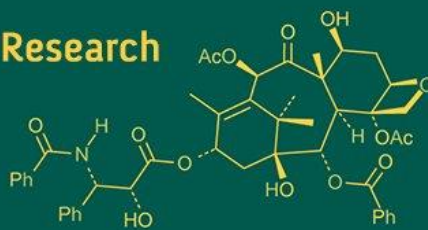


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## The evolution of plant breeding: Genetic foundations and future directions

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### Abstract

Plant breeding has progressed from empirical selection to precision design powered by quantitative genetics, multi-omics, artificial intelligence, and genome editing. This review traces the historical arc—from Mendelian inheritance and early quantitative theory to molecular markers, genome-wide association studies (GWAS), genomic selection (GS), and pangenomes—highlighting how foundational genetic principles have been repeatedly retooled by new technologies. We synthesize recent advances in speed breeding, doubled haploids and haploid induction, high-throughput phenotyping, and CRISPR-based base/prime editing, and we examine emerging paradigms such as de novo domestication and epigenetic breeding. We conclude with a forward look at systems-level breeding that integrates genotype-phenotype-environment (G×P×E) modeling, climate resilience, nutrition, and equity-centered deployment. Throughout, we emphasize recent literature (2023-2025) and identify research priorities to accelerate genetic gain while safeguarding biodiversity and societal trust.

**Keywords:** Plant breeding, quantitative genetics, genomic selection, pangenome, high-throughput phenotyping, speed breeding, CRISPR, base editing, prime editing, haploid induction, de novo domestication, epigenetic breeding, climate resilience

### 1. Introduction

Plant breeding is the art and science of creating new plant varieties with desirable traits, and its evolution reflects the broader progress in genetics, technology, and agricultural priorities. Initially rooted in simple visual selection practiced by early farmers thousands of years ago, the field gained a predictive foundation with the rediscovery of Mendel's laws at the turn of the 20th century. This enabled systematic hybridization and selection, allowing breeders to combine and fix beneficial traits more effectively.

The integration of quantitative genetics in the mid-20th century transformed plant breeding from a primarily observational practice into one guided by statistical principles. Concepts such as heritability, genetic variance partitioning, and selection intensity provided mathematical frameworks to predict genetic gain, forming the basis of modern breeding programs. The advent of molecular markers in the late 20th century further revolutionized the field, enabling marker-assisted selection and the precise tracking of genomic regions associated with complex traits.

Over the last two decades, advances in sequencing technology, bioinformatics, and automation have driven an era of genomic selection, where thousands of markers spread across the genome are used to predict the performance of breeding lines. Coupled with speed breeding, high-throughput phenotyping, and genome editing tools such as CRISPR, plant breeding is shifting from trial-and-error improvement toward intentional design. This transformation is not only enhancing the efficiency of crop improvement but also aligning breeding goals with contemporary challenges, including climate resilience, resource-use efficiency, and nutritional security.

Today, the discipline stands at a critical juncture, where foundational genetic knowledge meets powerful technological innovation. The convergence of pangenomics, artificial intelligence, epigenetics, and synthetic biology is unlocking new possibilities, from editing wild relatives to rapidly develop climate-adapted cultivars to re-domesticating crops with

entirely new trait combinations. The future of plant breeding will depend on how effectively these innovations are integrated into practical, equitable, and sustainable agricultural systems, balancing productivity with biodiversity conservation, farmer accessibility, and global food security.

## 2. Genetic foundations that still matter

Plant breeding innovations, regardless of technological sophistication, continue to rely on genetic principles discovered more than a century ago. These foundations provide the framework through which molecular tools, predictive analytics, and genome editing are translated into practical varietal improvement.

### 2.1 Mendelian and quantitative genetics

Mendelian genetics remains the cornerstone for understanding trait inheritance, guiding controlled crosses, and tracking allelic segregation in breeding populations. While single-gene traits follow predictable Mendelian ratios, most agronomic traits—such as yield, stress tolerance, and quality—are quantitative, controlled by multiple loci with small additive or interacting effects. The predictive power of breeding therefore depends on the accurate estimation of genetic variance components: additive (the primary driver of long-term gain), dominance (critical for hybrid vigor), and epistasis (gene-gene interactions that can amplify or mask effects).

Heritability, both in the broad and narrow sense, serves as a key predictor of the response to selection. High heritability indicates that observed phenotypic differences are largely due to genetic differences, allowing selection to be more effective. However, heritability is context-dependent, varying across environments and management practices. Thus, modern breeding increasingly considers genotype  $\times$  environment (G $\times$ E) interactions, employing multi-environment trials to capture performance stability and plasticity.

