Journal of Cereal Research
Volume 18 (1): 25-53
Homepage: http://epubs.icar.org.in/ejournal/index.php/JWR
Review Article

From Domestication to Genome Editing: The Evolution and Future of Barley Breeding

Madhu Patial[1†*], Vandana Thakur[2†], Santosh Kumar Bishnoi[3], Prem Lal Kashyap[3], Dharam Pal[1] and Kallol Kumar Pramanick[1]

[1] *ICAR-IARI, Regional Station, Tutikandi Centre, Shimla (H.P), India*
[2] *CSK Himachal Pradesh Agricultural University, Palampur, Palampur-176062, India*
[3] *ICAR-Indian Institute of Wheat and Barley Research, Karnal, India*
[†] *Contributed equally to this work*

Article history:
Received: 25 Mar., 2026
Revised: 29 Apr., 2026
Accepted: 29 Apr., 2026

Citation:
Patial M, V Thakur, SK Bishnoi, PL Kashyap, D Pal and KK Pramanick. 2026. From Domestication to Genome Editing: The Evolution and Future of Barley Breeding. *Journal of Cereal Research* ***18 (1):*** *25-53. http://doi.org/10.25174/2582-2675/2026/177379*

****Corresponding author:***
E-mail: mcaquarian@gmail.com

Abstract

Barley is one of the world's most important cereal crops, with critical roles in malting, animal feed, and human nutrition across diverse agro-ecological regions. Over the past century, barley breeding has evolved from phenotype-based selection to a highly data-driven technologies enabled by genomics and precision breeding. Recent phylogeography evidence indicated that domesticated barley possesses a mosaic genomic ancestry derived from multiple *Hordeum vulgare* ssp. *spontaneum* populations across the Fertile Crescent, Eastern Iran, Central Asia, and the Tibetan Plateau, challenging earlier single-origin domestication models. This genetic complexity highlights the continuing importance of wild and landrace as reservoirs of alleles for abiotic stress tolerance, disease resistance, and grain quality. It severs as a diploid model of the *Triticeae* tribe with relatively small genome (~5.3 Gb), resolved to near telomere-to-telomere continuity through the Morex V3 reference assembly. It has accelerated gene discovery, structural variant characterization, and the development of molecular breeding tools. This review synthesizes current knowledge on barley phylogeography and domestication, genomic architecture, breeding objectives, and technological milestones, with emphasis on modern barley improvement strategies including genomic selection, speed breeding, and genome editing. We also discuss future prospects for climate-resilient barley improvement in the era of artificial intelligence–assisted breeding and CRISPR-based precision genetics.

Key words: *Hordeum vulgare,* mosaic origins, *Triticeae* model system, doubled haploidy, marker-assisted selection, barley reference genome, genome editing

1. Introduction

Barley (*Hordeum vulgare* L.) is among the earliest domesticated cereal crops, with archaeological and genomic evidence indicating its domestication approximately 10,000 years ago in the Fertile Crescent from its wild progenitor *H. vulgare* ssp. *spontaneum.* Following domestication, barley spread across Eurasia during the early expansion of agriculture, adapting to diverse agro-climatic conditions and farming systems (Lister *et al.*, 2018). Modern molecular phylogeographic studies support a mosaic or polyphyletic model of domestication. This suggests that barley was not domesticated in just one location in the Levant; instead, several wild populations from different regions might have contributed to its domestication (Allaby, 2015; Poets *et al.*, 2015).

Barley is a diploid species (2n = 2x = 14) with a genome size of about 5.1 Gb. It serves as an important model for genetic and genomic studies within the *Triticeae* tribe (Sato, 2020). The high-quality barley reference genome assemblies, particularly those derived from the cultivar 'Morex', together with advances in long-read sequencing and pan-genome resources, has enhanced the understanding of both gene-rich and repetitive regions of the barley genome. These genomic resources have facilitated the identification of structural variation, gene presence/absence polymorphisms and regulatory elements for phenotypic diversity. Consequently, they are increasingly being exploited for crop improvement and breeding applications (Mascher *et al*., 2016; Jayakodi *et al*., 2024).

Globally, barley production has remained relatively stable amid climatic and geopolitical fluctuations, with production of approximately 140–150 million tonnes (FAO, 2024). Major barley producers include the European Union, Russia, Australia, Canada and Ukraine reflecting the crop's adaptability across a wide range of environments. In India, barley is primarily cultivated as a Rabi crop (winter season) in the North-Western plains and adjoining regions, with production of approximately 1.69 million tonnes from about 0.55 million hectares area and average productivity exceeding 3.0 t/ha during 2022-23 (FAO, 2024). Main barley production states include Rajasthan, followed by Uttar Pradesh, Haryana, Punjab and Madhya Pradesh, where barley is valued for its low water requirement and suitability to marginal and rain fed conditions.

Historically, barley has been used as food source (flat breads, porridges and soups), as a feed-grain for livestock and as the principal raw material for malting and brewing (Ullrich, 2011; Patial *et al*., 2023b). Therefore, current breeding programmes focus on multiple objectives that include grain yield and yield stability, resistance to major diseases (rusts, powdery mildew, net blotch, spot blotch, viral diseases), tolerance to abiotic stresses (drought, salinity, heat, cold), as well as improved end use quality for malting, feed and food markets. The wide genetic diversity preserved in landraces, wild relatives and specialized germplasm collections continues to provide novel alleles for these traits and remains central to future genetic gain (Poets *et al*., 2015). Barley breeding has pioneered key innovations in plant improvement, from early mutagenesis experiments by Stadler (1928) that led to the development of radiation-induced variety like 'Pallas' (Gustafsson *et al*., 1971); to doubled haploid technology developed by Kasha and Kao (Kasha and Kao, 1970), which achieves complete homozygosity in a single generation and shortens years of breeding cycles. Early hybrid systems, led to the development of cultivar 'Hembar' using balanced tertiary trisomics, demonstrated the feasibility of exploiting heterosis in barley despite its self-pollinating nature (Ramage and Ramage, 1965). During the 19th-century systematic mass selection in the development of world's first malt barley variety 'Chevalier' (or 'Chevallier') in Great Britain, which spread from a single farm and reached world-wide dominance – and thus marked the shift from domestication to improved selection programs (Hagenblad and Leino, 2022). Progress in barley improvement accelerated during the twentieth century with the introduction of semi-dwarf germplasm, with lodging resistance and high harvest index that enabled the development of cultivars adapted to diverse agro-ecological environments. Reduced-height barley mutants have been widely utilized in breeding programs. For instance, the cultivars Diamant and Triumph, derived from mutants selected in the M_2 generation of cv. Valticky following X-ray treatment, served as donors for nearly 150 cultivars developed in Europe during the twentieth century (Kuczy ska *et al*., 2013). At present, cultivars carrying the *sdw1/denso* locus occur in the pedigree of most modern barley cultivars bred globally (Dahleen *et al*., 2005). Adding to these advances, recent decade have witnessed the integration of modern genomic approaches, including high-quality reference genome assemblies such as those derived from the cultivar 'Morex', quantitative trait locus (QTL) mapping, genome-wide association studies (GWAS), genomic selection, speed breeding and genome editing technologies for targeted trait improvement (Ullrich, 2011; Mascher *et al*., 2021). Together, these genomic developments have transformed barley breeding into a precision-driven breeding, enabling the precise identification and improvement of genes underlying agronomic performance and resistance traits. Therefore, in the current era, barley functions not only as a significant global crop but also as a diploid model for studying the genetics of more complex *Triticeae* species, such as wheat, offering substantial potential for developing

climate-resilient agricultural systems under increasing environmental challenges (Poets *et al*., 2015).

2. Phylogeography and the Mosaic Origins of Barley Domestication

The domestication of barley from a wild grass into one of the important cereal represents a complex interaction between natural evolutionary processes and sustained human selection. Its wild progenitor, *Hordeum vulgare* ssp. *spontaneum*, is distributed across a broad geographic range extending from the Levant (modern-day Turkey, Syria, Jordan, and Israel) through the Zagros Mountains, the eastern Iranian Plateau and into Central Asia (Jakob *et al*., 2014). Early "Levantine-centric" hypotheses proposed a single domestication event in the western Fertile Crescent approximately 10,500 years ago, supported by archaeological findings from sites such as Abu Hureyra and Jericho and early molecular analyses of nucleotide diversity in barley populations (Morrell and Clegg, 2007; Morrell *et al*., 2014). However, advances in molecular phylogeography and population genomics use haplotype-based analyses and whole-genome sequencing to trace domestication, adaptation and genetic diversity in modern barley. These studies now support a more complex mosaic (polycentric) model of domestication involving multiple wild populations across different regions (Fuller *et al*., 2011) (Fig 1).

Genome-wide analyses of more than 250 domesticated barley accessions reveal distinct genetic differentiation between Asian landraces and those from Europe and North Africa, indicating at least two major domestication or introgression events (Fang *et al*., 2014). Evidence suggests an initial domestication occurred in the western Fertile Crescent followed by additional domestication or diversification processes occurring approximately 1,500–3,000 km farther east, possibly in the Hindu Kush or Eastern Iranian Plateau. In barley, there is a clear East–West pattern in key domestication genes that control how easily seeds shatter. Western barley populations mostly carry the *btr1* allele, while eastern populations tend to have *btr2* (Gao *et al*., 2024). This difference played a crucial role in domestication, allowing farmers to harvest more efficiently by minimizing seed shattering (Pourkheirandish *et al*., 2015).

Additional evidence points to the Qinghai–Tibetan Plateau as a potential secondary diversification center, where unique wild populations were identified using Diversity Array Technology (DArT) markers–contributed to the evolution of hull-less (naked) barley adapted to high-altitude environments. Transcriptomic and genomic analyses have revealed that genomic origin of modern cultivated barley is derived from wild-barley genotypes in the Fertile Crescent (mainly in chromosomes 1H, 2H, and 3H) and Tibet (mainly in chromosomes 4H, 5H, 6H, and

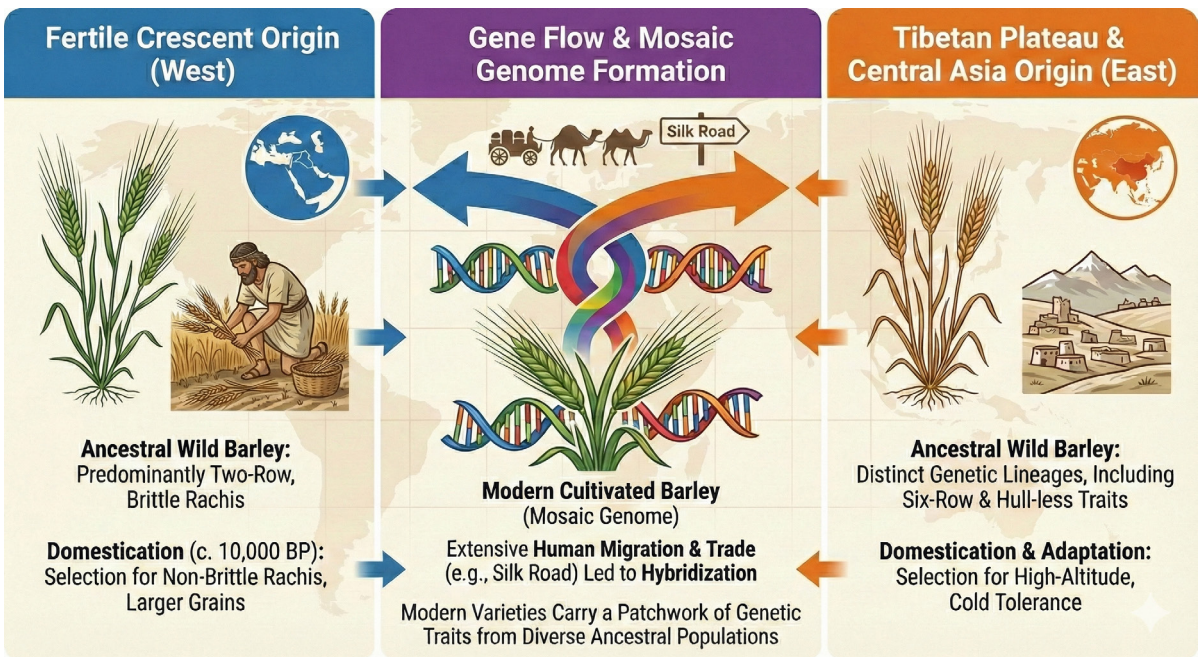

Fig 1. Understanding the Mosaic pattern of origins and gene flow in barley domestication

7H) (Dai *et al*., 2014). Archaeobotanical evidence supports prolonged interactions between wild and cultivated barley forms prior to full domestication. Evidences from the archaeological site of Ohalo II (~23,000 BP) and later domesticated remains from locations like Yoram Cave (~6,000 BP) suggested a gradual and progressive domestication. This transition involved recurrent genetic contributions from wild barley populations (Kislev *et al*., 1992; Fuller *et al*., 2011; Mascher *et al*., 2016). These findings confirm that barley domestication was not a one-time domestication occurrence but a prolonged and geographically widespread evolution.

The mosaic origin of barley has significant relevance for present-day breeding programmes. Germplasm derived from the wild and geographically diverse populations represent an important pool for promising alleles for stress adaptation, disease resistance and grain quality improvement. For instance, barley lineages originated from the Eastern regions, contributed to exhibit enhanced drought and salinity tolerance through improved physiological regulation, as observed in genotypes such as 'Zahna' (Alsamadany *et al*., 2024). In a similar way, wild *Hordeum* sources have contributed resistance loci such as *Rym14*^{Hb} that provides resistance to barley yellow mosaic viruses (BaYMV) (Pidon *et al*., 2021). In addition, numerous quantitative trait loci linked to rust and powdery mildew resistance have been identified from these sources (Ge *et al*., 2021; Pan *et al*., 2021). Genetic variation originated from different ancestral populations also contributed to grain quality traits, including β-glucan content and hull-less phenotypes which are linked to distinct genomic regions (Elouadi *et al*., 2021; Geng *et al*., 2022). These findings point towards the value of wild relatives and traditional landraces as genetic resource for maintaining long term genetic gain.

3. Historical innovations: A Global Journey

Barley occupies a distinctive position in the history of agricultural and was among the earliest domesticated cereals. Its wide ecological adaptability enabled cultivation across wide range of agro-ecological environments that includes arid regions as well as high latitudes and elevations (Yu *et al*., 2024). The progression of barley improvement reveals the overall transformation of plant breeding i.e. from initial unconscious selection by the farmers to later scientifically guided genetic improvement supported by modern molecular breeding approaches and molecular technologies (Fig 2, Table 1).

