REVIEW

The Plant Genome

Genomic approaches to enhance adaptive plasticity to cope with soil constraints amidst climate change in wheat

Roopali Bhoite[1,2] | Yong Han[1,3] | Alamuru Krishna Chaitanya[4] |
Rajeev K. Varshney[3] | Darshan Lal Sharma[1,3]

[1]Department of Primary Industries and Regional Development, South Perth, Western Australia, Australia

[2]The UWA Institute of Agriculture, The University of Western Australia, Perth, Western Australia, Australia

[3]Centre for Crop & Food Innovation, State Agricultural Biotechnology Centre, Murdoch University, Perth, Western Australia, Australia

[4]Grains Genetics Portfolio, University of Southern Queensland, Centre for Crop Health, Toowoomba, Queensland, Australia

Correspondence
Darshan Lal Sharma, Department of Primary Industries and Regional Development, 3 Baron-Hay Ct, South Perth 6151, Western Australia, Australia.
Email: Darshan.Sharma@dpird.wa.gov.au

Assigned to Associate Editor Alison Bentley.

Abstract

Climate change is varying the availability of resources, soil physicochemical properties, and rainfall events, which collectively determines soil physical and chemical properties. Soil constraints—acidity ($pH < 6$), salinity ($pH \leq 8.5$), sodicity, and dispersion ($pH > 8.5$)—are major causes of wheat yield loss in arid and semiarid cropping systems. To cope with changing environments, plants employ adaptive strategies such as phenotypic plasticity, a key multifaceted trait, to promote shifts in phenotypes. Adaptive strategies for constrained soils are complex, determined by key functional traits and genotype × environment × management interactions. The understanding of the molecular basis of stress tolerance is particularly challenging for plasticity traits. Advances in sequencing and high-throughput genomics technologies have identified functional alleles in gene-rich regions, haplotypes, candidate genes, mechanisms, and in silico gene expression profiles at various growth developmental stages. Our review focuses on favorable alleles for enhanced gene expression, quantitative trait loci, and epigenetic regulation of plant responses to soil constraints, including heavy metal stress and nutrient limitations. A strategy is then described for quantitative traits in wheat by investigating significant alleles and functional characterization of variants, followed by gene validation using advanced genomic tools, and marker development for molecular breeding and genome editing. Moreover, the review highlights the progress of gene editing in wheat, multiplex gene editing, and novel alleles for smart control of gene expression. Application of these advanced genomic technologies to enhance plasticity traits along with soil management practices will be an effective tool to build yield, stability, and sustainability on constrained soils in the face of climate change.

1 | INTRODUCTION

The world's population is projected to reach 8 billion in 2022, 8.5 billion in 2030, and 9.7 billion in 2050 (Carvajal-Yepes et al., 2019; UN, 2022), and global agriculture production must increase at least by 70% to meet food demand and security. Wheat is a major global cereal crop cultivated in more than 100 countries and is a staple food resource for 40% of the global population. Climate change has resulted in varying rainfall events, and the impacts are more acute in arid and semiarid cropping systems. Of the major cereals, wheat is grown in the most hostile and lowest yielding environments. Soil constraints (acidity, salinity, sodicity, and soil dispersion) significantly pose challenges to wheat production globally, and the intensity of yield losses is increasing with climate change (Reynolds & Braun, 2022). Developing climate-resilient wheats with enhanced plasticity for soil constraints will enhance food security to feed the future growing population.

Soil constraints arise naturally and are an ever-increasing problem due to anthropogenic activities and climate change. Globally, the FAO (2020) estimated that there were 434 and 397 million hectares of sodic and saline soils, respectively. Soil constraints are usually caused by high salt, disruption in soil structure and integrity, variable pH (potential of hydrogen), mineral deficiencies or toxicities, and climate change, which reduces cereal production. These constraints are getting more severe due to the shortage of water of high quality, deterioration of the soils, and efforts from the communities to shift away from the use of chemical intervention in agricultural production. The high levels of soil salinity and sodicity common in arid and semiarid areas present obstacles to the maintenance of global food security and environmental sustainability. Salt stress in soils is becoming increasingly common across both irrigated and dryland ecosystems (Husen, 2021). The soil management practices include the addition of lime on acid soils (pH < 4.5) and gypsum on saline–sodic and dispersive soils (pH > 8.0) to improve crop performances (Table 1) (DPIRD Report, 2018). However, there is a greater need to comprehend the genetic inheritance and mechanisms of tolerance to soil constraints to develop climate-proof elite cultivars for food security and farm sustainability.