Advanced modeling integrates molecular markers and environmental covariates, enabling the estimation of genomic-estimated breeding values (GEBVs). Training population size, genetic relatedness to selection candidates, marker density, and statistical models profoundly influence prediction accuracy (Alemu *et al.*, 2024) <sup>[2]</sup>. Recent progress focuses on incorporating non-additive effects, epistasis, and dynamic G $\times$ E patterns, often supported by functional genomics data, such as gene expression, regulatory networks, and epigenetic profiles, derived from pangenomes and transcriptomic resources (Crossa *et al.*, 2025) <sup>[8]</sup>. These developments transform classical breeding theory into data-rich, dynamic prediction systems capable of forecasting performance in yet-unseen environments.

### 2.2 Mapping to prediction: QTL, GWAS, and GS

The transition from mapping to prediction represents a paradigm shift in plant breeding. Early approaches centered on identifying quantitative trait loci (QTL) through biparental populations and linkage analysis, allowing breeders to tag regions of the genome linked to specific traits. Genome-wide association studies (GWAS) expanded this scope to diverse germplasm, identifying loci associated with traits by exploiting historical recombination events.

While QTL mapping and GWAS remain valuable for dissecting trait architecture, especially for monogenic or oligogenic traits, genomic selection (GS) has emerged as a powerful approach for complex traits influenced by many loci with small effects. GS does not aim to pinpoint individual QTL; instead, it estimates the combined effects of all genome-wide markers simultaneously to predict the total genetic merit of untested individuals.

Best practices in GS involve careful cross-validation strategies, training population optimization, and model selection, ensuring robustness across genetic backgrounds and environments. Multi-trait and multi-environment GS models leverage correlations among traits and across sites, increasing prediction accuracy and allowing simultaneous improvement of multiple objectives. Documented outcomes include increased realized selection intensity, shortened breeding cycles, and enhanced genetic gain per unit of time (Alemu *et al.*, 2024; Crossa *et al.*, 2025) <sup>[2, 8]</sup>. Importantly, integrating GS with speed breeding and doubled haploid production further accelerates varietal development, reinforcing the synergy between statistical prediction and experimental design.

### 3. The diversity substrate: pangenomes and graph references

The utility of genetic tools depends on the diversity available to breeding programs. Traditional reliance on a single reference genome has been shown to underestimate the extent of variation within species. Many important agronomic traits are controlled by structural variations, gene presence-absence polymorphisms, or copy-number changes absent from the reference genome.

Pangenomes, which aggregate the entire complement of genes present within a species (the “core” and “dispensable” genome), capture this hidden variation. Graph-based genome references further enhance this by representing multiple haplotypes and structural variants in a single framework, improving variant discovery, read mapping, and haplotype phasing. These approaches have already demonstrated significant impacts in cereals, legumes, and minor crops, where access to rare alleles has led to breakthroughs in stress resilience and quality improvement (He *et al.*, 2024) <sup>[15]</sup>.

Recent advances include “super-pangenomes” that integrate wild relatives and even multiple species, creating a reservoir of alleles for orphan crop improvement and novel trait assembly (Schreiber *et al.*, 2024; He *et al.*, 2024; He *et al.*, 2025) <sup>[20, 15, 16]</sup>. Perspectives highlight that while pangenomics has “come of age,” its routine application in breeding still faces challenges, including data standardization, computational infrastructure, and breeder-friendly analytical pipelines (Eisenstein, 2023) <sup>[9]</sup>.

**3.1 Implications for breeders:** To maximize the impact of pangenomics, breeding programs should integrate graph/pangenome-aware GWAS and GS pipelines, implement haplotype-based selection strategies, and design crossing schemes that leverage dispensable or stress-responsive genes. Such integration is particularly relevant for improving stress tolerance, nutritional quality, and niche adaptation—traits often enriched in structural variants and underutilized genomic regions.

#### 4. Making time an ally: Speed breeding and haploid technologies

##### 4.1 Speed breeding (SB)

Speed breeding accelerates the development of new varieties by compressing the time required for each generation cycle. Light intensity, photoperiod, and temperature-optimized protocols—implemented in controlled-environment growth chambers, greenhouses, and vertical farming systems—allow crops to complete reproductive cycles in as little as 6-8 weeks. By synchronizing with genomic selection (GS) pipelines, breeders can advance multiple generations per year (3-6 in several cereals and legumes) while applying data-driven selection pressure at each step (He *et al.*, 2024; Williams *et al.*, 2024; Ahtisham, 2025) <sup>[15, 3]</sup>. New approaches extend SB beyond controlled conditions, leveraging natural cues such as temperature and photoperiod manipulation in field environments (Gurumurthy *et al.*, 2024) <sup>[11]</sup>. These strategies combine accelerated turnover with operational scalability, increasing annual selection intensity and enhancing the rate of genetic gain.