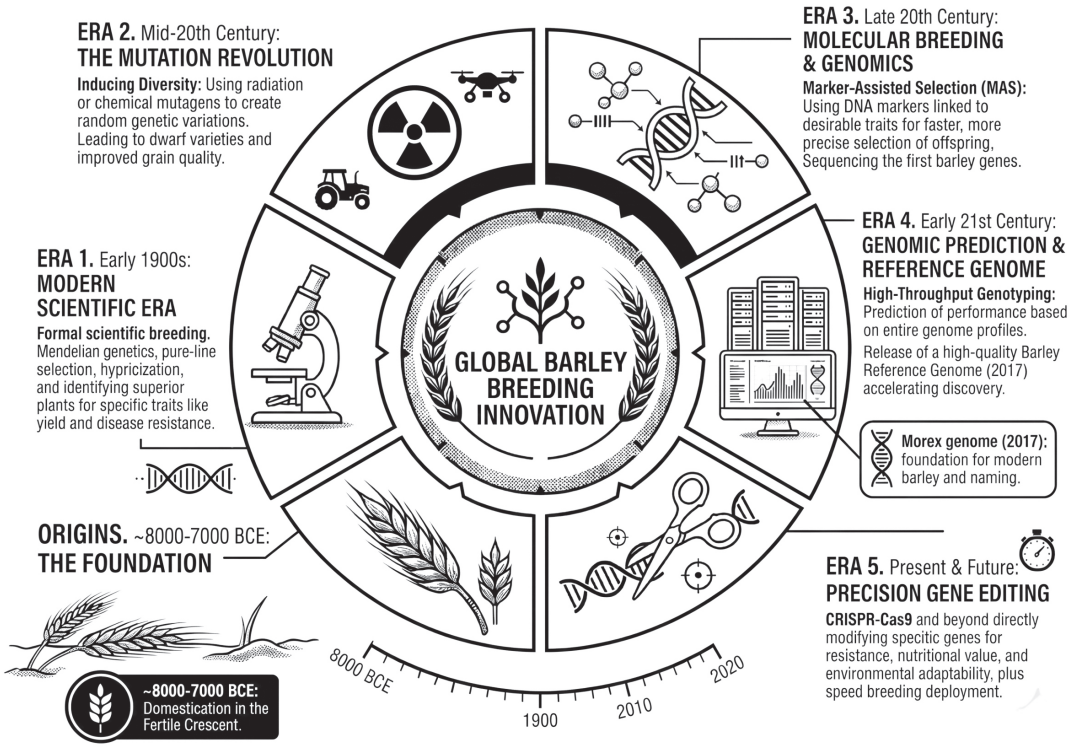

Fig 2. Conceptual illustration of the rise in global barley yield over time, highlighting key breeding milestones.

3.1 Selection and Early Trait Domestication (10,000 BCE – 2,000 BCE)

Barley is considered to have been domesticated in the Fertile Crescent around 10,000 years ago from its wild ancestor *Hordeum vulgare* ssp. *spontaneum*. During the early stages of agriculture practices, farmers gradually selected plants with key domestication traits i.e traits favourable for cultivation and harvesting. One of the most important traits was the selection from brittle to non-shattering rachis. This trait allowed mature spikelets to remain attached to the ear, facilitating harvesting with minimal seed loss (Pourkheirandish *et al*., 2015). This selection also favoured hull-less (naked) grain types in some regions which results reduction in post-harvest processing requirements for human consumption. Another important development involves the evolution of six-rowed types from the ancestral two-rowed form. This trait, governed by a specific gene, increased the number of grains per spike and ultimately contributed to higher yield potential (Pourkheirandish and Komatsuda, 2007). In addition, traits such as uniform germination, large seed size and improved threshability resulted in more uniform crop stands and better productivity. Collectively, these early selection practices laid the genetic foundation for the widespread cultivation of barley in ancient agricultural systems.

3.2 Global spread and advancement of Environmental Adaptation (6,000 BCE – 1700s CE)

Barley played a crucial role in the development of early agricultural civilization in the Near East and nearby regions. As one of the founder crops of Neolithic agriculture, it played a key role in the transition from hunter-gatherer lifestyle to settled farming societies (Mascher *et al*., 2016). Its tendency to adapt varying environmental conditions and comparatively brief growing season made it a reliable food source for early farmers. After its domestication, barley spread rapidly as the humans migrated beyond the Fertile Crescent. Archaeological evidence indicates its presence in the Indus Valley by approximately 6000 BCE, in ancient Egypt around 5000 BCE as a staple grain for preparing both bread and beer. Between 5000 and 4000 BCE, it spread across Europe where it adapted to diverse temperate environments. Around 3000 BCE, barley had also reached East Asia, where it complements the major crops such as rice and millet, especially in cold or high-altitude regions. Over many generations, farmer deliberately selected barley under varied environmental conditions that resulted in regionally adapted landraces exhibiting traits such as drought tolerance in arid regions and cold hardiness in northern latitudes. This diversification contributed to the development of barley as a resilient crop, well adapted to marginal conditions.

3.3 The Dawn of Systematic Breeding: from 18th – 19th Century

During the eighteenth to nineteenth centuries, the application of systematic agricultural practices shifted traditional cultivation towards more deliberate crop improvement practices and this period marked the beginning of formal plant breeding, through the establishment of agricultural experiment stations and the rediscovery of Mendel's laws in the early twentieth century. These advances gave rise to structured barley breeding programs across Europe. As a result, specialized malting barley varieties were developed in Bavaria and other brewing regions, showing how industrial demand has an influence on targeted trait selection (Fang *et al*., 2019; Hagenblad and Leino, 2022; Yu *et al*., 2024). The establishment of the United States Department of Agriculture's Office of Cereal Investigations in 1862 allowed researchers to introduce and test thousands of barley accessions across the globe. These initiatives helped improve traits such as winter hardiness, disease resistance, and yield potential (Tyagi *et al*., 2020). Together, these developments transformed barley from a subsistence crop to a scientifically managed agricultural commodity with both nutritional and industrial importance.

3.4 The Twentieth Century: Genetic advances and the Green Revolution

The 20th century witnessed revolutionary progress in barley breeding largely driven by the rediscovery of Mendelian genetics, the establishment and rise of formal breeding institutions, and the worldwide demand for increased food production. Early scientific efforts for barley improvement focused on systematic hybridization and careful selection strategies, influenced by pioneering seed breeders like the Vilmorin family (Gayon and Zallen, 1998). While the Green Revolution is commonly linked with wheat and rice, but similar principles – including reduced plant height, enhancing fertilizer efficiency, and improving key agronomic traits etc. were also applied to barley improvement from the mid-1900s onward

(Kuczyńska *et al*., 2013). For example the most significant milestone was the development and application of semi-dwarf germplasm i.e '*sdw1/denso'* locus, derived from mutant sources such as 'Abed Denso' and 'Jotun'. This lead to evolution of dwarf plants with lodging resistance and increased harvest index (HI), resulting notable yield gains under high-input agricultural conditions (Dockter and Hansson, 2015; Braumann *et al*., 2018). These advances progressed alongside the introduction of dwarfing genes in wheat and played a key role in upgrading barley production systems across the globe.

During this phase, breeding for disease resistance also gained momentum, targeting major pathogens that include powdery mildew, rusts, and scald. European breeding programs utilized both major resistance genes i.e *Mla* and *mlo* for powdery mildew as well as polygenic resistance sourced from wild germplasm. Worldwide resistance breakdown events in the 1970s and 1980s, forced breeders to eventually adopt gene pyramiding approaches to enhance resistance durability (Dreiseitl, 2020, 2024). Key leaf rust resistance loci, such as *Rph7*, was first identified in the cultivar 'Cebada Capa'. It was later incorporated into breeding programs in North America along with the cultivars including 'Larker' and 'Morex' functioning as key genetic resources for research and development (Steffenson *et al*, 1993). All India Coordinated Wheat and Barley Improvement Projects (AICW&BIP), a part of coordinated national initiatives, made significant contributions to the development of cultivars adapted to rain fed and stress-prone environments in India. These efforts led to the release of various varieties i.e. 'BL-2', 'RD 2035, and 'RD 2552' for salinity tolerant; 'Rajkiran' for resistance to cereal cyst nematode (CCN) etc. (https://www.raridurgapura.org/Scheme-Wheat-Barleys.htm), thereby enhancing both adaptation and resilience under varying agro-climatic conditions.

Improvement in malting quality progressed vis-à-vis agronomic breeding, with key contributions from European programs, especially the Carlsberg Research Laboratory in Denmark. Utilizing approaches such as pure-line selection, biochemical characterization of trait and the development of micro-malting evaluation systems, researchers were able to identify key genetic factors governing kernel plumpness, enzyme activity, and extract yield traits that laid the foundation for modern malting varieties. In addition, mutation breeding played a significant role in broadening genetic variability example, the semi-dwarf cultivar 'Golden Promise', derived from gamma-irradiated 'Maythorpe', combined reduced plant height due to mutation in the *ari-e.GP* dwarfing gene with excellent malting quality. This cultivar was popularized across regions in Europe during the 1970s and early 1980s (https://www.beerandbrewing.com/dictionary/COMO4SK5Y5).

The breeding efficiency was further upgraded by the use of technological advancements. One of the major developments was the production of doubled haploids (DH) through interspecific crosses between *Hordeum vulgare* and *Hordeum bulbosum*. This innovation enabled the speedy generation of completely homozygous lines within a very short span of single generation. Consequently, the duration for breeding cycles was substantially reduced and thus accelerating genetic gain and enabling more efficient crop improvement (Kasha and Kao, 1970; Czembor *et al*., 2019). During the 1980s and 1990, advances in molecular marker technologies, including Restriction Fragment Length Polymorphisms (RFLPs) and Simple Sequence Repeats (SSRs), and later Single Nucleotide Polymorphism (SNP) markers, transformed plant breeding approaches. These tools facilitated marker-assisted selection for improving disease resistance, abiotic stress tolerance and quality-related traits (Akar *et al*., 2009; Liu *et al*., 2010; Fang *et al*., 2019; Ishikawa *et al*., 2022).

By the late 20th century, barley had become dual-purpose crop with well-defined breeding pathways: a resilient food and feed crop suited to marginal environments and a highly specialized raw material optimized for the global malting and brewing industries. These developments laid the conceptual and technological foundations for modern genomics-assisted breeding strategies.

3.5 The Modern Era: Genomics and Precision Breeding

The development of high-quality reference genome assemblies, especially the chromosome-scale sequence of the cultivar 'Morex' produced by the International Barley Sequencing Consortium (IBSC) switched barley breeding towards precision based approaches. These genomic resources offered novel understanding for genome organization and enabled the discovery of high density molecular markers, thereby facilitating genome-wide association studies (GWAS) and accelerating the

identification of genes regulating important agronomic traits (Visioni *et al*., 2013; Alqudah *et al*., 2014; Ogrodowicz *et al*., 2023). Nowadays, dense genome-wide marker information is easily accessible that signaled a transition from established marker-assisted selection (MAS), that generally targets a restricted number of loci, toward genomic selection (GS), where vast number of markers are used simultaneously to estimate breeding values.

Therefore, early applications of genomic selection (GS) in barley studies exhibit its potential to upgrade prediction precision for complicated quantitative traits as compared to MAS approaches (Crossa *et al*., 2017). Methodological advancements, especially statistical models that allow incorporating genotype × environment interactions, further helped in improved prediction accuracy under varying environmental conditions. As a result, more robust selection decisions can be achieved under diverse climatic range (Montesinos-López *et al*., 2023). These advancements are crucial especially for traits regulated by polygenic inheritance like grain yield, malting quality and abiotic stress resistance.

Simultaneously, major progress was witnessed in phenotyping technologies where, during 2010s the widespread adoption of high-throughput phenotyping systems was noticed. Later includes unmanned aerial vehicles, hyperspectral sensors and thermal imaging

Table 1. Major technological innovations accelerating genetic gain in barley breeding

Technological Innovation	Approximate year	Impact	Reference
Systematic Selection	19th Century	Marked the beginning of deliberate crop improvement through phenotypic selection and seed purification	Bishnoi *et al.* (2022)
Semi-dwarf Genes (*sdw1/denso*)	1960s–1980s	Reduced lodging and improved harvest index, which enable more efficient selection	Börner *et al.* (1998); Kuczyńska *et al.* (2013)
Doubled Haploidy (*Hordeum bulbosum* method)	1970s	Shortened breeding duration by 4-5 years by generating completely homozygous lines in one generation	Kasha and Kao, (1970)
Marker-Assisted Selection (MAS)	1980s–1990s	Early and precise selection for major genes, reducing time spent on phenotypic screening	Tanksley *et al.* (1989); Liu *et al.* (2010); Ishikawa *et al.* (2022)
Barley Reference Genome (IBSC draft)	2012	Laid foundation for modern genomics, including QTL mapping, and molecular marker development	Mayer *et al.* (2012)
Genomic Selection (GS)	2009–2012	Improved selection for more complex traits using genome wide marker information	Lorenz *et al.* (2012); Heffner *et al.* (2009)
Genome Editing (CRISPR/Cas9)	2015 onward	Enabled precise and rapid modification of specific genes, accelerating trait development	Lawrenson and Harwood (2019); Lawrenson *et al.* (2024)
Speed Breeding (SB)	2018	Allowed multiple generations per annum under controlled conditions, greatly speed up breeding progress	Watson *et al.* (2018)

systems that allow large breeding populations to be analyzed efficiently and without physical disruption of the sample crop. Multiple imaging modalities in combination with RGB (Red, Green, and Blue) imaging, chlorophyll fluorescence, and canopy temperature measurements has strengthened the capacity to characterize and evaluate plant responses to drought and other stresses by simultaneously capturing structural and physiological features (Li *et al*., 2014; Mikołajczak *et al*., 2020; Leiva *et al*., 2024). These advanced tools and technologies facilitated the estimation of crop indices such as normalized difference vegetation index and physiological traits including stomatal conductance.

A further significant advancement in modern barley improvement has been the adoption of speed breeding methodologies. Controlled-environment protocols using extended photoperiods (approximately 22 hours of light per day) in combination with optimized LED lighting systems allows the production of up to six generations per year, considerably shortening crop breeding cycle and accelerating genetic gain (Watson *et al*., 2018). Speed breeding integrated with genomic selection allowed occurrence of recombination and selection steps more rapidly, resulting in enhanced overall breeding efficiency.

CRISPR/Cas systems are remarkable genome editing technologies that further strengthened the precision breeding toolkit by allowing targeted and heritable modifications in superior genetic backgrounds without comprehensive backcrossing. In barley, targeted mutagenesis of susceptibility genes such as *Mlo* has successfully conferred durable resistance to powdery mildew disease, revealing the translational potential of gene editing for improvement of disease resistance (Lyngkjær *et al*., 2000; Miklis *et al*., 2007; Kusch and Panstruga, 2017). Gene editing approaches have also been applied to grain quality traits, for example, knockout of lipoxygenase *(LOX)* genes reduces lipid oxidation and thus improving storage stability and flavour characteristics relevant to malting and dietary uses (Zeng *et al*., 2025). In recent times, modification of developmental pathways such as *Ppd-H1* through genome editing tools has enabled controlled flowering time and vegetative growth duration. This is providing opportunities to optimize biomass accumulation, forage production, and environmental responsiveness (Tezuka *et al*., 2024).

