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MODERN BREEDING AND MOLECULAR GENETIC APPROACHES TO ENHANCING WINTER BREAD WHEAT RESISTANCE TO BIOTIC AND ABIOTIC STRESSES UNDER GLOBAL CLIMATE CHANGE (REVIEW)

Yehor Kucherenko , **Andrii Yarosh** , **Zoya Usova** , **Natalia Kuzmyshyna** 

Yuriev Plant Production Institute of NAAS of Ukraine 
142 Heroiv Kharkova Ave., Kharkiv 61060, Ukraine

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Background. Winter bread wheat (*Triticum aestivum* L.) is one of the world's most important cereal crops, and its productivity is critical for global food security. Under ongoing climate change, the impact of biotic and abiotic stresses, including drought, high temperature, salinity, and frost, is increasing, leading to significant yield losses and reduced grain quality. This creates a strong need to integrate conventional breeding with modern molecular genetic and bioinformatics approaches to develop stress-resilient cultivars.

This review summarizes current breeding and molecular genetic strategies aimed at improving the resistance of winter bread wheat (*T. aestivum* L.) to biotic and abiotic stresses under changing climatic conditions. We analyze the applications of genetic markers, quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), genomic selection, and genome-editing technologies. Particular attention is given to integrating high-throughput phenotyping, molecular research, and digital tools into modern breeding pipelines, as well as to emerging sources of resistance and the development of an adaptive wheat gene pool.

Overall, this review highlights the importance of combining conventional breeding approaches with advanced molecular and genomic tools to enhance breeding efficiency. Such integration provides a coherent framework for developing next-generation wheat cultivars capable of maintaining stable yield performance under climate-related stress



conditions and thereby contributing to global food security. The review also outlines key future research directions for improving breeding efficiency under increasing environmental variability.

Keywords: resistance breeding, climate change, adaptive potential, QTL analysis, marker-assisted selection (MAS), genomic selection

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INTRODUCTION

Agricultural crops are significantly affected by global climate change, the major manifestations of which include increasing average annual temperatures (Bibi & Rahman, 2023), alterations in seasonal precipitation patterns (Huang *et al.*, 2024), and an increasing frequency of drought events, which intensify stress pressure on plants and contribute to soil degradation (Tang *et al.*, 2025). Global climate change is already causing statistically significant reductions in the productivity of major crops (Tran *et al.*, 2025), thereby necessitating the adaptation of breeding programs and agricultural technologies (Benitez-Alfonso *et al.*, 2023). Winter bread wheat is also substantially affected by climate change, particularly due to the reduction of optimal cultivation areas caused by rising temperatures and changes in soil moisture conditions (Guo *et al.*, 2024; Shoukat *et al.*, 2024). In Ukraine, the negative effects of drought on the growth and development of winter bread wheat have already been reported (Domaratskyi *et al.*, 2023). In addition, climate change increases the risk of the spread of diseases and pests, including the emergence of new climate-adapted pathogens (Campos-Avelar *et al.*, 2023). In recent years, considerable attention has been focused on the molecular genetic mechanisms underlying plant adaptation, particularly the role of stress-responsive genes, regulatory networks, and transcription factors in the formation of stress-resistant genotypes (Guo *et al.*, 2025; Wang *et al.*, 2024).

Despite the substantial number of recent review publications devoted to specific aspects of wheat improvement, such as genomic selection, genome-wide association studies (GWAS), marker-assisted selection, or resistance to particular biotic and abiotic stresses, a comprehensive analysis of these areas within the context of global climate change remains limited. Most studies focus on individual adaptation mechanisms or specific breeding tools. In contrast, the present review synthesizes current knowledge on the genetic basis of winter bread wheat resistance to a complex of biotic and abiotic factors, as well as contemporary breeding approaches for the development of climate-resilient cultivars. Particular attention is given to the integration of molecular genetic tools into practical breeding programs and to the utilization of modern sources of resistance under changing climatic conditions.

The genetic mechanisms underlying resistance in winter bread wheat are mediated through regulatory networks involved in responses to biotic and abiotic stress factors. Low temperature represents a key limiting factor for winter forms, while frost resistance determines overwintering success and yield stability (Wu *et al.*, 2024). Frost events occurring during the reproductive stage may reduce yield by more than

1% for each degree of temperature decrease (Ferrante *et al.*, 2024). The *TaDREB1*, *TaSnRK2.9*, and *TaHSP17.4* genes contribute to cold, drought, and heat adaptation (Jiang *et al.*, 2022; Wang *et al.*, 2023).