##### 4.2 Doubled haploids and haploid induction (HI)

Doubled haploid (DH) technology remains a gold standard for rapid fixation of desirable allelic combinations. Through chromosome doubling of haploid embryos, fully homozygous lines are obtained in a single generation, bypassing years of inbreeding. Traditional systems rely on *in vivo* haploid induction using donor lines carrying specific genetic factors, but breakthroughs in centromere engineering (CENH3-mediated haploid induction) are expanding the method's applicability across crop species. Recent work highlights parental-factor-mediated and BoCENH3-based induction systems, demonstrating their potential to streamline both hybrid and cytoplasmic male sterile (CMS) line development (Song *et al.*, 2024) <sup>[21]</sup>. A notable advance in Brassica oleracea demonstrates one-step CMS line creation via BoCENH3-mediated paternal haploid induction, effectively linking HI with hybrid seed production (Han *et al.*, 2024) <sup>[12]</sup>. Forward-looking analyses project wider crop coverage, higher induction efficiencies, and more flexible breeding pipelines using gene-edited HI lines that can be customized to target specific germplasm (Zhang *et al.*, 2025) <sup>[26]</sup>.

#### 5. Phenotyping at scale: UAVs, hyperspectral imaging, and analytics

High-throughput phenotyping (HTP) platforms are transforming how breeders observe and select for complex traits. Unmanned aerial vehicles (UAVs), piloted aircraft, and ground-based rovers now carry RGB, multispectral, hyperspectral, and LiDAR sensors capable of capturing canopy temperature, biomass, stress indices, and yield-related traits with high spatial and temporal resolution. These phenomic datasets feed directly into GS models, increasing the accuracy of predicting genetic merit, particularly for drought tolerance, nutrient-use efficiency, and yield components (Bongomin *et al.*, 2024; Alves *et al.*, 2024; Fu *et al.*, 2024; Mérida García *et al.*, 2024; Wang *et al.*, 2024) <sup>[5, 4, 10, 18, 2]</sup>. The next frontier is adaptive, near-real-time data assimilation: active learning loops where acquisition strategies dynamically adjust based on model uncertainty, enabling more efficient resource allocation and faster convergence on superior genotypes.

#### 6. Precision rewriting: CRISPR and next-gen editors

Genome editing has moved from proof-of-concept experiments to practical trait deployment. CRISPR/Cas systems—including Cas9 and Cas12 variants—are now joined by base and prime editors that allow precise nucleotide changes without generating double-strand breaks. Agricultural pipelines increasingly leverage multiplex editing to modify domestication traits, nutritional quality, disease resistance, and abiotic stress tolerance simultaneously (Chen *et al.*, 2024; Li *et al.*, 2024) <sup>[6, 17]</sup>. Early field trials, such as improved sweetness in tomato and yield gains in wheat, highlight the practical impact of these technologies as they progress through regulatory and commercialization pipelines. Annual reviews track diversification of Cas effectors, advances in specificity engineering, and plant-optimized editor architectures that expand the editing toolbox (Xu *et al.*, 2024) <sup>[24]</sup>. Integration of genome editing with speed breeding and DH technologies further compresses the edit-to-variety timeline, turning multi-year programs into streamlined, iterative cycles.

**6.1 Design breeding and de novo domestication:** A new paradigm is emerging where editing targets wild relatives and landraces to introduce key domestication traits while preserving adaptive resilience. This de novo domestication approach effectively creates “new crops,” combining stress tolerance with consumer-preferred qualities (Zhang *et al.*, 2023; Rogo *et al.*, 2024) <sup>[25, 19]</sup>. However, the release of edited wild species into agricultural systems raises ecological and weediness concerns, underscoring the need for thoughtful regulatory frameworks and risk assessments that balance innovation with environmental stewardship.

#### 7. Beyond DNA sequence: epigenetic and epibreeding strategies

Epigenetic mechanisms provide an additional layer of heritable phenotypic regulation beyond the DNA sequence itself. Stress memory, paramutation, histone modification, and small RNA-guided DNA methylation are increasingly recognized as drivers of variation that can persist across generations. Such mechanisms allow plants to “remember” prior exposure to environmental cues, influencing flowering time, stress resilience, and even hybrid vigor without altering the underlying nucleotide sequence. Reviews synthesize how epigenetic variation may be harnessed for heterosis exploitation, resilience under climate stress, and yield stability (Abdulraheem *et al.*, 2024; Chen, 2025; Wu *et al.*, 2025) <sup>[1, 7, 23]</sup>. However, challenges remain: stability of epigenetic marks under field conditions, predictability of trait inheritance, and methods for precise manipulation. Emerging pipelines integrate epigenomic profiling with genomic selection (epigenomic selection), leveraging methylation maps, chromatin accessibility data, and small RNA networks as predictive covariates in breeding models.