Overall, the integration of genomic selection (GS), speed breeding, high-throughput phenotyping and genome editing in combination with sustained use of allelic diversity from wild barley germplasm–has transformed barley breeding into a highly data-driven and precision-oriented field. These advances provide potential avenues in future to develop cultivars with enhanced productivity, improved resilience to climatic stresses, and better end-use quality.

4. Genomic Architecture and the Triticeae Model System

Barley has comparatively simple diploid genome (2n = 2x = 14; ~5.3 Gb) relative to the highly complex allohexaploid genome of bread wheat (2n = 6x = 42; ~17 Gb) due to which it occupies a central position as a genetic model system within the *Triticeae* tribe, especially for wheat and rye. Despite this apparent simplicity, the barley genome is dominated by repetitive DNA, with approximately 80–90% consisting of long terminal repeat (LTR) retro-transposons. This high repeat content posed major barriers for early sequencing efforts based on short-read technologies, limiting assembly continuity and resolution of genomic complex regions.

Early whole-genome shotgun sequencing efforts were able to anchor approximately 3.9 Gb of sequence to integrate genetic and physical maps. However, the draft status of the assembly along with the extensive repeat content, limited sequence contiguity and reduce the accuracy of gene annotation (International Barley Genome Sequencing Consortium, 2012). In subsequent years, remarkable progress was made with the release of the Morex V2 reference genome, which integrated short-read sequencing with optical mapping and Hi-C–based scaffolding through the TRITEX assembly pipeline. This strategy generated chromosome-scale pseudo-molecules spanning approximately 4.2–4.3 Gb and captured the majority of the gene space, although unresolved gaps remained in highly repetitive centromeric and telomeric regions (Mascher *et al*., 2016; Monat *et al*., 2019).

The advent of long-read sequencing technologies, including Pacific Biosciences high-fidelity reads or sequencing circular consensus sequencing (CCS), Oxford Nanopore sequencing, and complementary methods such as Bionano optical mapping, has markedly improved genome assembly quality. These innovations have

enabled highly contiguous, chromosome-scale assemblies, most notably the Morex V3 reference genome, which resolved previously inaccessible repetitive regions such as centromeres and ribosomal DNA arrays (Mascher *et al*., 2021) (Table 2). Incorporating long-range scaffolding techniques like as Hi-C within the TRITEX assembly framework further enhanced structural accuracy, achieving high gene completeness (~98.4%) and minimal sequence gaps (<0.1%) (Monat *et al*., 2019). Together, these resources provide a solid foundation for gene discovery, structural variant analysis, and functional genomics studies.

Beyond the use of single reference genome, a pan-genome analysis that integrates wild barley, traditional landraces and modern superior cultivars have provided deeper insights into genomic diversity responsible for phenotypic variation. These comparative analyses indicate that only about 20–30% of genes are shared across different accessions, while a large proportion of the genome varies considerably. This variation is reflected in the form of presence–absence variation (PAV), copy number variation (CNV) and structural variants (SVs) (Chapman *et al.,* 2026). Such studies have identified more than 15,000 PAVs and more than 10,000 SV, including huge chromosomal inversions on chromosome 2H. They have also revealed expansions in gene families associated with stress-responsiveness particularly those involved in dehydration tolerance in wild barley. In addition, domestication-related deletions affecting Btr1 and Btr2-genes, which are linked to the loss of seed shattering have been well documented (Pourkheirandish *et al.,* 2015). These findings together emphasize the value of wild germplasm as an important pool of adaptive alleles for crop improvement. The availability of high-quality genomic resources have further accelerated the identification of genes controlling key agronomic traits that include grain weight regulators such as GW2 (Wang *et al.,* 2019), cold tolerance genes within the HvCBF (Tondelli *et al.,* 2006) cluster and resistance loci for yellow mosaic disease such as Rym14Hb (Pidon *et al.,* 2021). These advancements played a significant role in strengthening comparative genomics and synteny analyses across Triticeae species. A recent important reference on the barley genome is the pangenome analysis of wild and domesticated barley, published recently (Jayakodi *et al.,* 2024). This study identified structural variation, including differences in the copy number of the HvTB1 gene, as well as six previously uncharacterized protein variants. Another notable resource is the barley pan-transcriptome, which provides insight into the functional consequences of genotypic diversity (Guo *et al.,* 2025).

Table 2. Major barley reference assemblies and their breeding relevance

Assembly / Resource	Timeline	Key Technologies	Major Attributes	Breeding Applications
IBSC Morex V1	2012	BAC-by-BAC approach with short-reads sequencing	Produced a ~3.9–4.8 Gb draft genome, highly fragmented, gene-rich BAC contigs mapped to chromosomes.	Served as first reference genome framework; enabled early gene/QTL anchoring and initiate marker development though resolution was limited.
Morex V2	2017–2019	Integration of Short reads, optical mapping, Hi C (TRITEX)	Generated Chromosome-scale pseudomolecules (~4.3 Gb), improved gene coverage, residual gaps in repeats.	Provided more reliable genome structure which improved QTL mapping, GWAS accuracy and positional cloning efforts
Morex V3	2021	PacBio HiFi long reads combined with optical mapping	Delivered a near complete (4.8~5.1 Gb) assembly, telomere to telomere-like assembly; greatly improved repeat and LTR regions.	High-precision mapping of resistance genes (e.g., *Ryd4Hb*), grain-size loci (GW2.1), and stress genes (HvCBF14).
Ensembl / Pan-genome resources	2024–2025	Multiple assemblies, haplotype-resolved pan-genome	Includes more genetic diversity than Morex alone, capturing variation from both cultivated and wild relatives.	Helps identify useful alleles, guides introgression strategies, and supports the development of reliable markers across diverse germplasm.

Barley serves as an excellent model crop as it has strong genome collinearity with other members of *Triticeae* species. A high degree of structural similarity exists between barley chromosomes and the wheat subgenomes that enable efficient use of comparative genomics for gene discovery, marker development and cross-species transfer of genomic information (Mayer *et al*., 2011; Poursarebani *et al*., 2013). Furthermore, pan-genome analyses have highlighted regions of the genome that are rich in structural variant. These hotspots are particularly valuable for gene validation and play important role in facilitating alien introgression of beneficial traits from related species into breeding germplasm (Jayakodi *et al*., 2024).

Overall, these genomic advancements further strengthen barley's role not only as an important crop but also as an experimental model crop for *Triticeae* genetics. The availability of advanced genomic resources now reinforces modern breeding strategies such as genomic prediction, haplotype-based selection and genome editing, ultimately shaping a more precise and efficient future of barley improvement.

5. Core Breeding Objectives

Barley breeding efforts have largely focused on improving grain yield by modifying key aspects in plant architecture such as increasing tiller number, grains per spike, and thousand-grain weight. The incorporation of "stay-green" phenotypes have attracted considerable interest, as prolonged photosynthetic activity during grain filling can enhance assimilate availability and final yield potential (Wang *et al*., 2019; Brunner *et al*., 2024). Genetic resources derived from landraces and wild *H. spontaneum* continue to offer valuable alleles for optimizing agronomic traits. Variation in the strigolactone signaling pathway has been linked to the regulation of the functional balance between tillering capacity and grain size in barley (Kelly *et al*., 2025).

Enhancing resistance to biotic stresses continues to be a major focus in barley breeding, with emphasis on durable and broad-spectrum protection. The *mlo* locus represents one of the most successful examples, which provides long-lasting resistance to powdery mildew across a wide range of environments (Kusch and Panstruga, 2017; Dreiseitl, 2024). Similarly, the *Yd2* gene located on chromosome 3HS provides tolerance to Barley Yellow Dwarf Virus (BYDV) (Collins *et al*., 1996). The pyramiding of resistance gene, involving *Rph* (leaf rust), *Rpg* (stem rust), and *Rps* (stripe rust) loci strengthens defense against multiple rust pathogens (Brueggeman *et al*., 2002). Similar efforts are being focused on improving quantitative trait loci resistance to other major diseases example, spot blotch (*Bipolaris sorokiniana*) resistance quantitative trait loci on chromosomes 3H and 7H (Roy *et al*., 2025) and net blotch (*Pyrenophora teres*) resistance loci (Afanasenko *et al*., 2022) are also being incorporated. These resistance sources are increasingly being combined through coordinated phenotypic screening and molecular strategies.

Breeding for abiotic stress tolerance in barley frequently exploits the rich adaptive diversity found in wild populations. Developmental escape from water stress mediated by deeper root systems and osmotic adjustment capacity (Nevo and Chen, 2010) are particularly valuable under water-limited conditions. Similarly, enhanced salinity tolerance was achieved through efficient ion exclusion mechanisms (Gharaghanipor *et al*., 2022) and improved reproductive resilience under heat stress that preserves pollen viability during anthesis (Ejaz and von Korff, 2017) are key target traits in breeding programs. Cold tolerance has also been closely linked with CBF/DREB transcriptional factors and antifreeze proteins, both of which play a critical role in contributing winter hardiness (Skinner *et al*., 2005).

Quality improvement objectives in barley breeding vary widely depending on end use, and breeding strategies are often shaped by strict industrial requirements. Malting barley requires relatively low grain protein concentrations (9.5–11.5% on dry basis) to achieve high extract yield (>80%). In addition, breeders look for plump, well-filled kernels, highly uniform germination (>95%), and strong diastatic power. This enzymatic strength, resulting from a good balance between α- and β-amylase activities, is critical for efficient starch breakdown during the brewing process (Bettenhausen *et al*., 2018). Genetic studies have identified several key genes, which influence important agronomic and quality traits in barley example: *VRS1* and *INTERMEDIUM-C* (*INT-C*) play central roles in determining spike morphology particularly row number and spikelet fertility. These genes have been exploited to develop varieties with characteristics desirable for specific end uses. The *VRS1* gene, in particular, regulates the two-rowed or six-rowed phenotype, allowing breeders to select

the preferred type depending on brewing applications (Ramsay *et al*., 2011). In contrast, feed barley breeding prioritizes nutritional value and rumen digestibility, targeting improved amino acid composition. This includes enhancing the amino acid profile-especially lysine and threonine along with maintaining moderate protein levels (12–15%). This balance helps support efficient livestock growth while minimizing excess nitrogen excretion. Food-grade hull-less barley focuses on nutritional functionality, especially elevated soluble β-glucan content (3–11%). These viscous fibers form gels in the gastrointestinal tract that slow carbohydrate digestion, reduce postprandial glucose responses by approximately 20–30%, and bind bile acids, contributing to reductions in low-density lipoprotein cholesterol of 5–10% (Bhatty, 1999).

6. Traditional Breeding: A Slow but Steady Path

Barley improvement has been rooted in traditional breeding practices, where the best performing plants from each harvest were selected by farmers and saved seed for the next growing season. In due course, this farmer approach gradually developed into breeding efforts that were more organized. By the early twentieth century, European scientists, including Erich von Tschermak, began using planned hybridization followed by careful selection. The aim was to improve adaptation and overall agronomic performance, particularly in winter two-row type barley (Stockinger, 2021).

A major methodological shift came during the 1910s–1920s, when H. V. Harlan at the United States Department of Agriculture, developed the mass-pedigree approach. This method involved intercrossing elite parent lines, raising early -generation progeny in bulk, and applying phenotypic selection for lodging resistance and yield (Ramage, 1987). Among the early barley improvement efforts, most of the improvements were made by selection within existing germplasm, as documented in early studies of barley cultivation and variety development. During the same time, breeders started releasing improved varieties adapted to particular environmental conditions, example-the malting barley 'Prior', was developed in Australia in 1925 by Albert E. Pugsley. In the following decades, these approaches were further refined. Harrington improved the efficiency of Harlan's mass-pedigree method, while breeding programs in Northern European regions strengthened pedigree breeding combined with multi-environment testing. These efforts played a crucial role in improving winter barley performance as well as for improving malting qualities (Ramage, 1987; Stockinger, 2021; Bishnoi *et al*., 2022).

During the 1920–1930s, at various research centers in India viz. Pusa, Kanpur and Sabour, efforts for systematic barley improvement began, where breeders developed NP, K, BR, and C series through mass and pure-line selection, with the major focus on adaptation to rainfed agro-ecological conditions (ICAR-IIWBR, 2024). A major institutional development took place in 1966 when All India Coordinated Research Project (AICRP) on Barley was established. This program brought together coordinated breeding efforts across diverse agro-ecological zones, combining pedigree and mass-pedigree strategies. Consequently, the program led to the release of more than 100 improved barley varieties, generally with better yield stability, wider adaptation and end-use quality traits (ICAR-IIWBR, 2024). At the same time, parallel progress was made internationally. In Australia, breeding programs supported by state agencies and the Grains Research and Development Corporation focus on elite crosses and multi-environment evaluation. These efforts facilitated the selection of cultivars with traits like early maturity for heat escape and strong malting. 'Baudin' is the well-known variety developed in Western Australia which gained wide acceptance (Paynter *et al*., 2004). During this period, resistance to Barley Yellow Dwarf Virus also emerged as an important objective, with genetic mapping and characterization of the *Yd2* locus, helps breeders its incorporation into elite germplasm (Collins *et al*., 1996; Jefferies *et al*., 2003).

From the 1980s till early 2000s, several dedicated breeders contributed significantly to both cultivar development and disease resistance. At North Dakota State University, Jerome D. Franckowiak was closely involved in the development of many barley cultivars and in genetic studies on disease resistance. His work included research on leaf rust resistance genes and the use of Bowman backcross-derived lines for genetic analysis. At the international level, the ICARDA–CIMMYT barley breeding program, led by Hugo E. Vivar focused on developing barley cultivars suited for wide range of environments, with particular emphasis on resistance

to multiple diseases. In India, parallel efforts led to the release of improved feed and malting barley cultivars such as DWRUB 52, BHS352, BHS400 and RD2552 as part of national improvement efforts (Kumar *et al*., 2020; Verma *et al*., 2022).

Altogether, these traditional breeding methods viz. mass selection, pure-line development, and pedigree-based breeding–resulted steady gains in productivity, adaptation and grain quality, even in the absence of advanced genetic tools (Table 3). Significantly, established the foundation was laid by generating valuable germplasm and breeding populations that continue to support modern molecular and genomic breeding efforts.