Frost resistance in winter bread wheat is a polygenic trait associated with genes involved in cold acclimation, developmental regulation, and photoperiod response. A key role is played by the *FR-A1/VRN-A1* and *FR-A2* loci, which coordinate vernalization and cold adaptation, whereas increased expression of *VRN-A1* may reduce cold acclimation capacity (Ahres *et al.*, 2025). The *CBF* cluster located within the *FR-A2* locus activates *COR* genes associated with membrane stabilization and osmoprotection. Interactions among *VRN-A1*-, *CBF*-, and *ICE*–*CBF*–*COR*-dependent pathways ensure a balance between plant development and stress adaptation (Ahad *et al.*, 2023; Whiting *et al.*, 2025; Raza *et al.*, 2023). Genotypes with a high vernalization requirement generally exhibit greater frost resistance but slower reproductive development (Zhang *et al.*, 2022; Ahres *et al.*, 2025). Under conditions of climatic instability, the balance between vernalization requirement and frost resistance determines the optimal phenotypic type of winter bread wheat, while the *VRN*–*CBF* regulatory axis enables the integration of cold adaptation and productivity. Crop adaptation also depends on the seasonal sequence of stresses, which necessitates the development of multi-stress tolerance (Zhu *et al.*, 2022; Ahlawat *et al.*, 2025). **Fig. 1** presents the major seasonal abiotic stresses and critical developmental stages of winter bread wheat.

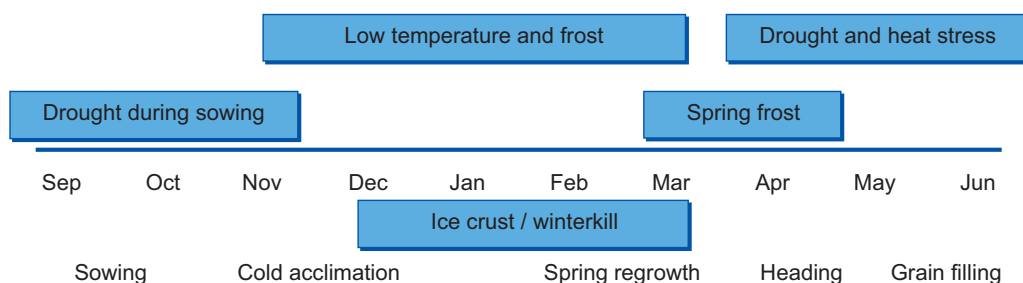


Fig. 1. Seasonal dynamics of major abiotic stresses affecting winter bread wheat during the vegetation period

An important role in wheat resistance to pathogens is played by genes of the NLR family, which are responsible for effector recognition and activation of immune responses. The genome of bread wheat contains more than 1,500–2,100 NLR-like genes, a substantial proportion of which are organized in clusters. The integration of additional domains, alternative splicing, and changes in gene expression expand the spectrum of pathogen recognition and contribute to the development of complex resistance to biotic stresses (Hao *et al.*, 2023).

Snow mold caused by *Microdochium* spp., *Typhula* spp., and *Sclerotinia* spp. can lead to significant yield losses in winter bread wheat (Yarosh *et al.*, 2024). Resistance to snow mold is associated with QTLs involved in cold acclimation, while the induction of *UGT80A2-like* and *NAI1-like* genes during cold acclimation confirms the link between frost resistance and pathogen resistance (Gołębiowska *et al.*, 2021; Sertse *et al.*, 2026). Root and crown rots caused by *Fusarium* spp. and *Microdochium* spp. weaken plants after overwintering. Resistance to these diseases has a polygenic basis, whereas the *Fhb1* QTL is associated with mycotoxin detoxification (Pu *et al.*, 2025;

Mapuranga *et al.*, 2026; Zhang *et al.*, 2026). Genes involved in cold acclimation participate in the formation of freezing tolerance, which is supported by GWAS analyses revealing the polygenic nature of this trait, while cold stress activates antioxidant systems associated with ROS homeostasis in wheat (H. Wang *et al.*, 2026; Shenoda *et al.*, 2026). The severity of foliar diseases caused by *Blumeria graminis* and *Zymoseptoria tritici* increases in spring due to the weakened physiological state of plants after winter stress, while resistance to these pathogens is controlled by both race-specific and polygenic mechanisms (Ngou *et al.*, 2022; Zhang *et al.*, 2022).

GWAS in winter bread wheat has identified SNPs and QTLs on chromosomes 2A, 2B, 3B, 5A, and 7B associated with drought and frost resistance, root architecture, and stress recovery via ABA signaling and transcriptional regulation (Schierenbeck *et al.*, 2023). These results confirm the polygenic nature of adaptive traits and support the use of genomic and marker-assisted selection. Resistance mechanisms operate at multiple levels, from NLR-based race-specific resistance to QTL-controlled quantitative resistance and regulatory networks involving CBF, DREB, and VRN genes. Overall, winter bread wheat resistance represents an integrated system linking development, stress adaptation, and immunity. The summary of key genes (**Table 1**) demonstrates the multilevel organization of resistance, ranging from R genes to regulatory networks involved in cold and hormonal responses.

