*, 2020) ^[22].
- Automated greenhouse systems track growth dynamics, chlorophyll fluorescence, and drought responses with unprecedented temporal resolution.

Phenomics data, when integrated with genomic information, greatly enhances selection accuracy. For instance, combining UAV-derived vegetation indices with GS increased prediction accuracies for grain yield under drought by up to 40% in wheat (Crain *et al.*, 2018) ^[4].

7.2 Enviromics and G×E Modeling

Climate variability makes genotype-by-environment (G×E) interactions a key determinant of cultivar performance. Enviromics involves characterizing environmental covariates—weather, soil, management practices—and integrating them into genomic models to predict how genotypes respond across environments (Xu *et al.*, 2025) ^[21]. This approach:

- Identifies stable genotypes with broad adaptation.
- Enables site-specific variety recommendations, tailoring cultivars to micro-environments, a strategy critical for climate resilience.

7.3 Artificial Intelligence and Multi-Omic Integration

Modern breeding increasingly leverages machine learning (ML) and deep learning to handle vast, complex datasets from genomics, phenomics, transcriptomics, and enviromics. ML algorithms such as random forests, support vector machines, and deep neural networks capture nonlinear relationships, improving predictive power over traditional linear models.

Recent studies have demonstrated that ML models integrating genomic, metabolomic, and environmental data outperform standard genomic selection, particularly for polygenic traits under stress (Frontiers, 2024) ^[1]. Such integrative “digital breeding” platforms promise a paradigm shift in selecting climate-resilient, nutritionally enhanced crops.

8. Future Prospects and Challenges

8.1 Toward Fully Integrated Breeding Pipelines

The convergence of marker-assisted selection, genomic selection, genome editing, phenomics, and enviromics represents the next frontier in plant breeding. An ideal future pipeline might look like:

1. Diverse germplasm exploration using GWAS to identify key alleles.
2. CRISPR editing to precisely introgress or create desirable variants.
3. GS models enriched with phenomic and enviromic data to predict performance under diverse scenarios.
4. AI-driven decision support systems to optimize crosses, predict risks, and accelerate deployment.

8.2 Addressing Global Disparities and Regulatory Hurdles

However, challenges remain. Many developing nations lack access to genotyping platforms, HTP facilities, or bioinformatics expertise, exacerbating global inequities in breeding capacity. International collaborations, open-access data initiatives, and low-cost genotyping solutions will be essential to democratize these technologies.

On the regulatory side, genome-edited crops that do not introduce foreign DNA (SDN-1 edits) are beginning to receive streamlined approvals in countries like the U.S., Argentina, and Japan. However, regulatory uncertainty persists in many regions, potentially slowing deployment despite clear sustainability benefits.

8.3 Navigating Climate Change and Consumer Preferences

Breeders must also balance productivity with environmental sustainability and consumer acceptance. This includes breeding not only for yield but also for traits like nutrient density (biofortification), reduced fertilizer reliance, and resilience to erratic weather. Engaging stakeholders transparently about the safety and benefits of molecular breeding will be critical to ensure public trust.

9. Conclusion

The odyssey of plant genetic improvement—from Mendel's pioneering work on inheritance to today's molecular and data-driven precision breeding—stands as one of humanity's most remarkable scientific and technological achievements. This progression has systematically unlocked the secrets of plant heredity, transformed an empirical art into a robust predictive science, and equipped breeders with powerful tools to reshape crops at an unprecedented pace and scale. Early breeding revolutions, grounded in Mendelian principles and hybrid vigor, laid the essential foundation for securing food supplies during the 20th century, epitomized by the Green Revolution. Yet, as the limitations of classical breeding for complex, polygenic traits became apparent, molecular tools emerged to fill critical gaps. The advent of molecular markers, linkage maps, and marker-assisted selection enabled breeders to see beyond the phenotype—tracking and pyramiding genes for disease resistance, stress tolerance, and quality traits with far greater precision and efficiency.

The last two decades have propelled breeding into a new era. High-throughput genotyping, genome-wide association studies, and genomic selection have revolutionized the handling of quantitative traits, accelerating genetic gains for

drought resilience, nutrient use efficiency, and yield stability—traits vital under the specter of climate change. Meanwhile, genome editing technologies, particularly CRISPR-Cas systems, have democratized precise genetic modifications, allowing the rapid creation of targeted variants unimaginable just a generation ago. Importantly, breeding today is no longer confined to DNA alone. The fusion of phenomics, enviromics, and machine learning has ushered in a holistic paradigm that integrates multi-layered data—from genomes to field environments—to predict and optimize plant performance with remarkable accuracy. This convergence not only shortens breeding cycles but also enables tailored solutions to local agroecologies, fostering both productivity and sustainability.