Table 3. Traditional barley breeding methods used for different breeding objective

Geographical Origin	Traditional Method	Primary Outcome	Major Breeding Goals
India	Pure-line selection, Introductions and pedigree breeding	Improved varieties development from landraces (NP series); along with BHS 400, RD 2907	Focus on feed/food use; Malting quality; resistance to biotic and abiotic stresses and overall Yield improvement
Kazakhstan	Interspecific hybridization and both simple/complex crosses	Development of donor lines with desirable seed quality traits and seed weight	Emphasis on Quality malt; Seed size and weight, protein content optimization
New Zealand	Crossing and selection based on introduced material	Replacement of older varieties like 'Kenia'; with improved cultivars such as Kaniere, and Mata (derived from diverse pedigrees)	Malt/Quality improvement; Seed trait and adaptation to varying rainfall conditions
Czech Republic	Mutation breeding (gamma irradiation) followed by selection	Development of semi-dwarf varieties such as Diamant	Improvement of lodging resistance, yield stability, malting quality and control of beta-glucan content
Spain	Backcross integrated with pedigree selection	Raising Cierzo-derived lines from SBCC042/SBCC073	Targeted improvement for end use, drought tolerance and adaptation to Mediterranean heat stress
South Africa	Phenotypic selection, Mass selection	Superior individuals for resistance	Feed/Malt; Spot blotch resistance (biotic stress), quality
Ethiopia	Mass and pure-line selection from landraces	HB-series, Ratta	Food/Feed; Drought/scald resistance (biotic/abiotic), malt quality
China	Hybridization and pedigree crosses	Salt-tolerant two/six-row lines	Feed/Fodder; Salt/abiotic stresses, aphid biotic resistance, fodder yield

7. Technological Frontiers in Breeding

Contemporary barley breeding is undergoing a major transformation driven by genomics-enabled germplasm characterization and rapidly advancing molecular technologies. Traditional phenotype-based selection is increasingly complemented by DNA-based approaches that allow breeders to make more precise and informed decisions at earlier stages of the breeding cycle. Marker-assisted selection (MAS) relies on molecular markers linked to genes or quantitative trait loci controlling desirable traits, enabling efficient introgression of specific alleles into elite genetic backgrounds. In contrast, genomic selection (GS) evaluates genome-wide marker information simultaneously to predict breeding values for complex quantitative traits such as yield, stress tolerance, and quality, thereby accelerating selection gains compared with conventional approaches.

Sequencing of the large barley genome, together with high-throughput genotyping platforms and improved computational tools, now enables genome-scale analysis of genetic variation and prediction of trait performance with increasing accuracy (Ganal *et al*., 2009). Genome-wide association studies (GWAS) further complement these approaches by examining diverse germplasm panels with dense single nucleotide polymorphism (SNP) markers to identify loci associated with important agronomic traits.

Such studies have successfully detected robust allelic variants derived from breeding history, including genes controlling photoperiod response, *Ppd-H1* (Turner *et al*., 2005); vernalization, *VRN*$_3$ (Yan *et al*., 2006); and plant height, *sdw1* (Lukina *et al*., 2024), which contribute to adaptation, flowering regulation, and lodging resistance.

Together, these technological innovations provide powerful opportunities to integrate genetic diversity, predictive breeding and precision trait improvement into modern barley breeding pipelines. The major molecular breeding tools currently applied for barley improvement are summarized below (Table 4).

Table 4. Molecular breeding tools transforming barley improvement

Tool	Key Mechanism	Primary Advantages	Example Applications in Barley	Reference
Marker-Assisted Selection	Linked markers for known QTL/genes	Early selection; precise introgression	*Rph5* leaf rust resistance; mlo powdery mildew resistance; *Yd2* for barley yellow dwarf; frost, quality	Jefferies *et al.* (2003); Mammadov *et al.* (2003); Akar *et al.* (2009); Kusch and Panstruga (2017)
Genomic Selection	Genome-wide SNP prediction models	Polygenic trait capture; rapid cycles	Yield, drought tolerance, malt quality, disease resistance	Lorenz *et al.* (2012); Maurer *et al.* (2016); Roy *et al.* (2025)
QTL Mapping	Bi-parental cross segregation analysis	Precise locus detection in structured populations	Heading date, tillering, grain size, malting, drought, biotic stress	Fan *et al.* (2015); Fang *et al.* (2019); Wang *et al.* (2019); Pan *et al.* (2021)
GWAS	Association in diverse panels	Broad allelic discovery; historical recombinations	*Ppd-H1*, *VRN-3*, lodging QTLs	Alqudah *et al.* (2014); Ogrodowicz *et al.* (2023)

7.1 Marker-Assisted Selection (MAS) and Genomic Selection (GS)

Marker-assisted selection (MAS) has significantly enhanced the efficiency of barley breeding by enabling early identification of desirable genotypes for traits which are difficult, time-consuming, or expensive to assess phenotypically, including yield components, disease resistance and abiotic stress tolerance. Through the combined use of foreground selection for target loci and background selection to minimize linkage drag, MAS allows more rapid recovery of elite genetic backgrounds compared with conventional phenotypic selection (Table 5). The integration of high-density SNP genotyping platforms, such as the Illumina 9K iSelect and 50K iSelect arrays, together with functional markers for major genes, has accelerated marker-assisted breeding by improving selection efficiency and enabling earlier identification of superior genotypes (Bayer *et al*., 2017).

MAS have proven particularly effective for traits controlled by major loci, including *rym*-mediated resistance to barley yellow mosaic viruses and important malting quality quantitative trait loci. In elite breeding populations, MAS also facilitates the pyramiding of multiple resistance genes and serves as a complementary approach to genomic selection for complex traits through the estimation of genomic breeding values. The development of optimized marker panels has further improved the practicality of molecular breeding; for example, core marker sets such as HvCoreSet_v1, comprising 768 genome-wide markers, provided a cost-effective framework for genomic-assisted selection and multi-trait prediction, Japanese barley breeding materials demonstrating substantial prediction accuracies across agronomic and quality traits (Ishikawa *et al*., 2022).

Table 5. Key Markers in Barley Breeding for MAS

Trait	Key Markers/ QTL	Chromosome	Linked Gene/QTL	Effect/Utility	References
Disease Resistance	Bmac0029 (SSR)	3H	*rym4/rym5*	*BaYMV/BaMMV* resistance; distinguishes alleles for dual-pathotype protection	Graner *et al.* (1999); Pellio *et al.* (2005)
	mlo functional SNP	4H	*mlo*	Recessive powdery mildew resistance	Büschges *et al.* (1997); Kusch and Panstruga, (2017)
	Rym14Hb KASP	4H	*Rym14Hb*	Yellow mosaic virus resistance	Pidon *et al.* (2021)
Abiotic Stress	*HvCBF14* SNPs	5H	CBF cold response	Freezing tolerance; introgressed from winter landraces	Francia *et al.* (2004; Visioni *et al.* (2013)
	HvPIP2;5 indel	7H	Aquaporin	Drought tolerance via root hydraulics	Knipfer *et al.* (2011)
Malting Quality	*beta-amylase* SNPs	4H	*bmAmy1*	Thermostability for malt extract; >80% correlation with malt quality	Eglinton *et al.* (1998)
Yield Components	*VRS1* diagnostic	2H	*vrs1*	Six-row vs two-row; naked kernel (*nud*) pyramid	Komatsuda *et al.* (2007)
	HvGW2 SNPs	2H	*Grain size*	10-15% TGW increase; syntenic to wheat	Zombori *et al.* (2020)

Genomic selection (GS) represents a further advancement by enabling the simultaneous analysis of thousands of genome-wide markers to predict breeding performance for quantitatively inherited traits. The feasibility of GS in barley was first demonstrated by Lorenz *et al.* (2012), who reported prediction accuracies of 0.72 for Fusarium head blight (Lorenz et al., 2012). Genomic approaches offer a powerful strategy for developing improved barley varieties with enhanced traits, including better organoleptic qualities that are preferred by end users (Sangwan *et al.,* 2026).Therefore, Genomic Selection offers a more powerful tool to accelerate the improvement of complex traits that are challenging to enhance through conventional selection methods alone.

7.2 Quantitative Trait Loci (QTL) Mapping and Genome-Wide Association Studies (GWAS)

Quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS) have become integral approaches for understanding the genetic architecture of complex traits in barley (Table 6). Traditional QTL mapping typically relies on structured bi-parental populations–such as F_2 generations, recombinant inbred lines (RILs), and doubled haploid (DH) populations. Later developed from parents that differ markedly in key target characteristic that includes heading date, plant height, tillering ability, grain size, and disease resistance (Collard *et al.*, 2005; Ajayi *et al.*, 2023). These controlled populations make the detection of genomic regions with

Table 6. Major QTLs associated with yield and stress tolerance in barley

Target Traits	Genomic loci (QTL)	Population (s)	Chromosome Number	Results	Reference
Grain yield & components	*qTGW7-1, qTGW7-3, qGWP7-3/4, qGWS2-3/7-8*	Bi-parental RILs evaluated across three varying environments	2H and 7H	Several stable QTL were identified for thousand grain weight (up to 16% phenotypic variation), grains per spike, grain weight per plant under irrigated as well as drought conditions	Wang *et al.* (2019)
Malting quality (β amylase, MN, DP, extract traits)	*Bmy1& HvSBP16/β* amylase	DH population (Navigator × Admiral)	4H and 7H	Major QTL associated with β amylase activity (diastatic power) and cluster QTLs influencing soluble protein, wort β glucan, Kolbach index and related traits.	Cu *et al.* (2016); Fang *et al.* (2019)
Seed quality (protein, dormancy)	Protein content QTL, *Qsd1,Qsd2*	Multi parent RILs, GWAS panels, and wild × cultivar population	5H	Major seed dormancy QTLs regulates dormancy duration, prevent pre harvest sprouting along with protein content influenced by dormancy alleles	Sato *et al.* (2016); Nakamura *et al.* (2017)
Root architecture & drought	*qRL1H 5, qRL3H 2, qRL5H 2 / qRL6H 2* (and additional root QTL regions)	RILs and GWAS panels focusing on root and seedling traits	1H, 2H, 3H, 5H and 6H	Multiple QTLs linked to root length and biomass contribute to root architecture variation and enhanced drought adaptation	Ajayi *et al.* (2023); Farooqi *et al.* (2023); Ogrodowicz *et al.* (2023)
Agronomic traits (heading, height)	*Ppd-H1 and sdw1*	European elite and spring barley GWAS panels	2H and 3H	Well known pleiotropic loci affecting flowering time, plant height and root traits; with pleiotropic effects on yield related performance	Ogrodowicz *et al.* (2023)
Grain-yield related traits	Yield/Harvest Index loci	Two row spring barley GWAS panels across multi environment	2H and 6H	SNP associations near flowering genes and other loci linked to harvest index and overall grain yield under wide conditions	Genievskaya *et al.* (2025)
Terminal Heat stress	Major QTL clusters under heat stress	DH/RILs or mapping population evaluated under terminal heat stress	2H, 5H and 7H	Stable genomic regions identified contributing to stress response and yield stability under high temperature conditions	Sabouri *et al.* (2025)
Nitrogen utilizing efficiency	*QTgw.sau 2H & Qhi.sau 5H*	RIL population under different nitrogen levels	2H, 4H and 7H	Nitrogen-responsiveness QTLs linked to yield and NUE; some alleles perform better under low nitrogen suggesting potential for sustainable production	Chen *et al.* (2024)

relatively large phenotypic effects that segregate between the two parental lines and have long served as the basis for evaluating loci significant to crop improvement.

More recently, GWAS has broadened the scope of genetic analysis by exploiting historical recombination and natural variation in diverse germplasm collections. With the help of GWAS has uncovered major loci associated with agronomic traits using dense genome-wide marker. These include grain yield, root system architecture, drought tolerance, phenological development and lodging resistance across global barley panels (Pasam *et al.,* 2012; Maurer *et al.,* 2016). Interestingly, several of these loci detected through GWAS coincide with well-characterized developmental genes, including Ppd-H1 (Comadran *et al.,* 2012), VRN-3 (Muñoz-Amatriaín *et al.,* 2020), and sdw1/denso (Kuczyńska *et al.,* 2013). GWAS have proven valuable in identifying genetic loci associated with complex quantitative traits, including abiotic stress resilience, β-glucan content, malting quality and yield components. The overlap between QTL mapping and GWAS findings not only confirms the role of major regulatory genes but also highlights additional minor loci that may contribute to stability of trait and wider adaptation to diverse environment.

Overall, QTL mapping and GWAS complement each other, offers deeper understanding into the genetic control over complex traits. Together they facilitate marker development, candidate gene identification, and thus strengthen precision breeding strategies aimed at improving barley performance under varying growing conditions.

7.3 CRISPR–Cas9 Gene Editing

Genome editing technologies, particularly CRISPR/Cas9, have brought a high level of precision to barley improvement by facilitating site specific modification of endogenous genes without the introduction of foreign DNA. This approach make it possible to improve traits such as stress resilience, agronomic performance, and grain quality traits while preserving the genetic background of elite cultivars (Fig 3). In barley, several successful editing applications have already demonstrated practical value of this approach. For instance, directed disruption of the Eukaryotic Translation Initiation Factor 4E (*eIF4E*) gene has been shown to confer resistance to potyviruses. This highlights the value of editing host susceptibility factors to achieve durable disease resistance (Hoffie *et al*., 2021). Similarly, editing of *HvERF62*, a transcription factor involved in stress responses, has been shown to improve tolerance to waterlogging by enhancing root aerenchyma formation and facilitating better oxygen transport under oxygen deficient conditions (Zhu *et al*., 2025). Recent progress in precision gene editing has also enabled manipulation of plant architecture traits. For instance, targeting gene editing of the *HvGA20ox2* gene led to the identification of a novel semi-dwarf allele, *sdw1.ZU9*. This gene reduces plant height and improves lodging resistance, along with preserving overall yield potential (Xie *et al*., 2024). More recently, genes associated with salinity and drought tolerance have been identified in wild species and are being introgressed to enhance stress resilience in barley (Safhi, 2025).

Grain quality traits have also been targeted using genome editing tools. For example, targeted mutations in *Qsd1* and *Qsd2* have been shown to reduce pre-harvest sprouting susceptibility while strengthening grain dormancy and increases crop stability under field conditions (Hisano *et al*., 2022). On the other hand, editing of lipoxygenase genes (*HvLOXA* and *HvLOXC1*) responsible for lipid oxidation has been reported to prolong grain storability and preserves the flavor during storage and processing (Zeng *et al*., 2025). Researchers have also initiated working on genes linked to nutrient use efficiency and malting quality. Targeted edits in *HvPAPhy_a* gene regulating phytic acid metabolism and *ENGase* loci governing carbohydrate modification, have shown promising outcomes. These efforts laid foundation for improving mineral availability and processing performance in barley grain (Holme *et al*., 2017; Kapusi *et al*., 2017). Zeng et al. (2020) elucidated the vitamin E biosynthesis pathway in barley by generating functional mutants of the *Hvhpt* (homogentisate phytyl transferase) and *Hvhggt* (homogentisate geranylgeranyl transferase) genes using the CRISPR/Cas9 system. Disease resistance in barley has also been targeted using the CRISPR/Cas9 system with engineered transgenic barley plants with enhanced resistance to wheat dwarf virus (WDV) by suppressing replication of the viral genome (Kis *et al*., 2019).