Table 1. Key resistance genes of winter bread wheat associated with biotic and abiotic stress factors

Gene	Type of resistance	Pathogen / stress factor	Pathogen / stress factor	Reference
<i>Lr34 / Yr18 / Sr2 / Lr46 / Yr29</i>	Adult plant resistance (APR)	Rust diseases	ABC transporter, pleiotropic effect, partial non-specific resistance	Krattinger <i>et al.</i> , 2009; Sychala <i>et al.</i> , 2024
<i>Pm21</i>	Race-specific	Powdery mildew	NLR protein, strong vertical resistance	Xing <i>et al.</i> , 2018
<i>Stb6</i>	Race-specific	Septoria tritici blotch	Recognition of pathogen effectors	Saintenac <i>et al.</i> , 2018
<i>Fhb1</i>	Quantitative (QTL)	Fusarium head blight	DON toxin detoxification	Cuthbert <i>et al.</i> , 2006
QTL (2B, 7B)	Quantitative	Snow mold	Associated with cold acclimation and stress response	Kruse <i>et al.</i> , 2017
<i>CBF (CBF14, CBF15)</i>	Abiotic	Frost resistance	Regulation of COR genes, cold acclimation	Campoli <i>et al.</i> , 2009; Badawi <i>et al.</i> , 2007
<i>DREB1</i>	Abiotic	Cold, drought	Transcription factor, stress-induced expression	Nakashima <i>et al.</i> , 2014; Liu <i>et al.</i> , 2018
<i>VRN1</i>	Phenological / adaptive	Vernalization	Regulation of transition to the reproductive stage	Yan <i>et al.</i> , 2003; Milec <i>et al.</i> , 2023
<i>FR-A2 (CBF cluster)</i>	Abiotic	Frost resistance	Cluster of cold response genes	Miller <i>et al.</i> , 2006; Motomura <i>et al.</i> , 2013
<i>TaSnRK2.9</i>	Abiotic	Drought	ABA-dependent signaling	Feng <i>et al.</i> , 2019; Rehman <i>et al.</i> , 2019

Current winter bread wheat breeding approaches include MAS, GS, GWAS, and CRISPR/Cas technologies. MAS is effective for monogenic traits (e.g., *Pm21*, *Fhb1*) but limited for polygenic traits such as drought and frost resistance. GS improves the prediction of polygenic traits but is resource-intensive, while GWAS provides high-resolution mapping without always identifying causality. CRISPR/Cas is constrained by trait polygenicity and field validation requirements. The most effective strategy is integrating MAS for major genes, GWAS for locus detection, and GS for complex trait prediction.

Winter bread wheat resistance to biotic and abiotic stresses is governed by an integrated signaling–genetic network involving stress perception, signal transduction, gene regulation, and adaptive phenotype formation. Stress is initially perceived by cellular sensors: membrane fluidity changes under low temperature activate ion channels and Ca^{2+} fluxes, water deficit triggers osmosensing systems, and biotic stress is recognized by PRRs detecting PAMPs (Zhang *et al.*, 2022; Gusain *et al.*, 2023). Early responses include ROS production and ion homeostasis changes acting as secondary messengers. Signal transduction proceeds via Ca^{2+} sensors, MAPK cascades, and hormonal pathways, with ABA mediating drought and cold responses, and SA and JA regulating immune signaling (Gupta *et al.*, 2023).

Under cold stress conditions, the ICE–CBF–COR signaling cascade is activated, where ICE induces the expression of CBF transcription factors that regulate cold-responsive *COR* genes (Liu *et al.*, 2022). **Fig. 2** illustrates a generalized scheme of the immune signaling system of winter bread wheat in response to biotic stress.