#### 8. AI-augmented breeding: data fusion and decision support

Artificial intelligence (AI) is reshaping breeding pipelines through integration of heterogeneous data streams. Deep learning models now process genomic, phenomic, environmental, and management data to predict performance across multiple environments. Mechanistic crop models are being embedded into decision-support platforms, enabling breeders to explore multi-objective



ideotype design and prioritize lines with superior stability. Genomic prediction increasingly incorporates non-linear kernels and AI-based feature engineering to capture epistatic interactions and rare allelic effects. Industrial deployments link AI-assisted CRISPR target selection, multiplex edit optimization, and active variant prioritization to accelerate trait discovery and advancement, while public sector programs experiment with Bayesian optimization loops where phenotyping is directed by model uncertainty (Alemu *et al.*, 2024; Crossa *et al.*, 2025) [2, 8]. Model architecture, training-set composition, and data curation have emerged as dominant factors influencing realized genetic gain, highlighting the importance of transparent pipelines and collaborative data sharing.

### 9. Climate-smart and nutrition-forward breeding

Breeding priorities are shifting toward climate resilience and nutritional security. Modern pipelines increasingly focus on heat, drought, flooding, salinity, and pest variability while maintaining or improving nutritional quality. Pangenome-guided allele mining has identified previously hidden diversity in stress tolerance loci, including key regulators of ion transport, ABA signaling, cuticular wax deposition, and root system architecture. Editing of these “stress hubs” accelerates the assembly of multi-stress-tolerant ideotypes. Simultaneously, consumer-facing traits—including micronutrient density, reduced antinutritional factors, and improved flavor profiles—are regaining prominence. Case studies, such as enhanced sweetness in tomato via targeted gene editing, illustrate the potential for traits that combine agronomic and sensory value. Transparent communication and participatory breeding approaches may improve societal acceptance of such innovations, aligning them with sustainability and health goals.

### 10. Responsible innovation: regulation, equity, and biodiversity

The rapid pace of plant breeding innovation necessitates equally agile and responsible governance. Regulatory frameworks for gene-edited crops remain heterogeneous, with several jurisdictions adopting product-based evaluations, particularly when no foreign DNA is introduced. Best practices across contexts emphasize trait-linked environmental risk assessments, including evaluation of weediness potential in *de novo* domestication candidates and management strategies for resistance durability. Equity considerations include benefit-sharing with custodians of genetic resources, support for smallholder access, and capacity-building for underrepresented regions. Conservation of crop wild relatives and on-farm genetic diversity remains essential for long-term resilience and sustained genetic gain (Nature Plants Editorial, 2023). A balanced approach—protecting ecosystems while enabling innovation—will define the trajectory of next-generation plant breeding.

### 11. Conclusion

Plant breeding has traversed an extraordinary journey from ancient farmer-led selection to sophisticated, data-driven crop design. Its evolution reflects the continual interplay of foundational genetics, technological innovation, and shifting agricultural priorities. Today, breeders possess an unprecedented toolbox: high-resolution genomics, predictive analytics, speed breeding, genome editing, and

even epigenetic manipulation. These tools not only accelerate the pace of genetic gain but also broaden the scope of traits that can be addressed—yield stability, climate resilience, nutritional enhancement, and resource efficiency. The future of plant breeding lies in integration. Combining genomic, epigenomic, and phenomic data with mechanistic models, artificial intelligence, and climate projections will enable systems-level decision-making that accounts for genotype-by-environment-by-management interactions. Equally critical will be ensuring equitable access, ethical deployment, and biodiversity stewardship. Public-private collaborations, capacity building in developing regions, transparent regulatory frameworks, and farmer-centric innovation pathways will determine whether the full promise of next-generation breeding translates into global food and nutritional security.

In an era defined by climate uncertainty, growing populations, and evolving consumer preferences, plant breeding remains a cornerstone of agricultural resilience and sustainability. Its continued evolution must balance speed with responsibility, precision with diversity, and innovation with trust. If executed thoughtfully, the next decades will see not only more productive crops but also more resilient food systems—capable of nourishing people and the planet alike.

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