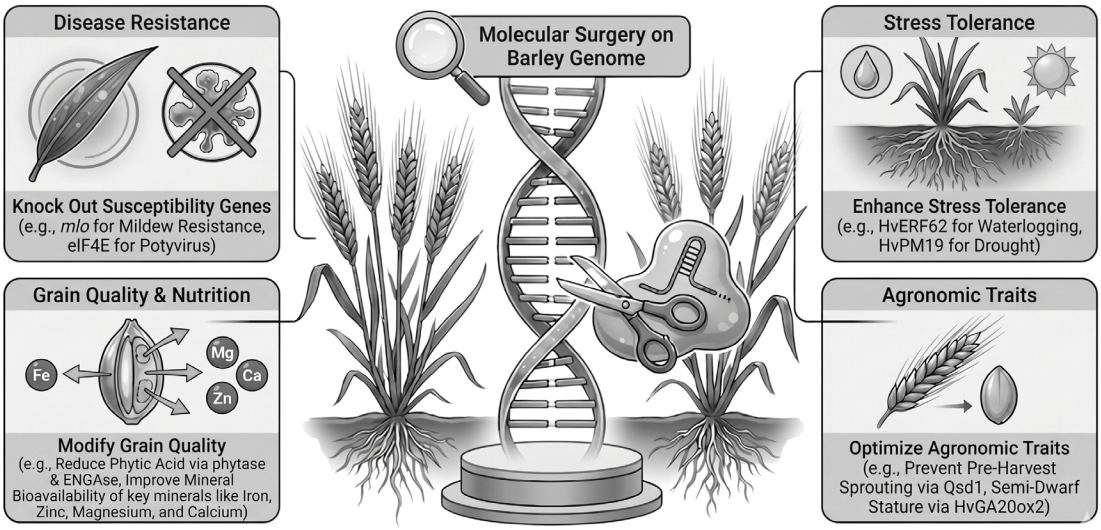

Fig 3. Applications of CRISPR–Cas9 gene editing in barley for improving disease resistance, abiotic stress tolerance, grain quality, and agronomic traits through targeted modification of key functional genes

7.4. Doubled Haploid

Doubled haploid (DH) technology proved to be a key tool in barley breeding as it allows breeders to generate completely homozygous lines in just one generation. This resulted in shortening breeding cycles by 4–5 years as compared to conventional breeding that require several generations of selfing. DH production in barley involve both *in-vitro* and *in-vivo* strategies. Anther culture is an *in-vitro* method that involves excising and culturing immature anthers (pre-meiotic to early uninucleate stage) on different media supplemented with auxins and cytokinins. Under appropriate conditions, these anthers undergo androgenesis, yielding embryogenic calli or direct embryos that regenerate into green/albino plantlets. This is followed by colchicine treatment for chromosome doubling to restore fertility and stable double haploid lines. Recovery rates are highly variable and depend on genotype and treatment protocol. To improve consistency and reduce somaclonal variation, isolated microspore culture has been developed as a more refined method of tissue culture. Microspore are removed and cultured directly after applying stress cold/heat shock pre-treatments in order to enhance green plants. On the other hand, the predominant in-vivo methodology relies on chromosome elimination technique–typically using *H. vulgare* × *H. bulbosum* crosses. In this strategy, selective elimination of *H. bulbosum* chromosomes occurs to yield haploid barley plants followed by colchicine-induced genome doubling of the resulting haploids. Consequently, fertile and genetically uniform DH plants can be raised for immediate selection and evaluation (Ho and Kasha, 1975).

Other advanced strategies such as parthenogenetic haploid inducer systems and CRISPR/Cas9-mediated centromere disruption, is promising technique for genotype-independent, high-throughput haploid production with minimal somaclonal variation (Kuppu *et al.,* 2020; Song *et al.,* 2024). These approaches, collectively allows fixation of traits like yield, disease resistance, and malting quality. This is more advantaging when combined with marker-assisted and genomic selection methods. However, certain constraints like albinism and genotype dependence still need to be addressed.

Scientific studies have clearly shown that valuable Double Haploid technique is very significant for barley improvement. Early work by Kasha and Kao (1970) introduced the *H. vulgare* × *H. bulbosum* hybridization approach, which later became a key method for quickly producing haploid and doubled haploid lines in breeding programs. Since then, DH technology has been widely adopted–almost half of modern European barley varieties are believed to have been developed using these systems (Forster *et al.,* 2007).

Further studies have been undertaken to refine the process example, Jacquard *et al.* (2009) found that cold/heat shock pre-treatments of anthers can significantly improve embryo formation and the recovery of green plants. This helps breeders to recover fully homozygous lines more efficiently for complex traits such as yield and malting

quality. Likewise, Hickey *et al.* (2011) successfully mapped the adult plant resistance gene *Rph20* on chromosome 5HS using a DH population along with PCR-based markers, making it easier to incorporate this resistance into breeding lines. Xu *et al.* (2021) signified the molecular insights with DH lines, identifying 1,027 genes that showed altered expression in the DH line 'DH45' under low nitrogen conditions, consequently, providing useful targets for improving nutrient-use efficiency in barley.

In barley androgenesis, microspores which normally develop into pollen can be reprogrammed to follow embryogenic sporophytic pathway than gametophytic route. This shift enables the production of haploid and doubled haploid plants, which are highly useful for genetic mapping and crop improvement (Chu *et al.*, 1975; Bilynska, 2020; Patial *et al.*, 2023a). Chromosome doubling may occur spontaneously or can be induced *via* chemical treatments, though the efficiency of later process depend on genotype, culture conditions, auxin concentration and pre-treatment steps which can significantly affect embryo induction and subsequent plant regeneration. For example, cultivars such as 'Igri' exhibit remarkably higher androgenic competence than less responsive genotypes (van Bergen S *et al.*, 1999; Kruczkowska *et al.*, 2005).

Double Haploid (DH) technology has made a significant impact on barley breeding at the commercial level too, leading to the worldwide release of numerous successful cultivars (Table 7). Much of this progress has been achieved through the *H. vulgare* × *H. bulbosum* crossing system and androgenesis-based strategies. It may be substantiated by a unique example from New Zealand cultivar *Mingo,* which was developed through a doubled haploid barley breeding program. Similarly, several Australian cultivars such as Dhow, Sloop SA, Flagship, Navigator, and Skipper, demonstrated the effectiveness of doubled haploidy for accelerating the development of uniform, commercially useful barley lines by shortening breeding time (Patial *et al.*, 2023a).

Table 7. Representative barley cultivars developed using doubled haploid

Registered Cultivar Name	Release Year	Country of origin	Breeding Approach	Key Features	Scientist(s) / Reference
Mingo	1979	Canada	Developed using *H. bulbosum* method	Known for its high yield potential and desirable malting trait	Ho and Jones (1980)
Rodeo	1984	Canada	Derived through *H. bulbosum* technique	A two-row malting type with better disease resistant	Campbell *et al.* (1984)
DH45	2021	China	Produced *via* F_1 microspore embryogenesis	Exhibits enhanced nitrogen use efficiency, suitable for low input conditions	Xu *et al.* (2021)

8.10 Speed Breeding

Speed breeding has emerged as a powerful tool for speeding up barley improvement through carefully regulating the growing environmental conditions to shorten crop cycle. Using extended photoperiods (up to 22 h light provided by LED systems at approximately 300–500 µmol m^{-2} s^{-1}), controlled temperature regimes (around 22/17 °C day/night), and, in some cases, increased CO_2 concentrations (~700 ppm) may result in shortening of generation cycles from the usual 4–6 months under field conditions to roughly 8–10 weeks (Watson *et al.*, 2018; Wanga *et al.*, 2021). This enables up to 5-6 generations per year, substantially increasing the rate of genetic gain in breeding programs. The feasibility of rapid cycling in barley was clearly demonstrated by Watson et al. (2018), who achieved 5–6 generations annually in spring barley under controlled environmental conditions. Rossi et al. (2024) provided genetic insights into photoperiod responsiveness under accelerated

growth conditions. This study highlights the key role of *PPD-H1* in controlling plant development when crops were grown under speed breeding regimes, emphasizing its significance in governing flowering and growth under longer photoperiods.

Speed breeding is now being effectively combined with other modern and advanced breeding approaches to make crop improvement even faster and more efficient. When integrated with doubled haploid technology, it facilitates breeders to obtain completely homozygous lines in comparatively shorter durations, reducing the time needed to stabilize useful recombination events. Similarly, the integration of genomic selection allows breeders to make early prediction-based selection within these accelerated cycles, leading to identification of promising lines without waiting for extensive field evaluations. Genome-editing strategies further empower this approach by enabling precise and targeted genetic modifications. This adds another level of efficiency and control to modern breeding programs (Varshney *et al*., 2020).

8. Challenges and Limitations in Barley Improvement

Despite the great transformative potential of genomics-assisted breeding, various challenges still limit the pace of genetic improvement in barley (Fig 4). One major constrain is the relatively narrow genetic diversity within elite breeding material. Years of Intensive selection and repeated use of closely related parents have narrowed the genetic base as compared to its wild progenitors thus it is difficult to identify novel alleles through even the modern approaches like GWAS. To address this, breeders increasingly rely on introgression from wild barley, land races and other exotic germplasm to broaden the barley genetic base. However, these donors usually lack good agronomic performance; therefore multiple back crossing over many generation (6-8 cycles) with elite varieties is required to recover desirable traits. As a result, this pre-breeding process becomes both time consuming and resource intensive.

Genotype × environment interactions represent another major limitation, particularly for complex quantitative traits such as yield, stress tolerance and grain quality. The expression and stability of QTLs often decline substantially across contrasting environments due to variation in climate, soil conditions and crop management practices. This variability reduces the predictive accuracy of genomic selection models and complicates marker deployment across target environments. More actionable progress will require environment-specific breeding schemes, including multi-location phenotyping, climate-smart genomic prediction, and selection indices that combine yield stability with stress adaptation rather than yield alone. Breeding for barley in climate-vulnerable regions should therefore emphasize early flowering, terminal heat escape, water-use efficiency, and lodging resistance, alongside grain quality targets relevant to end use.

The application of genome editing technologies such as CRISPR-Cas systems also faces practical constraints. Editing efficiencies remain highly variable across genotypes and transformation protocols, and regeneration capacity is strongly genotype dependent, especially in better performing cultivars. Although next-generation nucleases tools such as Cas12a provide precision in targeting specific DNA regions, there are still concerns regarding unintended off-target mutations. In addition, unclear or still evolving regulatory policies continue to influence how widely and quickly these genome-editing tools are deployed in breeding programs. To improve field impact, genome editing should be directed toward high-priority, large-effect traits such as resistance to key diseases, flowering-time adjustment, and abiotic stress resilience, rather than diffuse trait modification with uncertain gain.

Intensive integrated and multidisciplinary approach is required to overcome these limitations. Emerging multi-omics platforms that bring together genomics, phonemics, transcriptomics and metabolomics are opening up better opportunities to effectively understand and resolve complex trait architecture. At the same time, improved modeling of Genotype × Environment (G×E) interactions, especially the incorporation of climate forecasting and environmental data into genomic prediction, may enhance accuracy and reliability of selection under variable conditions. Furthermore, systematic pre-breeding efforts to utilize wild germplasm, coupled with clear and science-based regulatory frameworks for genome-edited crops will play a key role in realizing sustainable genetic gains in barley under intensifying climate pressures.

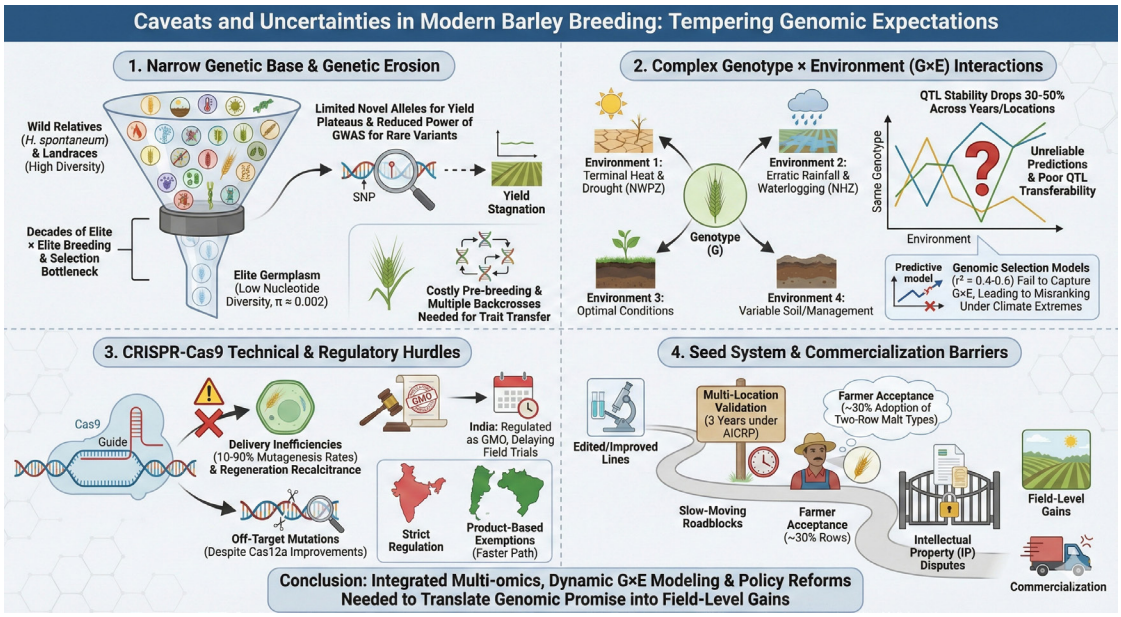

Fig 4. Constraints and Translational Bottlenecks in Modern Barley Breeding: From Genomic Potential to Field-Level Impact

10. Future Prospects and Conclusion

Barley breeding has undergone transformation, progressing from conventional mass and pedigree selection toward an integrated precision-breeding framework that combines genomics, doubled haploid technology, marker-assisted and genomic selection, speed breeding, and CRISPR/Cas-based genome editing. The convergence of these approaches provides unprecedented opportunities to address persistent constraints in barley production, including yield stagnation, climate variability, and inefficient resource utilization, while enabling systematic harnessing of genetic diversity from wild *H. spontaneum* and landrace germplasm. Yet, despite these breakthroughs, significant challenges persist. Climate change poses a formidable threat, manifesting in heat stress, drought and salinity issues that compromise yield stability. Barley's adaptability to marginal environments makes it a crucial crop for food security, but breeding for resilience requires a deeper understanding of stress physiology and the integration of diverse genetic resources. Disease resistance remains another pressing concern, as pathogens continually evolve to overcome existing defenses. The arms race between crops and pathogens necessitates durable resistance strategies, combining conventional breeding with molecular innovations. Genetic bottlenecks, a legacy of domestication and selective breeding, further constrain progress by limiting the pool of adaptive traits available. Addressing these challenges demands a holistic approach that embraces diversity, innovation and sustainability. In the near future, several trait targets show strong translational potential. Genome editing of susceptibility genes such as *eIF4E* offers promising routes to durable resistance against potyviruses, while modification of regulatory loci including *HvERF62* may enhance tolerance to waterlogging stress through improved root anatomical adaptation. Similarly, alleles associated with nitrogen use efficiency provide opportunities to reduce fertilizer inputs substantially without compromising the yield, thereby improving both economic and environmental sustainability. Continued improvement of harvest index, grain number per spike and grain weight remains central to achieving sustained genetic gain across diverse rainfed and marginal production environments.