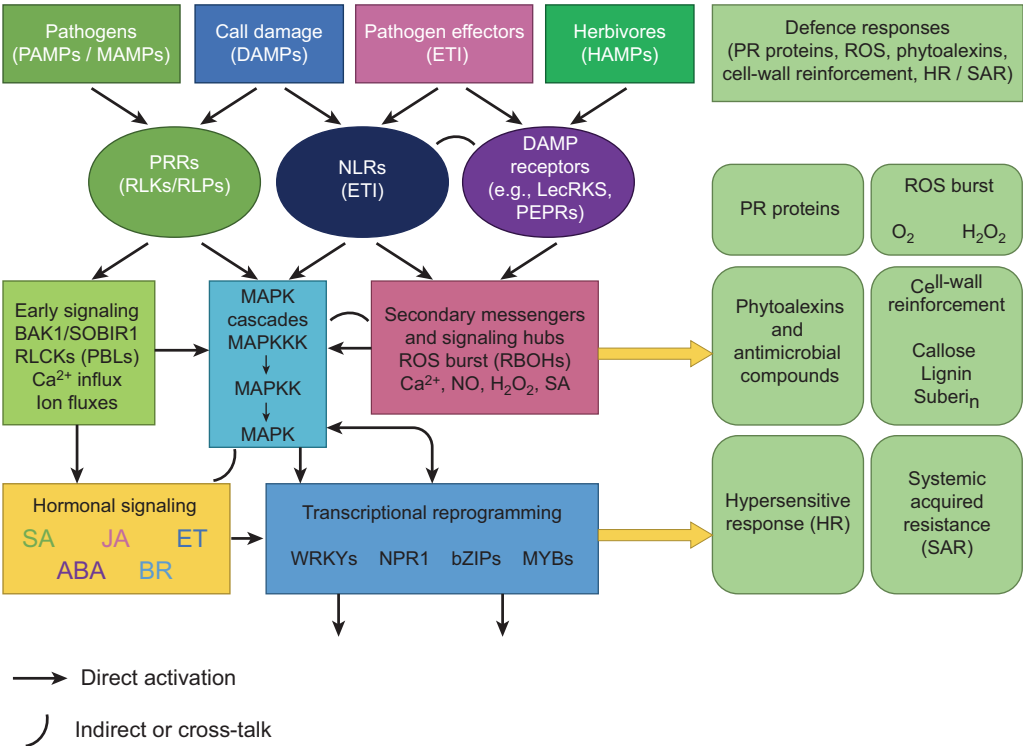


Fig. 2. Simplified scheme of the immune signaling network activated in winter bread wheat upon perception of biotic stressors (PAMPs, DAMPs, and effectors) to downstream defense responses

Integration of signaling and genetic mechanisms leads to adaptive phenotype formation. Low temperature induces frost tolerance via membrane stabilization, osmoprotectant accumulation, and enhanced antioxidant defenses; drought stress maintains water balance and metabolic adjustment; pathogen attack triggers localized infection control and defense responses. Resistance operates through a “perception–signaling–gene expression–phenotype” framework with overlapping pathways. Interaction among the CBF cascade, *VRN-A1*, and immune networks underpins cross-tolerance. However, application of these mechanisms is limited by polygenic control, complex regulation, genotype – environment interactions, and the cost and difficulty of functional validation and field translation.

Modern breeding approaches and genomic technologies for improving winter bread wheat

are based on the integration of high-throughput genotyping, precise phenotyping, and predictive models, which together form a unified workflow for developing adaptive cultivars. This approach is particularly important for winter forms, where selection is aimed at combining frost resistance, pathogen resistance, and stable productivity under climate change conditions. The evolution of molecular markers in winter bread wheat breeding reflects a transition from low-throughput to high-throughput technologies (Merrick *et al.*, 2022; Budhlakoti *et al.*, 2022). Microsatellite markers (SSRs), which were long used for genetic diversity analysis and cultivar identification, have largely been replaced in modern breeding programs by SNP markers due to their lower genomic coverage density and limited scalability (Paux *et al.*, 2022). Modern genotyping platforms include SNP arrays, GBS, DArTseq, and KASP markers, which are widely used in GWAS, genomic selection, and marker-assisted selection (Mahmood *et al.*, 2022; Zeng *et al.*, 2022). High-throughput technologies are mainly applied to identify marker–trait associations, whereas KASP markers are used for routine selection of target alleles in breeding populations (Paux *et al.*, 2022). The main molecular marker technologies used in modern winter bread wheat breeding are summarized in **Table 2**. Examples of the practical application of modern molecular approaches in winter bread wheat breeding are presented in **Table 3**.

Table 2. Major molecular marker technologies used in modern winter bread wheat breeding

Technology	Marker type	Main application	Advantages	Limitations
SSR	Microsatellite markers	Genetic diversity analysis, cultivar identification	Codominant and reproducible	Low throughput
SNP arrays	Single- nucleotide polymorphisms	GWAS and genomic selection	High genome coverage	Relatively expensive
KASP	Allele-specific SNP markers	Marker-assisted selection	Fast and cost-effective	Limited number of loci
GBS	Sequencing-based SNP discovery	Genome-wide genotyping	High marker density	Complex bioinformatic analysis
DArTseq	Reduced-representation sequencing	High-throughput genotyping	Simultaneous SNP discovery and genotyping	Requires specialized platforms

Table 3. Examples of practical applications of modern molecular approaches in winter bread wheat breeding