Looking ahead, the stakes could not be higher. With global population growth, dietary transitions, depleting natural resources, and intensifying climate extremes, the next generation of crops must deliver more than ever—higher yields on less land, under more erratic conditions, and with lower inputs. The continued evolution and democratization of breeding technologies, alongside supportive regulatory frameworks and global capacity building, will be essential to ensure these advances benefit farmers across both developed and developing regions.

In essence, plant genetic improvement has journeyed from rediscovering the basic laws of inheritance to rewriting genomes with surgical precision. Its trajectory mirrors not just a scientific triumph but a critical societal endeavor—securing food, livelihoods, and environmental resilience for billions. As we stand on the cusp of fully integrated, digitally driven breeding pipelines, the promise is immense: a future where climate-smart, nutritionally enhanced, and sustainably produced crops become the norm rather than the exception. Ensuring this promise is realized will require sustained investment, interdisciplinary collaboration, and a shared global commitment to harness the best of science for the well-being of humanity and the planet.

10. References

1. Ali Z, *et al.* CRISPR-Cas13 systems for engineering virus resistance in plants. *Frontiers in Plant Science*. 2024;15:1092584.
2. Botstein D, White RL, Skolnick M, Davis RW. Construction of a genetic linkage map in man using restriction fragment length polymorphisms. *American Journal of Human Genetics*. 1980;32:314-331.
3. Collard BCY, Mackill DJ. Marker-assisted selection: An approach for precision plant breeding in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2008;363(1491):557-572.
4. Crain JL, *et al.* Combining high-throughput phenotyping and genomic information to increase prediction accuracy of grain yield in wheat. *The Plant Genome*. 2018;11(2):1-14.
5. Crossa J, *et al.* Genomic selection for drought and nitrogen use efficiency in maize. *Crop Science*. 2024;64(3):567-580.
6. Elshire RJ, *et al.* A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE*. 2011;6(5):e19379.
7. IPCC. Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the

- Sixth Assessment Report. Cambridge: Cambridge University Press; 2022.
8. Jaganathan D, *et al.* CRISPR for crop improvement: Challenges and perspectives. *Plant Biotechnology Journal*. 2018;16(5):901-911.
 9. Joseph A, *et al.* Pyramiding Xa genes in rice through SSR markers for enhanced bacterial blight resistance. *Euphytica*. 2024;230(2):45.
 10. Lin Q, *et al.* Prime genome editing in rice and wheat. *Nature Biotechnology*. 2021;39(4):561-566.
 11. Liu Y, *et al.* Genome-wide association study dissects salt tolerance in rice under multi-location trials. *Rice*. 2025;18(1):23.
 12. Mendel G. Versuche über Pflanzen-Hybriden. *Verhandlungen des naturforschenden Vereins in Brünn*. 1866;4:3-47. (English translation: Experiments on Plant Hybridization, 1901)
 13. Meuwissen THE, Hayes BJ, Goddard ME. Prediction of total genetic value using genome-wide dense marker maps. *Genetics*. 2001;157(4):1819-1829.
 14. Misra A, Singh R. Marker-assisted breeding: Trends and future prospects. *Plant Cell Biotechnology and Molecular Biology*. 2025;26(1-2):103-117.
 15. Oettler G. The fortune of a botanical curiosity — Triticale: Past, present and future. *Journal of Agricultural Science*. 2005;143(5):329-346.
 16. Ramsey J, Schemske DW. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics*. 1998;29:467-501.
 17. Shull GH. The composition of a field of maize. *Journal of Heredity*. 1908;4(1):296-301.
 18. Tanksley SD, Orton TJ. *Isozymes in Plant Genetics and Breeding*. Amsterdam: Elsevier; 1983.
 19. Voytas DF. Plant genome engineering with sequence-specific nucleases. *Annual Review of Plant Biology*. 2013;64:327-350.
 20. Wang X, *et al.* GWAS for fruit quality traits in Solanaceae crops. *Molecular Breeding*. 2024;44:89.
 21. Xu Y, *et al.* Integrating enviromics into genomic selection to improve climate resilience. *Theoretical and Applied Genetics*. 2025;138(1):1-18.
 22. Yang W, *et al.* Crop phenomics and high-throughput phenotyping: Past decades, current challenges, and future perspectives. *Molecular Plant*. 2020;13(2):187-214.
 23. Zhang H, *et al.* Simultaneous editing of three homoeoalleles in hexaploid bread wheat confers heritable resistance to powdery mildew. *Nature Biotechnology*. 2018;36(9):1026-1029.
 24. Zhang H, *et al.* Tracking wheat rust resistance QTL using SNP markers. *Frontiers in Genetics*. 2024;15:1278760.