Future advances in barley improvement will depend on the development of fully integrated breeding platforms that combine accelerated generation turnover with predictive analytics. The integration of conventional pedigree selection with doubled haploid production and speed breeding protocols–enabling up to six generations annually–can substantially shorten breeding cycles. At the same time, genomic selection models incorporating dynamic genotype × environment interactions, together with systems biology approaches that integrate multi-omics datasets and high-throughput phenotyping technologies such as drone-based imaging, will enhance prediction accuracy under variable climatic conditions.

Equally important are the translational considerations beyond genetics. Strengthening pre-breeding pipelines, improving farmer-centric seed delivery systems, and clarifying intellectual property and regulatory frameworks will be essential to ensure that technological innovations are converted into measurable on-farm benefits.

Overall, barley occupies a unique position among cereal crops as both are a globally important commodity and a tractable genetic model for the *Triticeae*. Its long history of domestication and adaptation, combined with rapidly advancing genomic resources and breeding technologies, positions barley as a key platform for developing climate-resilient cropping systems. The continued integration of diverse genetic resources with precision breeding strategies will be critical for meeting future demands for food, feed and industrial uses under increasingly constrained environmental conditions.

Acknowledgments

Research was supported by the Indian Council of Agricultural Research, Department of Agricultural Research and Education, Government of India. The authors acknowledge ICAR-IARI, New Delhi for in-house project on rust resistance barley breeding at ICAR-IARI, Regional Station, Tutikandi Centre, Shimla (H.P).

Conflict of Interest

The authors declare no conflicts of interest relevant to this article.

Author Contributions

The review was written and enriched by Madhu Patial and Vandana Thakur. Santosh Kumar Bishnoi, Prem Lal Kashyp, Dharam Pal and Kallol Kumar Pramanick comprehensively edited all sections. All authors read, edited, and approved the final manuscript.

Ethical Approval

Ethical approval was not required for this study as it did not involve human or animal subjects.

Generative AI or AI/Assisted Technologies use in Manuscript Preparation

The figures were edited using AI tools.

References

1. Afanasenko O, I Rozanova, A Gofman, N Lashina, F Novakazi, N Mironenko, O Baranova and A Zubkovich. 2022. Validation of Molecular Markers of Barley Net Blotch Resistance Loci on Chromosome 3H for Marker-Assisted Selection. *Agriculture*, **12**, Multidisciplinary Digital Publishing Institute.
2. Ajayi OO, P Bregitzer, K Klos, G Hu, JG Walling, and R Mahalingam. 2023. QTL mapping of shoot and seed traits impacted by Drought in Barley using a recombinant inbred line Population. *BMC Plant Biol* **23**:283.
3. Akar T, E Francia, A Tondelli, F Rizza, AM Stanca, and N Pecchioni. 2009. Marker-assisted characterization of frost tolerance in barley (*Hordeum vulgare* L.). *Plant Breeding*, **128**:381–386.
4. Allaby RG. 2015. Barley domestication: the end of a central dogma? *Genome Biol*, **16**:176.
5. Alqudah AM, R Sharma, RK Pasam, A Graner, B Kilian, and T Schnurbusch. 2014. Genetic dissection of photoperiod response based on GWAS of pre-anthesis phase duration in spring barley. *PLoS One*, **9**:e113120.
6. Alsamadany H, AS Abdulbaki, and Y Alzahrani. 2024. Unravelling drought and salinity stress responses in barley genotypes: physiological, biochemical, and molecular insights. *Front Plant Sci*, **15**.
7. Bayer MM, P Rapazote-Flores, M Ganal, PE Hedley, M Macaulay, J Plieske, L Ramsay, J Russell, PD Shaw, W Thomas, and R Waugh. Development and Evaluation of a Barley 50k iSelect SNP Array. *Front Plant Sci*. 2017: **8**:1792. doi: 10.3389/fpls.2017.01792.
8. Bettenhausen HM, L Barr, CD Broeckling, JM Chaparro, C Holbrook, D Sedin, and AL Heuberger. 2018. Influence of malt source on beer chemistry, flavor, and flavor stability. *Food Research International*, **113**:487–504.
9. Bhatty RS. 1999.The Potential of Hull-less Barley. *Cereal Chemistry*, **76**:589–599.
10. Bilynska O. 2020. Influence of Spike Pretreatment at Low Temperatures on Efficiency of Spring Barley Haploid Production in Anther Culture in Vitro. *Problems of Cryobiology and Cryomedicine*, **30**:68–76.
11. Bishnoi SK, M Patial, C Lal, and RPS Verma. 2022. Barley Breeding, in *Fundamentals of Field*

Crop Breeding (Yadava DK, Dikshit HK, Mishra GP, and Tripathi S eds), pp 259–308, Springer Nature Singapore, Singapore.

12. Börner A, V Korzun, and AJ Worland. 1998. Comparative genetic mapping of loci affecting plant height and development in cereals. *Euphytica*, **100**:245–248.
13. Braumann I, W Urban, A Preuß, C Dockter, S Zakhrabekova, and M Hansson. 2018. Semi-dwarf barley (*Hordeum vulgare* L.) *brh2* and *ari-l* mutants are deficient in a U-box E3 ubiquitin ligase. *Plant Growth Regul*, **86**:223–234.
14. Brueggeman R, N Rostoks, D Kudrna, A Kilian, F Han, J Chen, A Druka, B Steffenson, and A Kleinhofs. 2002. The barley stem rust-resistance gene *Rpg1* is a novel disease-resistance gene with homology to receptor kinases. *Proceedings of the National Academy of Sciences*, **99**:9328–9333.
15. Brunner SM, E Dinglasan, S Baraibar, S Alahmad, C Katsikis, S van der Meer, J Godoy, D Moody, M Smith, L Hickey, and H Robinson. 2024. Characterizing stay-green in barley across diverse environments: unveiling novel haplotypes. *Theor Appl Genet*, **137**:120.
16. Büschges R, K Hollricher, R Panstruga, G Simons, M Wolter, A Frijters, R van Daelen, Lee T van der, P Diergaarde, J Groenendijk, S Töpsch, P Vos, F Salamini, and P Schulze-Lefert. 1997. The Barley *Mlo* Gene: A Novel Control Element of Plant Pathogen Resistance. *Cell*, **88**:695–705, Elsevier.
17. Campbell KW, RI Brawn, and Ho KM. Rodeo Barley. 1984. *Can J Plant Sci*, **64**:203–205.
18. Chapman B, V Dang, T He, C Hill, H Hu, P Wang, PE Bayer, D Edwards, G Keeble-Gagnère, J Tibbits, and C Li. 2026. The graphical barley pangenome reveals micro- and macro-scale genetic variation. *Agriculture Communications*, **4**:100131.
19. Chen B, Y Hou, Y Huo, Z Zeng, D Hu, X Mao, C Zhong, Y Xu, X Tang, X Gao, J Ma, and G Chen. 2024. QTL Mapping of Yield, Agronomic, and Nitrogen-Related Traits in Barley (*Hordeum vulgare* L.) under Low Nitrogen and Normal Nitrogen Treatments. *Plants*, **13**.
20. Chu C, Wang C-c, SC San, H Chen, YK Chu, CC Yin, and BF Yun. 1975. Establishment of an Efficient Medium for Anther Culture of Rice through Comparative Experiments on the Nitrogen Sources. *Scientia Sinica*, 18:659–668.
21. Collard BCY, MZZ Jahufer, JB Brouwer and ECK Pang. 2005. An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. *Euphytica*, **142**:169–196.
22. Collins NC, NG Paltridge, CM Ford, and RH Symons. 1996. The Yd2 gene for barley yellow dwarf virus resistance maps close to the centromere on the long arm of barley chromosome 3. *Theor Appl Genet*, **92**:858–864.
23. Comadran J, B Kilian, J Russell, L Ramsay, N Stein, M Ganal, P Shaw, M Bayer, W Thomas, and D Marshall. 2012. Natural variation in a homolog of Antirrhinum CENTRORADIALIS contributed to spring growth habit and environmental adaptation in cultivated barley. *Nature genetics*, **44**:1388–1392.
24. Crossa J, P Pérez-Rodríguez, J Cuevas, O Montesinos-López, D Jarquín, G de Los Campos, J Burgueño, JM González-Camacho, S Pérez-Elizalde, Y Beyene, S Dreisigacker, R Singh, X Zhang, M Gowda, M Roorkiwal, J Rutkoski and RK Varshney. 2017. Genomic Selection in Plant Breeding: Methods, Models, and Perspectives. *Trends Plant Sci*, **22**:961–975.
25. Cu ST, TJ March, S Stewart, S Degner, S Coventry, A Box, D Stewart, B Skadhauge, RA Burton, GB Fincher, and J Eglinton. 2016. Genetic analysis of grain and malt quality in an elite barley population. *Mol Breeding*, **36**:129.
26. Czembor JH, A Pietrusińska, U Piechota, and D Mańkowski. 2019. Resistance to powdery mildew in barley recombinant lines derived from crosses between *Hordeum vulgare* and *Hordeum bulbosum*. *Cereal Research Communications*, **47**:463–472, Akadémiai Kiadó.
27. Dahleen LS, LJ Vander Wal, and JD Franckowiak. 2005. Characterization and Molecular Mapping of Genes Determining Semidwarfism in Barley. *J Hered*, **96**:654–662.

28. Dai F, Z-H Chen, X Wang, Z Li, G Jin, D Wu, S Cai, N Wang, F Wu, E Nevo, and G Zhang. 2014. Transcriptome profiling reveals mosaic genomic origins of modern cultivated barley. *Proc Natl Acad Sci U S A*, **111**:13403–13408.

29. Dockter C, and M Hansson. 2015. Improving barley culm robustness for secured crop yield in a changing climate. *Journal of Experimental Botany*, **66**:3499–3509.

30. Dreiseitl A. 2024. Mlo-Mediated Broad-Spectrum and Durable Resistance against Powdery Mildews and Its Current and Future Applications. *Plants*, **13**:138.

31. Dreiseitl A. 2020. Specific resistance of barley to powdery mildew, its use and beyond: A concise critical review. *Genes*, **11**:971, MDPI.

32. Eglinton JK, P Langridge, and DE Evans. 1998. Thermostability variation in alleles of barley *beta*-amylase. *Journal of Cereal Science*, **28**:301–309.

33. Ejaz M, and M von Korff. 2017. The Genetic Control of Reproductive Development under High Ambient Temperature. *Plant Physiol*, **173**:294–306.

34. Elouadi F, A Amri, A El-Baouchi, Z Kehel, G Salih, A Jilal, B Kilian, and M Ibriz. 2021. Evaluation of a set of *Hordeum vulgare* subsp. *spontaneum* accessions for -Glucans and microelement contents. *Agriculture*, **11**:950, MDPI.

35. Fan Y, S Shabala, Y Ma, R Xu, and M Zhou. 2015. Using QTL mapping to investigate the relationships between abiotic stress tolerance (drought and salinity) and agronomic and physiological traits. *BMC Genomics*, **16**:43.

36. Fang Y, X Zhang, and D Xue. 2019. Genetic analysis and molecular breeding applications of malting quality QTLs in barley. *Frontiers in Genetics*, **10**:352, Frontiers Media SA.

37. Fang Z, AM Gonzales, MT Clegg, KP Smith, GJ Muehlbauer, BJ Steffenson, and PL Morrell. 2014. Two Genomic Regions Contribute Disproportionately to Geographic Differentiation in Wild Barley. *G3 (Bethesda)*, **4**:1193–1203.

38. FAO. (2024). World food and agriculture – Statistical yearbook 2024. Food and Agriculture Organization of the United Nations. https://www.fao.org/faostat/en/ - data/QCL

39. Farooqi MQU, D Moody, G Bai, A Bernardo, P St. Amand, AJ Diggle, and Z Rengel. 2023. Genetic characterization of root architectural traits in barley (*Hordeum vulgare* L.) using SNP markers. *Front Plant Sci*, **14**.

40. Forster BP, E Heberle-Bors, KJ Kasha, and A Touraev. The resurgence of haploids in higher plants. *Trends Plant Sci* 2007, **12**:368–375.

41. Francia E, F Rizza, L Cattivelli, AM Stanca, G Galiba, B Tóth, PM Hayes, JS Skinner, and N Pecchioni. 2004. Two loci on chromosome 5H determine low-temperature tolerance in a 'Nure' (winter) × 'Tremois' (spring) barley map. *Theor Appl Genet*, **108**:670–680.

42. Fuller DQ, G Willcox, and RG Allaby. 2011. Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. *World Archaeology*, **43**:628–652.

43. Ganal MW, T Altmann, and MS Röder. 2009. SNP identification in crop plants. *Current Opinion in Plant Biology*, **12**:211–217.

44. Gao G, L Yan, Y Cai, Y Guo, C Jiang, Q He, S Tasnim, Z Feng, J Liu, J Zhang, T Komatsuda, M Mascher, and P Yang. 2024. Most Tibetan weedy barleys originated via recombination between *Btr1* and *Btr2* in domesticated barley. *Plant Commun*, **5**:100828.

45. Gayon J, and DT Zallen. 1998. The Role of the Vilmorin Company in the Promotion and Diffusion of the Experimental Science of Heredity in France, 1840–1920. *Journal of the History of Biology*, **31**:241–262.

46. Ge C, E Wentzel, N D'Souza, K Chen, RP Oliver, and SR Ellwood. 2021 Adult resistance genes to barley powdery mildew confer basal penetration resistance associated with broad-spectrum resistance. *The Plant Genome*, **14**:e20129.

47. Geng L, M Li, G Zhang, and L Ye. 2022. Barley: a potential cereal for producing healthy and functional foods. *Food Quality and Safety* **6**, Oxford University Press (OUP).

48. Genievskaya Y, S Abugalieva, and Y Turuspekov. 2025. Identification of QTLs associated with grain yield-related traits of spring barley. *BMC Plant Biol*, **25**:554.

49. Gharaghanipor N, A Arzani, M Rahimmalek, and R Ravash. 2022. Physiological and Transcriptome Indicators of Salt Tolerance in Wild and Cultivated Barley. *Front Plant Sci*, **13**.

50. Graner A, S Streng, A Kellermann, A Schiemann, E Bauer, R Waugh, B Pellio, and F Ordon. 1999. Molecular mapping and genetic fine-structure of the *rym5* locus encoding resistance to different strains of the Barley Yellow Mosaic Virus Complex. *Theor Appl Genet*, **98**:285–290.

51. Guo W, M Schreiber, VB Marosi. 2025. et al. A barley pan-transcriptome reveals layers of genotype-dependent transcriptional complexity. *Nat Genet*, **57**:441–450.

52. Gustafsson Å, A Hagberg, G Persson, and K Wiklund. 1971. Induced mutations and barley improvement. *Theoret Appl Genetics*, **41**:239–248.