Approach	Gene / locus	Trait	Technology / marker	Practical outcome	Reference
MAS	<i>Lr34</i>	Leaf rust resistance	KASP marker	Selection of resistant genotypes	Fang <i>et al.</i> , 2020
MAS	<i>Fhb1</i>	Fusarium head blight resistance	SNP/KASP	Improved resistance to Fusarium	Buerstmayr <i>et al.</i> , 2009; Su <i>et al.</i> , 2018; Su <i>et al.</i> , 2019
GWAS	CBF cluster (FR-A2)	Frost tolerance	SNP arrays	Identification of cold tolerance loci	Würschum <i>et al.</i> , 2017; Babben <i>et al.</i> , 2018; Motomura <i>et al.</i> , 2013
GS	Polygenic loci	Yield and adaptability	Genomic prediction	Acceleration of the breeding cycle	Budhlakoti <i>et al.</i> , 2022; Meuwissen <i>et al.</i> , 2001; Crossa <i>et al.</i> , 2017
DARtseq	Winter hardiness QTLs	Winter hardiness	DARtseq genotyping	Mapping of adaptive QTLs	Vaitkevičiūtė <i>et al.</i> , 2023; Bolouri <i>et al.</i> , 2023
CRISPR / Cas	TaMLO	Powdery mildew resistance	Genome editing	Development of resistant lines	Wang <i>et al.</i> , 2014
CRISPR / Cas	TaHRC	Fusarium resistance	Gene editing	Reduced spike infection severity	Su <i>et al.</i> , 2019; Chen <i>et al.</i> , 2022
KASP	<i>Yr15</i>	Stripe rust resistance	KASP assay	Rapid selection of resistant plants	Klymiuk <i>et al.</i> , 2018; Chugunkova <i>et al.</i> , 2025
GWAS	TaDREB1	Drought tolerance	SNP genotyping	Identification of stress-associated loci	Liu <i>et al.</i> , 2018; Mondini <i>et al.</i> , 2012
AI / ML + GS	Integrated genomic datasets	Prediction of productivity	Machine learning	Improved prediction accuracy	Jeon <i>et al.</i> , 2026; Tsega <i>et al.</i> , 2026; Xie <i>et al.</i> , 2026; T. Wang <i>et al.</i> , 2026

Despite advances in genotyping, phenotyping remains a key bottleneck in modern plant breeding (Robles-Zazueta *et al.*, 2022). The assessment of frost resistance, winter hardiness, and disease resistance requires multi-year field trials and is strongly influenced by genotype × environment interactions (Sabir *et al.*, 2023). The implementation of high-throughput phenotyping, remote sensing, and digital indices improves the accuracy of complex trait evaluation (Ali *et al.*, 2026); however, challenges related to reproducibility across different environments persist. Genomic selection (GS) is an important tool in winter bread wheat breeding, enabling the prediction of breeding values based on genomic data without complete phenotyping of each generation. Unlike marker-assisted selection (MAS), GS accounts for the cumulative effects of multiple genes, which is critical for polygenic traits such as frost resistance and yield (Budhlakoti *et al.*, 2022; Merrick *et al.*, 2022). This approach reduces the breeding cycle and increases selection

efficiency. In recent years, AI- and machine learning (ML)-based approaches have been increasingly applied in wheat breeding for the analysis of large-scale phenotypic and genotypic datasets and for predicting genotype productivity and adaptability, thereby combining the precision of molecular methods with field-based evaluations (Chang-Brahim *et al.*, 2024). The overall integration of modern breeding technologies is illustrated in **Fig. 3**.

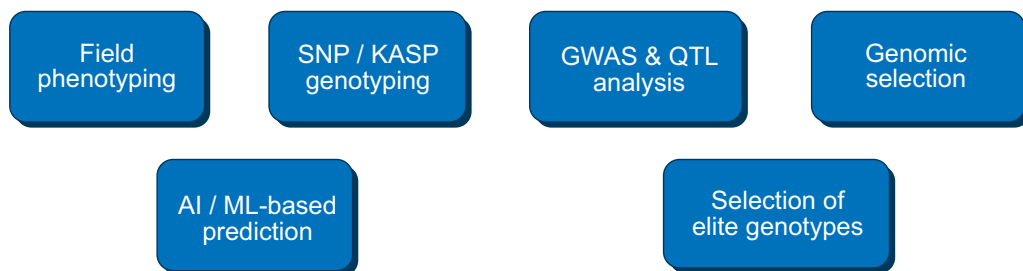


Fig. 3. Integrated workflow of modern breeding technologies used in winter wheat improvement

Despite the high potential of modern breeding technologies, their application remains limited by several factors. Marker-assisted selection (MAS) is effective for traits with simple genetic control but less suitable for polygenic traits such as frost resistance. Genomic selection provides higher prediction accuracy, although it requires large training populations, extensive phenotypic data, and advanced computational infrastructure (Budhlakoti *et al.*, 2022; Merrick *et al.*, 2022). Additional constraints include high genotyping costs, limited access to advanced technologies, and difficulties in integrating diverse datasets. In Ukraine, these challenges are aggravated by the impact of military actions on scientific and breeding infrastructure. Therefore, modern winter bread wheat breeding increasingly relies on integrated approaches combining genotyping, phenotyping, and genomic prediction to improve resistance to biotic and abiotic stresses under climate change conditions. Modern winter bread wheat breeding is increasingly focused on integrating pangenomics, multi-omics, CRISPR/Cas technologies, and AI/ML-based approaches within the concept of “data-driven breeding.” Pangenomics expands the genetic basis of breeding by enabling the analysis of structural variations and stress-resistance alleles from wild relatives, although its application is limited by high sequencing costs and the complexity of wheat genome bioinformatics (Tiwari *et al.*, 2024). Multi-omics approaches, including genomics, transcriptomics, proteomics, and metabolomics, provide systems-level insight into regulatory networks involved in stress responses and adaptation to cold and drought stress. However, their implementation is constrained by difficulties in integrating multidimensional datasets and the dependence on high-quality phenotyping (Sehgal *et al.*, 2023).