53. Hagenblad J, and MW Leino. 2022. Chevalier barley: The influence of a world-leading malting variety. *Crop Science*, **62**:235–246.

54. Heffner EL, ME Sorrells, and JL Jannink. 2009. Genomic Selection for Crop Improvement. Crop Science, **49**(1):1-12.

55. Hickey LT, W Lawson, GJ Platz, M Dieters, VN Arief, S Germán, S Fletcher, RF Park, D Singh, S Pereyra, and J Franckowiak. 2011. Mapping *Rph20*: a gene conferring adult plant resistance to Puccinia hordei in barley. *Theor Appl Genet*, **123**:55–68.

56. Hisano H, RE Hoffie, F Abe, H Munemori, T Matsuura, M Endo, M Mikami, S Nakamura, J Kumlehn, and K Sato. 2022. Regulation of germination by targeted mutagenesis of grain dormancy genes in barley. *Plant Biotechnology Journal*, **20**:37–46.

57. HO KM, and JONES. 1980. Mingo barley. *Can J Plant Sci*, **60**:279–280.

58. Ho KM, and KJ Kasha. 1975. Genetic Control of Chromosome Elimination during Haploid Formation in Barley. *Genetics*, **81**:263–275.

59. Hoffie RE, I Otto, D Perovic, N Budhagatapalli, A Habekuß, F Ordon, and J Kumlehn. 2021.Targeted Knockout of Eukaryotic Translation Initiation Factor 4E Confers Bymovirus Resistance in Winter Barley. *Front Genome Ed*, **3**.

60. Holme I, T Wendt, J Gil-Humanes, L Deleuran, C Starker, D Voytas, and H Brinch-Pedersen. 2017. Evaluation of the mature grain phytase candidate HvPAPhy_a gene in barley (*Hordeum vulgare* L.) using CRISPR/Cas9 and TALENs. *Plant Molecular Biology*, **95**.

61. ICAR-Indian Institute of Wheat and Barley Research. (2024). Barley cultivars released in India: Names, parentages, origins and adaptations. Karnal, India: ICAR-IIWBR.

62. Ishikawa G, H Sakai, N Mizuno, E Solovieva, T Tanaka, and K Matsubara. 2022. Developing core marker sets for effective genomic-assisted selection in wheat and barley breeding programs. *Breed Sci*, **72**:257–266.

63. Jacquard C, F Mazeyrat-Gourbeyre, P Devaux, K Boutilier, F Baillieul, and C Clément. 2009Microspore embryogenesis in barley: anther pre-treatment stimulates plant defense gene expression. *Planta*, **229**:393–402.

64. Jakob SS, D Rödder, JO Engler, S Shaaf, H Özkan, FR Blattner, and B Kilian. 2014. Evolutionary History of Wild Barley (*Hordeum vulgare* subsp. *spontaneum*) Analyzed Using Multilocus Sequence Data and Paleodistribution Modeling. *Genome Biol Evol*, **6**:685–702.

65. Jayakodi M, Q Lu, H Pidon, MT Rabanus-Wallace, M Bayer, T Lux, Y Guo, B Jaegle, A Badea, W Bekele, GS Brar, K Braune, B Bunk, KJ Chalmers, B Chapman, ME Jørgensen, J-W Feng, M Feser, A Fiebig, H Gundlach, W Guo, G Haberer, M Hansson, A Himmelbach, I Hoffie, RE Hoffie, H Hu, S Isobe, P König, SM Kale, N Kamal, G Keeble-Gagnère, B Keller, M Knauft, R Koppolu, SG Krattinger, J Kumlehn, P Langridge, Li C Langridge, MP Marone, A Maurer, KFX Mayer, M Melzer, GJ Muehlbauer, E Murozuka, S Padmarasu, D Perovic, K Pillen, PA Pin, CJ Pozniak, L Ramsay, PR Pedas, T Rutten, S Sakuma, K Sato, D Schüler, T Schmutzer, U Scholz, M Schreiber, K Shirasawa, C Simpson,

B Skadhauge, M Spannagl, BJ Steffenson, HC Thomsen, JF Tibbits, MTS Nielsen, C Trautewig, D Vequaud, C Voss, P Wang, R Waugh, S Westcott, MW Rasmussen, R Zhang, X-Q Zhang, T Wicker, C Dockter, M Mascher, and N Stein. 2024. Structural variation in the pangenome of wild and domesticated barley. *Nature*, **636**:654–662.

66. Jefferies SP, BJ King, AR Barr, P Warner, SJ Logue, and P Langridge. 2003. Marker-assisted backcross introgression of the *Yd2* gene conferring resistance to barley yellow dwarf virus in barley. *Plant Breeding*, **122**:52–56.

67. Kapusi E, M Corcuera-Gómez, S Melnik, and E Stoger. 2017. Heritable Genomic Fragment Deletions and Small Indels in the Putative ENGase Gene Induced by CRISPR/Cas9 in Barley. *Front Plant Sci*, **8**.

68. Kasha, K.J., Kao, K.N. 1970.High frequency haploid production in barley (*Hordeum vulgare* L.). *Nature*, **225**:874–876.

69. Kelly JH, AJ Gilmore, A Situmorang, KD Porker, M Marzec, MR Tucker, and PB Brewer. 2025. Strigolactones coordinate barley tillering and grain size. *J Exp Bot*, **76**:4538–4554.

70. Kis A, É Hamar, G Tholt, R Bán, and Z Havelda. 2019. Creating highly efficient resistance against wheat dwarf virus in barley by employing CRISPR/Cas9 system. *Plant Biotechnol J.*, **17**:1004-1006. doi: 10.1111/pbi.13077.

71. Kislev ME, D Nadel, and I Carmi. 1992. Epipalaeolithic (19,000 BP) cereal and fruit diet at Ohalo II, Sea of Galilee, Israel. *Review of Palaeobotany and Palynology*, **73**:161–166.

72. Knipfer T, M Besse, J-L Verdeil, and W Fricke. 2011. Aquaporin-facilitated water uptake in barley (*Hordeum vulgare* L.) roots. *J Exp Bot*, **62**:4115–4126.

73. Komatsuda T, Pourkheirandish M, He C, P Azhaguvel, H Kanamori, D Perovic, N Stein, A Graner, T Wicker, A Tagiri, U Lundqvist, T Fujimura, M Matsuoka, T Matsumoto, and M Yano. 2007. Six-rowed barley originated from a mutation in a homeodomain-leucine zipper I-class homeobox gene. *Proceedings of the National Academy of Sciences*, **104**:1424–1429, Proceedings of the National Academy of Sciences.

74. Kruczkowska H, H Pawlowska, and B Skuci ska. 2005. Effect of 2,4-D Concentration on the Androgenic Response in Anther Culture of Barley. *Cereal Research Communications*, **33**:727–732.

75. Kuczyńska A, M Surma, T Adamski, K Mikołajczak, K Krystkowiak, and P Ogrodowicz. 2013. Effects of the semi-dwarfing *sdw1/denso* gene in barley. *J Appl Genet*, **54**:381–390.

76. Kumar S, M Patial, and R Sharma. Efficient Barley Breeding. 2020 *In*: Accelerated Plant Breeding, Volume 1 (Gosal SS, and Wani SH eds), pp 309–364, Springer International Publishing, Cham.

77. Kuppu S, M Ron, MPA Marimuthu, G Li, A Huddleson, MH Siddeek, J Terry, R Buchner, N Shabek, L Comai, and AB Britt. 2020. A variety of changes, including CRISPR/Cas9-mediated deletions, in CENH3 lead to haploid induction on outcrossing. *Plant Biotechnol J*, **18**:2068–2080.

78. Kusch S, and R Panstruga. 2017. mlo-Based Resistance: An Apparently Universal "Weapon" to Defeat Powdery Mildew Disease. *MPMI*, **30**:179–189, Scientific Societies.

79. Lawrenson T, M Clarke, R Kirby, M Forner, B Steuernagel, JKM Brown, and W Harwood. 2024. An optimised CRISPR Cas9 and Cas12a mutagenesis toolkit for Barley and Wheat. *Plant Methods*, **20**:123.

80. Lawrenson T, and WA Harwood. Creating Targeted Gene Knockouts in Barley Using CRISPR/Cas9, in *Barley* (Harwood WA ed) 2019, pp 217–232, Springer New York, New York, NY.

81. Leiva F, R Dhakal, K Himanen, R Ortiz, and A Chawade. 2024. The Combination of Low-Cost, Red–Green–Blue (RGB) Image Analysis and Machine Learning to Screen for Barley Plant Resistance to Net Blotch. *Plants (Basel)*, **13**:1039.

82. Li L, Q Zhang, and D Huang. 2014. A Review of Imaging Techniques for Plant Phenotyping. *Sensors*, **14**:20078–20111.

83. Lister DL, H Jones, HR Oliveira, CA Petrie, X Liu, J Cockram, CJ Kneale, O Kovaleva, and MK Jones. 2018. Barley heads east: Genetic analyses reveal routes of spread through diverse Eurasian landscapes. *PLoS One*, **13**:e0196652.

84. Liu F, R Lance, R Loughman, S Gupta, Li C, M Jones, and X-Q Zhang. 2010 PCR markers for selection of adult plant leaf rust resistance in barley (*Hordeum vulgare* L.). *Molecular Breeding*, **28**.

85. Lorenz AJ, KP Smith, and JL Jannink. 2012. Potential and optimization of genomic selection for Fusarium head blight resistance in six-row barley. *Crop Science*, **52**:1609–1621.

86. Lukina KA, IV Porotnikov, OYu Antonova, and ON Kovaleva. 2024. Determination of the Allelic Composition of the *sdw1/denso* (HvGA20ox2), uzu1 (HvBRI1) and ari-e (HvDep1) Genes in Spring Barley Accessions from the VIR Collection. *Plants (Basel)*, **13**:376.

87. Lyngkjær M, A Newton, J Atzema, and S Baker. 2000. The Barley *mlo*-gene: an important powdery mildew resistance source. *Agronomie*, **20**:745–756.

88. Mammadov JA, JC Zwonitzer, RM Biyashev, CA Griffey, Y Jin, BJ Steffenson, and MAS Maroof. 2003. Molecular Mapping of Leaf Rust Resistance Gene *Rph5* in Barley. *Crop Science*, **43**:388–393.

89. Mascher M, VJ Schuenemann, U Davidovich, N Marom, A Himmelbach, S Hübner, A Korol, M David, E Reiter, S Riehl, M Schreiber, SH Vohr, RE Green, IK Dawson, J Russell, B Kilian, GJ Muehlbauer, R Waugh, T Fahima, J Krause, E Weiss, and N Stein. 2016. Genomic analysis of 6,000-year-old cultivated grain illuminates the domestication history of barley. *Nat Genet*, **48**:1089–1093.

90. Mascher M, T Wicker, J Jenkins, C Plott, T Lux, CS Koh, J Ens, H Gundlach, LB Boston, Z Tulpová, S Holden, I Hernández-Pinzón, U Scholz, KFX Mayer, M Spannagl, CJ Pozniak, AG Sharpe, H Šimková, MJ Moscou, J Grimwood, J Schmutz, and N Stein. 2021. Long-read sequence assembly: a technical evaluation in barley. *Plant Cell*, **33**:1888–1906.

91. Maurer A, V Draba, and K Pillen. 2016. Genomic dissection of plant development and its impact on thousand grain weight in barley through nested association mapping. *J Exp Bot*, **67**:2507–2518.

92. Mayer KFX, M Martis, PE Hedley, H Šimková, H Liu, JA Morris, B Steuernagel, S Taudien, S Roessner, H Gundlach, M Kubaláková, P Suchánková, F Murat, M Felder, T Nussbaumer, A Graner, J Salse, T Endo, H Sakai, T Tanaka, T Itoh, K Sato, M Platzer, T Matsumoto, U Scholz, J Doležel, R Waugh, and N Stein. 2011. Unlocking the Barley Genome by Chromosomal and Comparative Genomics. *Plant Cell*, **23**:1249–1263.

93. Mayer KFX, R Waugh, P Langridge, TJ Close, RP Wise, A Graner, T Matsumoto, K Sato, A Schulman, GJ Muehlbauer, N Stein, R Ariyadasa, D Schulte, N Poursarebani, R Zhou, B Steuernagel, M Mascher, U Scholz, B Shi, P Langridge, K Madishetty, JT Svensson, P Bhat, M Moscou, J Resnik, TJ Close, GJ Muehlbauer, P Hedley, H Liu, J Morris, R Waugh, Z Frenkel, A Korol, H Bergès, A Graner, N Stein, B Steuernagel, U Scholz, S Taudien, M Felder, M Groth, M Platzer, N Stein, B Steuernagel, U Scholz, A Himmelbach, S Taudien, M Felder, M Platzer, S Lonardi, D Duma, M Alpert, F Cordero, M Beccuti, G Ciardo, Y Ma, S Wanamaker, TJ Close, N Stein, F Cattonaro, V Vendramin, S Scalabrin, S Radovic, R Wing, D Schulte, B Steuernagel, M Morgante, N Stein, R Waugh, T Nussbaumer, H Gundlach, M Martis, R Ariyadasa, N Poursarebani, B Steuernagel, U Scholz, RP Wise, J Poland, N Stein, KFX Mayer, M Spannagl, M Pfeifer, H Gundlach, KFX Mayer, H Gundlach, C Moisy, J Tanskanen, S Scalabrin, A Zuccolo, V Vendramin, M Morgante, KFX Mayer, A Schulman, M Pfeifer, M Spannagl, P Hedley, J Morris, J Russell, et al. 2012. A physical, genetic and functional sequence assembly of the barley genome. *Nature*, **491**:711–716, Nature Publishing Group.

94. Miklis M, C Consonni, RA Bhat, V Lipka, P Schulze-Lefert, and R Panstruga. 2007. Barley MLO modulates actin-dependent and actin-independent antifungal defense pathways at the cell periphery. *Plant Physiol*, **144**:1132–1143.

95. Mikołajczak K, P Ogrodowicz, H Ćwiek-Kupczyńska, K Weigelt-Fischer, SR Mothukuri, A Junker, T Altmann, K Krystkowiak, T Adamski, M Surma, A Kuczyńska, and P Krajewski. 2020. Image Phenotyping of Spring Barley (*Hordeum vulgare* L.) RIL Population under Drought: Selection of Traits and Biological Interpretation. *Front Plant Sci*, **11**.

96. Monat C, S Padmarasu, T Lux, T Wicker, H Gundlach, A Himmelbach, J Ens, C Li, GJ Muehlbauer, AH Schulman, R Waugh, I Braumann, C Pozniak, U Scholz, KFX Mayer, M Spannagl, N

Stein, and M Mascher. 2019. TRITEX: chromosome-scale sequence assembly of Triticeae genomes with open-source tools. *Genome Biol*, **20**:284.