CRISPR/Cas technology enables targeted modification of genes associated with stress resistance, including VRN, CBF, and R genes, accelerating the development of novel alleles without prolonged crossing cycles. However, its application in wheat remains limited by complex transformation procedures, low regeneration efficiency, and regulatory barriers (Hussain *et al.*, 2022). AI- and machine learning (ML)-based approaches are increasingly applied to predict yield, stress resistance, and genomic breeding values using large-scale genotypic and phenotypic datasets, especially in

combination with high-throughput phenotyping technologies such as UAV monitoring and spectral indices. Their implementation, however, is constrained by the need for large training populations, challenges in model interpretation, and high computational costs (Kaushal *et al.*, 2024; Wójcik-Gront *et al.*, 2024).

Ukrainian winter bread wheat breeding has a long-standing scientific tradition, with leading roles in the development of modern cultivars being played by the V.M. Remeslo Myronivka Institute of Wheat of the National Academy of Agrarian Sciences of Ukraine, the Plant Production Institute named after V.Ya. Yuriev of the National Academy of Agrarian Sciences of Ukraine, the Plant Breeding and Genetics Institute – National Center of Seed and Cultivar Investigation, and the Institute of Plant Physiology and Genetics of the National Academy of Sciences of Ukraine.

The main directions of modern wheat breeding are focused on improving cultivar adaptability to climate change, combining high yield potential with drought and frost resistance, as well as resistance to major pathogens. Ukrainian breeding programs are aimed at developing cultivars of a universal adaptive type with stable productivity under variable environmental conditions, where winter hardiness, adaptability, and resistance to abiotic stresses are of key importance (Bazalii *et al.*, 2023). Cultivars developed through Ukrainian breeding programs are characterized by high adaptability and stable productivity across diverse agroecological conditions of Ukraine. In particular, the cultivars Haiok, MIP Lada, and Dyvo demonstrated yields ranging from 6.5 to 8.9 t/ha, whereas the cultivar Optyma Odeska exhibited increased frost resistance (7 points) and stable survival under winter stress conditions of the Forest-Steppe zone of Ukraine (Yarosh *et al.*, 2022).

Under the drought-prone conditions of the Steppe zone of Ukraine, modern winter bread wheat cultivars demonstrate considerable variability in drought resistance. In the most adaptive genotypes, yield losses ranged from 10 to 20 %, whereas in less resistant cultivars they reached up to 30–40 %, indicating substantial genetic differentiation of this trait within the Ukrainian wheat gene pool (Konovalova *et al.*, 2023). Ukrainian cultivars also produce a thousand-kernel weight ranging from 38 to 45 g, combining high productivity with ecological plasticity, which confirms their breeding value for modern agricultural production systems (Chuhrii *et al.*, 2022).

For a more systematic overview of achievements in Ukrainian winter wheat breeding, key cultivars together with their agronomic performance, resistance traits, and recommended agro-ecological zones of cultivation are summarized in **Table 4**.

The implementation of DArTseq, GWAS, and genomic selection in Ukraine is limited by the high cost of genotyping, insufficient infrastructure, and restricted access to bioinformatics platforms, which results in a gap compared to leading international breeding programs. At the same time, Ukrainian research actively employs analyses of adaptability, plasticity, and yield stability for the selection of stress-resistant genotypes, thereby creating a basis for the integration of conventional and genomic breeding approaches (Moskalets *et al.*, 2023).

Following the onset of Russia's full-scale invasion of Ukraine, the sown areas and overall production of cereal crops, particularly winter wheat, declined substantially due to the occupation of part of the country's territory, contamination of agricultural land with mines and unexploded ordnance, destruction of infrastructure, and disruptions to logistical and export supply chains (Han *et al.*, 2025). The greatest losses were recorded in the frontline regions of southern and eastern Ukraine, where a substantial proportion of arable land became unsuitable or inaccessible for agricultural cultivation (Deininger *et al.*, 2023).

Table 4. Overview of Ukrainian winter wheat cultivars: agronomic characteristics, resistance traits, and agro-ecological adaptation zones