97. Montesinos-López OA, S Ramos-Pulido, CM Hernández-Suárez, BA Mosqueda González, FA Valladares-Anguiano, P Vitale, A Montesinos-López, and J Crossa. 2023. A novel method for genomic-enabled prediction of cultivars in new environments. *Front Plant Sci*, **14**.

98. Morrell PL, and MT Clegg. 2007. Genetic evidence for a second domestication of barley (*Hordeum vulgare*) east of the Fertile Crescent. *Proc Natl Acad Sci U S A*, **104**:3289–3294.

99. Morrell PL, AM Gonzales, KKT Meyer, and MT Clegg. 2014. Resequencing data indicate a modest effect of domestication on diversity in barley: a cultigen with multiple origins. *J Hered*, **105**:253–264.

100. Muñoz-Amatriaín M, J Hernandez, D Herb, PS Baenziger, AM Bochard, F Capettini, A Casas, A Cuesta-Marcos, C Einfeldt, S Fisk, A Genty, L Helgerson, M Herz, G Hu, E Igartua, I Karsai, T Nakamura, K Sato, K Smith, E Stockinger, W Thomas, and P Hayes. 2020. Perspectives on Low Temperature Tolerance and Vernalization Sensitivity in Barley: Prospects for Facultative Growth Habit. *Front Plant Sci*, **11**.

101. Nakamura S, M Pourkheirandish, H Morishige, M Sameri, K Sato, and T Komatsuda. 2017. Quantitative Trait Loci and Maternal Effects Affecting the Strong Grain Dormancy of Wild Barley (*Hordeum vulgare* ssp. *spontaneum*). *Front Plant Sci*, **8**.

102. Nevo E, and G Chen. 2010. Drought and salt tolerances in wild relatives for wheat and barley improvement. *Plant Cell Environ*, **33**:670–685.

103. Ogrodowicz P, K Mikołajczak, M Kempa, M Mokrzycka, P Krajewski, and A Kuczy ska. 2023. Genome-wide association study of agronomical and root-related traits in spring barley collection grown under field conditions. *Front Plant Sci*, **14**, Frontiers.

104. Pan Y, J Zhu, Y Hong, M Zhang, C Lv, B Guo, H Shen, X Xu, and R Xu. 2021. Identification of novel QTL contributing to barley yellow mosaic resistance in wild barley (*Hordeum vulgare* spp. *spontaneum*). *BMC Plant Biol*, **21**:560.

105. Pasam RK, R Sharma, M Malosetti, FA van Eeuwijk, G Haseneyer, B Kilian, and A Graner. 2012. Genome-wide association studies for agronomical traits in a worldwide spring barley collection. *BMC Plant Biol*, **12**:16.

106. Patial Madhu, R Chauhan, HK Chaudhary, KK Pramanick, AK Shukla, V Kumar, and RPS Verma. 2023b. Au-courant and novel technologies for efficient doubled haploid development in barley (*Hordeum vulgare* L.). *Crit Rev Biotechnol*, **43**:575–593.

107. Patial M., M Kumar, SK Bishnoi, D Pal, KK Pramanick, AK Shukla, and Gandhi S. 2023. Genetic variability and trait association for grain yield in barley (*Hordeum vulgare* L.). *Journal of Cereal Research* 2023a, **15** (2): 284-293.

108. Paynter B, R Jettner, R Lance, C Li, A Tarr, and L Schultz. 2004. Characterising new malting barley cultivars – Hamelin and Baudin – from Western Australia. Proceedings of the 5th Australian Barley Technical Symposium, Fremantle, Western Australia: 20-23.

109. Pellio B, S Streng, E Bauer, N Stein, D Perovic, A Schiemann, W Friedt, F Ordon, and A Graner. 2005. High-resolution mapping of the Rym4/Rym5 locus conferring resistance to the barley yellow mosaic virus complex (BaMMV, BaYMV, BaYMV-2) in barley (*Hordeum vulgare* ssp. *vulgare* L.). *Theor Appl Genet*, **110**:283–293.

110. Pidon H, N Wendler, A Habekuβ, A Maasberg, B Ruge-Wehling, D Perovic, F Ordon, and N Stein. 2021. High-resolution mapping of *Rym14Hb*, a wild relative resistance gene to barley yellow mosaic disease. *Theor Appl Genet*, **134**:823–833.

111. Poets AM, Z Fang, MT Clegg, and PL Morrell. 2015. Barley landraces are characterized by geographically heterogeneous genomic origins. *Genome Biol*, **16**:173.

112. Pourkheirandish M, G Hensel, B Kilian, N Senthil, G Chen, M Sameri, P Azhaguvel, S Sakuma, S Dhanagond, R Sharma, M Mascher, A Himmelbach, S Gottwald, SK Nair, A Tagiri, F Yukuhiro, Y Nagamura, H Kanamori, T Matsumoto, G Willcox, CP Middleton, T Wicker, A Walther, R Waugh, GB Fincher, N Stein, J Kumlehn, K Sato, and T Komatsuda. 2015. Evolution of the Grain Dispersal System in Barley. *Cell*, **162**:527–539.

113. Pourkheirandish M, and T Komatsuda. 2007. The Importance of Barley Genetics and Domestication in a Global Perspective. *Ann Bot*, **100**:999–1008.

114. Poursarebani N, R Ariyadasa, R Zhou, D Schulte, B Steuernagel, MM Martis, A Graner, P Schweizer, U Scholz, K Mayer, and N Stein. 2013. Conserved synteny-based anchoring of the barley genome physical map. *Funct Integr Genomics*, **13**:339–350.

115. Ramage RT. 1987. A History of Barley Breeding Methods, in *Plant Breeding Reviews*, pp 95–138, John Wiley & Sons, Ltd.

116. Ramage RT, and RT Ramage. 1965. Balanced tertiary trisomics for use in hybrid seed production. *Crop Sci*, **5**:177–78.

117. Ramsay L, J Comadran, A Druka, DF Marshall, WTB Thomas, M Macaulay, K MacKenzie, C, Fuller J Simpson, N Bonar, PM Hayes, U Lundqvist, JD Franckowiak, TJ Close, GJ Muehlbauer, and R Waugh. 2011. INTERMEDIUM-C, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene TEOSINTE BRANCHED 1. *Nat Genet*, **43**:169–172.

118. Rossi N, W Powell, IJ Mackay, L Hickey, A Maurer, K Pillen, K Halliday, and R Sharma. 2024. Investigating the genetic control of plant development in spring barley under speed breeding conditions. *Theor Appl Genet*, **137**:115.

119. Roy D, E Dinglasan, R Fowler, G Platz, R Lance, L Synman, J Franckowiak, LT Hickey, K Voss-Fels, and H Robinson. 2025. Genomic regions associated with spot blotch resistance in elite barley breeding populations. *Mol Breeding*, **45**:16.

120. Sabouri H, B Kazerani, F Taliei, Z Pezeshkian, and S Ghasemi. 2025. New insights into the genetic basis of terminal heat tolerance in Iranian barley via important genomic regions controlling chlorophyll fluorescence parameters. *Plant Gene*, **44**:100535.

121. Safhi FA. 2025 Enhancing barley resilience: advanced genetic techniques to improve drought tolerance for sustainable cultivation under current climatic fluctuations. *Cereal Res Commun*, 53(1):17–33.

122. Sangwan N, J Jadaun, S Budhwar. 2026. et al. Innovative insights of barley genomics and biotechnology for nutraceuticals, sustainable agriculture, and bioeconomy. *Discov Food*, **6**:117.

123. Sato K. 2020. History and future perspectives of barley genomics. *DNA Res*, **27**:dsaa023.

124. Sato K, M Yamane, N Yamaji, H Kanamori, A Tagiri, JG Schwerdt, GB Fincher, T Matsumoto, K Takeda, and T Komatsuda. 2016. Alanine aminotransferase controls seed dormancy in barley. *Nat Commun*, **7**:11625, Nature Publishing Group.

125. Skinner JS, J von Zitzewitz, P Szűcs, L Marquez-Cedillo, T Filichkin, K Amundsen, EJ Stockinger, MF Thomashow, THH Chen, and PM Hayes. 2005. Structural, Functional, and Phylogenetic Characterization of a Large CBF Gene Family in Barley. *Plant Mol Biol*, **59**:533–551.

126. Song J, R Datla, J Zou, and D Xiang. 2024. Haploid induction: an overview of parental factor manipulation during seed formation. *Front Plant Sci*, **15**:1439350.

127. Stadler LJ. 1928. Mutations in Barley Induced by X-Rays and Radium. *Science* 1928, **68**:186–187.

128. Steffenson BJ, Y Jin, and CA Griffey. 1993. Pathotypes of *Puccinia hordei* with virulence for the barley leaf rust resistance gene *Rph7* in the United States. *Plant Dis*, **77**:867–869.

129. Stockinger EJ. 2021. The Breeding of Winter-Hardy Malting Barley. *Plants*, **10**.

130. Tanksley SD, ND Young, AH Paterson, and MW Bonierbale. 1989. RFLP mapping in plant breeding: New tools for an old science. *Bio/Technology*, **7**:257–264.

131. Tezuka D, H Cho, H Onodera, Q Linghu, T Chijimatsu, M Hata, and R Imai. **2024.** Redirecting barley breeding for grass production through genome editing of Photoperiod-H1. *Plant Physiol*, **95**:287–290.

132. Tondelli A, E Francia, D Barabaschi, A Aprile, JS Skinner, EJ Stockinger, AM Stanca, and N Pecchioni. 2006. Mapping regulatory genes as candidates for cold and drought stress tolerance in barley. *Theor Appl Genet*, **112**:445–454.

133. Turner A, J Beales, S Faure, RP Dunford, and DA Laurie. 2005. The Pseudo-Response Regulator *Ppd-H1* Provides Adaptation to Photoperiod in Barley. *Science*, **310**:1031–1034.

134. Tyagi V, SR Jacob, K Gupta, and P Brahmi. 2020. Status of introduction and conservation in barley

(*Hordeum vulgare* L.). *Journal of Cereal Research*, **12**:13–18.

135. Ullrich SE. 2011. Barley: production, improvement, and uses, John Wiley & Sons.
136. van Bergen S null, MJ Kottenhagen, RM null van der Meulen, and M Wang. 1999. The Role of Abscisic Acid in Induction of Androgenesis: A Comparative Study Between *Hordeum vulgare* L. Cvs. Igri and Digger. *J Plant Growth Regul*, **18**:135–143.
137. Varshney RK, P Sinha, VK Singh, A Kumar, Q Zhang, and JL Bennetzen. 2020. 5Gs for crop genetic improvement. *Curr Opin Plant Biol*, **56**:190–196.
138. Verma RPS, SK Bishnoi, R Malik, A Kumar, C Lal, L Kumar, J Singh, V Kumar, C Singh, D Kumar, AS Kharub, OV Singh and GP Singh. 2022. Barley varieties and genetic stocks: A compendium, ICAR-Indian Institute of wheat and barley research, Karnal-132001 (Haryana).. *Research Bulletin*.
139. Visioni A, A Tondelli, E Francia, A Pswarayi, M Malosetti, J Russell, W Thomas, R Waugh, N Pecchioni, I Romagosa, and J Comadran. 2013. Genome-wide association mapping of frost tolerance in barley (*Hordeum vulgare* L.). *BMC Genomics*, **14**:424.
140. Wang Q, G Sun, X Ren, B Du, Y Cheng, Y Wang, C Li, and D Sun. 2019. Dissecting the Genetic Basis of Grain Size and Weight in Barley (*Hordeum vulgare* L.) by QTL and Comparative Genetic Analyses. *Front Plant Sci*, **10**.
141. Wanga MA, H Shimelis, J Mashilo, and MD Laing. 2021. Opportunities and challenges of speed breeding: A review. *Plant Breeding*, **140**:185–194.
142. Watson A, S Ghosh, MJ Williams, WS Cuddy, J Simmonds, M-D Rey, M Asyraf Md Hatta, A, Steed A Hinchliffe, D Reynolds, NM Adamski, A Breakspear, A Korolev, T Rayner, LE Dixon, A Riaz, W Martin, M Ryan, D Edwards, J Batley, H Raman, J Carter, C Rogers, C Domoney, G Moore, W Harwood, P Nicholson, MJ Dieters, IH DeLacy, J Zhou, C Uauy, SA Boden, RF Park, BBH Wulff, and LT Hickey. 2018. Speed breeding is a powerful tool to accelerate crop research and breeding. *Nat Plants*, **4**:23–29.
143. Xie S, F Wang, M Li, Z Hu, H Wang, Z Zhang, X Chen, Z Gu, G Zhang, and L Ye. 2024. Enhancing barley yield potential and germination rate: gene editing of HvGA20ox2 and discovery of novel allele sdw1.ZU9. *Plant J*, **119**:814–827.
144. Xu H, Y Li, R Gao, R Xu, G Guo, R Lu, NG Halford, Z Chen, and C Liu. 2021. Rapid Generation and Analysis of a Barley Doubled Haploid Line with Higher Nitrogen Use Efficiency Than Parental Lines by F1 Microspore Embryogenesis. *Plants (Basel)*, **10**:1588.
145. Yan L, D Fu, C Li, A Blechl, G Tranquilli, M Bonafede, A Sanchez, M Valarik, S Yasuda, and J Dubcovsky. 2006. The wheat and barley vernalization gene *VRN3* is an orthologue of FT. *Proc Natl Acad Sci U S A*, **103**:19581–19586.
146. Yu A, Z Guo, and W Liu. 2024. Malting Barley: The Botanical Evolution and Domestication History from Wild Grain to Brewing Staple. *Triticeae Genomics and Genetics*, **15**.
147. Zeng Z, H Wang, Y Luo, W Chen, M Xu, H Wei, Z Chen, T Xiang, L Wang, N Han, X Huang, and H Bian. 2025. CRISPR/Cas9-mediated editing of barley lipoxygenase genes promotes grain fatty acid accumulation and storability. *GM Crops Food*, **16**:482–497.
148. Zeng Z, N Han, C Liu, B Buerte, C Zhou, J Chen, M Wang, Y Zhang, Y Tang, M Zhu, J Wang, Y Yang, and H Bian. 2020. Functional dissection of HGGT and HPT in barley vitamin E biosynthesis via CRISPR/Cas9-enabled genome editing. *Ann Bot*, **6**:929–942.
149. Zhu J, Y Zhang, M Zhang, Y Hong, C Sun, Y Guo, H Yin, C Lv, B Guo, F Wang, and R Xu. 2025. Natural variation and CRISPR/Cas9 gene editing demonstrate the role of a group VII ethylene response factor, HvERF62, in regulation of barley waterlogging tolerance. *J Exp Bot*, **76**:5071–5085.
150. Zombori Z, B Nagy, R Mihály, J Pauk, A Cseri, L Sass, V GH, and D Dudits. 2020. RING-Type E3 Ubiqitin Ligase Barley Genes (HvYrg1–2) Control Characteristics of Both Vegetative Organs and Seeds as Yield Components. *Plants*, **9(12)**, 1–15. https://doi.org/10.3390/plants9121693.