Cultivar	Key resistance genes / QTL	Biotic stress resistance	Yield (t/ha)	Agro-ecological zone	Reference
Podolianka	Mainly field resistance; partially described QTL for rust resistance	Leaf rust, powdery mildew (field resistance)	6.0–8.0	Forest-steppe, Steppe	Kovalov <i>et al.</i> , 2025; Demydov <i>et al.</i> , 2024
Smuhlianka	Yr, Lr (partial), Pm (field resistance)	Leaf rust, powdery mildew	5.5–7.5	Forest-steppe, Steppe	Shakalii <i>et al.</i> , 2022
Bohdana	Frost tolerance-related QTL; stress adaptation traits	Rusts, Septoria (partial resistance)	5.8–7.8	Steppe, Forest-steppe	Shakalii <i>et al.</i> , 2022
MIP Lada	Yield stability QTL; adaptive traits	Moderate powdery mildew resistance	6.5–8.0	Forest-steppe	Demydov <i>et al.</i> , 2024
MIP Yuvileina	Complex field resistance	Fungal diseases	6.5–8.2	Forest-steppe	Demydov <i>et al.</i> , 2024
MIP Fortuna	Yield stability QTL	Moderate resistance	6.8–8.5	Forest-steppe	Demydov <i>et al.</i> , 2024
MIP Lakomka	Productivity-related QTL	Moderate resistance	6.5–8.3	Forest-steppe	Demydov <i>et al.</i> , 2024
Horytsia Myronivska	Partial Yr, Lr	Rusts, powdery mildew	5.8–7.5	Forest-steppe, Polissia	Demydov <i>et al.</i> , 2024
Berehynia Myronivska	Resistance QTL for fungal diseases	Complex resistance	6.0–7.8	Forest-steppe, Polissia	Demydov <i>et al.</i> , 2024
Svitanok Myronivskyi	Pm + field resistance	Powdery mildew	6.0–7.6	Forest-steppe, Polissia	Demydov <i>et al.</i> , 2024

Military operations have significantly restricted farmers’ access to agricultural fields, accelerated land degradation, and increased production costs, thereby directly contributing to the decline in cereal crop production in Ukraine. In particular, according to FAO estimates (2026), approximately 13 % of agricultural households in frontline regions lost access to arable land due to landmine contamination and explosive remnants of war, effectively removing substantial areas of productive farmland from cultivation. Furthermore, comprehensive assessments by the World Bank, as reported by Ukrinform (2025), indicate that the direct losses incurred by Ukraine’s agricultural sector exceed USD 11 billion, including damage to agricultural machinery, grain elevators, storage facilities, and losses of agricultural products. Collectively, war-related risks and the reduction in available production areas are expected to result in an approximately

10 % decline in total grain output, as reported by Reuters (Polityuk, 2025). According to Reuters (Braun, 2025), Ukraine's grain production in 2025–2026 is projected to reach approximately 51–56 million tonnes, depending on weather conditions and the intensity of war-related risks. This figure remains substantially below the pre-war level recorded in 2021, when grain production exceeded 80 million tonnes.

An additional factor is the intensification of climate-related risks, which act synergistically with war-induced challenges. In particular, during 2024–2025, many regions of Ukraine experienced the lowest levels of plant-available soil moisture recorded in the past seven years, adversely affecting the development of winter crops and the establishment of optimal plant density. Insufficient precipitation resulted in poor seedling development and uneven overwintering of plants, further reducing yield potential (Chen *et al.*, 2024). The combined impact of war-related factors (landmine contamination, loss of access to agricultural land, and destruction of infrastructure) and climatic stresses (drought and soil moisture deficit) has created a new and highly challenging agroecological environment. This situation necessitates the development of adaptive breeding strategies aimed at enhancing cultivar resilience to biotic, abiotic, and anthropogenic stresses.

Knowledge gaps and research priorities in winter bread wheat breeding.

Future research in winter wheat breeding should focus on the development of integrated genomic prediction models that combine high-density genotyping data, multi-environment phenotyping, and climate modelling to predict genotype performance under the simultaneous influence of multiple stress factors. Particularly promising is the application of genomic selection models that incorporate genotype-by-environment (G×E) interactions and integrate ecological and climatic parameters, which would enhance the accuracy of selecting adaptive genotypes under changing climate conditions (Liu *et al.*, 2025; Thomsen *et al.*, 2026; Gogna *et al.*, 2026). An additional important direction is the improvement of yield prediction systems based on the integration of genomic data, crop growth models, and climate scenarios to evaluate the breeding potential of germplasm under future environmental conditions. Equally relevant remains the issue of field validation of CRISPR/Cas-edited wheat lines across diverse agroecological environments, particularly under Ukrainian conditions characterized by drought, high temperatures, unstable water regimes, and increased pathogen pressure. Despite significant advances in genome editing, most studies are still conducted under controlled conditions, whereas the assessment of the stability of edited trait expression under field conditions requires further investigation (Waqas *et al.*, 2025; T. Wang *et al.*, 2026). A promising direction is also the integration of artificial intelligence, machine learning, high-throughput phenotyping, and multi-omics technologies to accelerate the identification of valuable genotypes and optimize breeding decisions. The application of machine learning algorithms to large-scale genomic, transcriptomic, phenotypic, and environmental datasets enables a substantial improvement in the prediction of agronomically important traits and resistance to complex stress factors (Tsega *et al.*, 2026; Xie *et al.*, 2026).

Alongside genomic selection, GWAS analyses, and genome editing technologies, the investigation of epigenetic regulatory mechanisms and plant–microbiome interactions represents a promising avenue for enhancing wheat resistance to biotic and abiotic stresses. Current research indicates that DNA methylation, histone modifications, chromatin remodeling, and small RNA-mediated regulation play important roles in controlling the expression of genes involved in responses to drought, salinity, and both high and low temperature stresses. Epigenetic changes may establish so-called

“stress memory” in plants, enabling more efficient adaptation to repeated exposure to adverse environmental conditions, thereby opening new opportunities for the development of climate-resilient wheat cultivars (Zaid *et al.*, 2026; Nishanth *et al.*, 2025; Lodhi & Srivastava, 2025). An equally promising area of research is the study of the rhizosphere microbiome in shaping wheat resilience to stress factors. Plant-associated microorganisms have been shown to enhance nutrient uptake, regulate phytohormonal balance, strengthen antioxidant defense systems, and induce systemic resistance to pathogens. Recent studies indicate that specific rhizosphere microbial communities can increase wheat tolerance to salinity, drought, and other abiotic stresses, while also contributing to yield stability under changing climatic conditions (Fouad *et al.*, 2025; Smith *et al.*, 2025; Yaghoubi Khanghahi *et al.*, 2025). In the future, the integration of genomic, epigenomic, and microbiome-based approaches may substantially expand the potential of winter wheat breeding and facilitate the development of next-generation cultivars with comprehensive resistance to both biotic and abiotic stresses.

Priority directions for future research include the development of integrated genotype–phenotype–environment databases, advancement of digital phenotyping, identification of novel genes conferring broad-spectrum resistance, and improvement of genomic prediction models for multi-factor stress conditions. For applied breeding, the integration of molecular markers with long-term field evaluations of adaptability is particularly important, as it enables the accelerated development of high-yielding and stress-resilient winter wheat cultivars.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

Conceptualization, [Y.K.; A.Y.]; resources, [Y.K.; A.Y.]; writing – original draft preparation, [Y.K.]; writing – review and editing, [Y.K.; A.Y.; Z.U.; N.K.]; supervision, [Z.U.]. All authors have read and agreed to the published version of the manuscript.

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СУЧАСНІ СЕЛЕКЦІЙНІ ТА МОЛЕКУЛЯРНО-ГЕНЕТИЧНІ ПІДХОДИ ПІДВИЩЕННЯ СТІЙКОСТІ ПШЕНИЦІ М'ЯКОЇ ОЗИМОЇ ДО БІО- Й АБІОТИЧНИХ СТРЕСІВ В УМОВАХ ГЛОБАЛЬНИХ КЛІМАТИЧНИХ ЗМІН (ОГЛЯД)

Єгор Кучеренко, Андрій Ярош, Зоя Усова, Наталія Кузьмишина

*Інститут рослинництва імені В. Я. Юр'єва НААН
просп. Героїв Харкова, 142, Харків 61060, Україна*

Обґрунтування. Пшениця м'яка озима (*Triticum aestivum* L.) є однією з провідних зернових культур світу, продуктивність якої має важливе значення для глобальної продовольчої безпеки. В умовах кліматичних змін посилюється дія біо- й абіотичних стресів, зокрема, посухи, високих температур, солоності та морозу, що призводить до втрат урожайності й погіршення якості зерна. Це зумовлює необхідність інтегрувати традиційну селекцію зі сучасними молекулярно-генетичними та біоінформаційними підходами для створення стійких сортів. Мета цього огляду – узагальнити сучасні селекційні та молекулярно-генетичні стратегії підвищення стійкості пшениці м'якої озимої до біо- й абіотичних стресів в умовах кліматичних змін. У роботі проаналізовано застосування генетичних маркерів, QTL-аналізу, GWAS, геномної селекції і технологій редагування геному. Особливу увагу приділено інтеграції фенотипування, молекулярних досліджень і цифрових технологій у селекційних програмах. Узагальнено тенденції щодо використання нових джерел стійкості та формування адаптивного генофонду пшениці. Отримані узагальнення мають важливе практичне значення для вдосконалення стратегій селекції пшениці м'якої озимої з урахуванням сучасних кліматичних викликів. Їх можна використовувати для формування адаптивних програм добору вихідного матеріалу, спрямованих на підвищення стійкості рослин до комплексу біо- й абіотичних стресів. Результати огляду створюють наукове підґрунтя для інтеграції класичних селекційних методів зі сучасними молекулярно-генетичними технологіями. Це сприятиме підвищенню ефективності створення сортів нового покоління, здатних стабільно реалізовувати потенціал урожайності в умовах глобальних кліматичних змін і гарантувати продовольчу безпеку. Визначено ключові напрями подальших досліджень, спрямованих на підвищення ефективності селекції в умовах кліматичних ризиків. Огляд може бути корисним для селекціонерів, генетиків і фахівців із біоінформатики, що працюють у сфері створення та вдосконалення сортів пшениці м'якої озимої.

Ключові слова: селекція на стійкість, кліматичні зміни, адаптаційний потенціал, QTL-аналіз, маркер-асоційована селекція (MAS), геномна селекція