Since the *Arabidopsis thaliana* reference genome was decoded in 2000 (The Arabidopsis Genome Initiative, 2020), more than 100 crops have been sequenced over the last two decades, including the most important cereals wheat, rice, maize, and barley (Purugganan & Jackson, 2021; Varshney et al., 2021). The advancement in technologies from short-read sequencing to combined highly accurate long-read sequencing, optical mapping, and chromosome conformation capture enables the decoding of genomes more efficiently and cost-effectively (Athiyannan et al.,

Core Ideas

- Genetic and genomic research on tolerance to soil constraints in wheat in the wake of climate change.
- Tolerances to complex belowground constraints are quantitatively inherited.
- Modern genetic and genomic tools bring out rapid pre-breeding solutions.
- Rapid genetic solutions accelerate breeding program.
- High-yielding wheat cultivars with stable traits also enable farm sustainability.

2022; Garg et al., 2021). Recently, the first fully annotated reference genome of the *Triticum aestivum* variety "Chinese Spring" was accomplished (Alaux et al., 2018), which can significantly boost research combined with breeding practices for developing the next-generation varieties of wheat with climate resilience. Despite the bread wheat genome's size and intricacy, high-quality pangenome representing 16 wheat genotypes has also become available (Walkowiak et al., 2020). The pangenome not only enriches the genomic pool of sequence and structure variations among wheat germplasms but also serves as an invaluable resource for genome mining and gene editing. In particular, the pangenome accessions may offer a selection of diverse genetic backgrounds for targeted trait improvement through gene editing (Khan et al., 2020), which can partially bypass the genotype dependency on the wheat transformation references such as Bobwhite and Fielder (Wang et al., 2022). The wheat diversity panel also paves the way for functional gene discovery and subsequent development of cultivars with improved adaptation to various environments.

There is a greater need to address crop improvement in a specific target environment. Many agronomic traits related to soil constraints are complex in nature and subject to high genotype × environment × management interactions (G × E × M) (Chenu, 2015; Chenu et al., 2018). Crop improvement programs for complex soil constraints should incorporate a number of components—climatic variations, local management practices, type of soil constraints, genetic variability for the target environment, heritability of complex traits, and precise phenotyping and resourceful genotyping systems. Interactions amongst the favorable genes controlling plasticity in changing environment and management practices affect the rate of selection progress and genetic gain in breeding programs (Mace et al., 2013; Messina et al., 2011).

Chromatin profiling is the current advancement in root trait assessment under changing soil conditions. Chromatin profiling has been attempted in cereals (Li et al., 2019; Omrane

et al., 2017; Reynoso et al., 2022) to identify functional elements, including genes, promoters, enhancer-like elements, transcription factors, and transposons. Identification of new genic regions and *cis*-regulatory elements by studying patterns of chromatin for root traits will offer a comprehensive view of gene expressions and transcription factors controlling cellular events. The epigenomic map for annotations of *cis*-regulatory elements is now available for bread wheat (Li et al., 2019), and this resource can be successfully deployed in pre-breeding research to analyze root and phenotypic plasticity traits for soil constraints. Tolerances to soil constraints are quantitative traits. The review highlights soil constraints (acidity, salinity, sodicity, and dispersion) and the effect of climate change on wheat yield. Mechanisms and epigenetic regulation of plasticity primary and secondary traits are discussed. The mapped genomic locations for plasticity traits in wheat are also summarized. The demonstration of best genetic and genomic tools and potential tools available for pre-breeding investigations, specifically molecular, genome editing, and validation tools to identify potential alleles and allele mining are discussed for quantitative traits.

2 | SOIL CONSTRAINTS

Soil constraints (acidity, sodicity, and salinity) are naturally occurring soil conditions that affect wheat productivity. Soil acidity results from a fall in soil pH (<5), which is induced by the continuous addition of H^+ and huge volumes of acid-forming compounds, including urea and ammonia. All basic cations, including Na, Ca, Mg, K, and Si, as well as pH-buffering minerals, such as carbonates, are leached away year-round in a warm, humid climate, exposing acidic Fe and aluminum oxide minerals, which increases the proportion of Al^{3+} and H^+ in comparison to other cations (Caires et al., 2008). Soluble aluminum and pyrite minerals release protons into the soil environment, increasing acidity (Figure 1b) through the reaction, $Al^{3+} + H_2O \rightarrow AlOH^{2+} + H^+$. Another concern is the fact that soil acidity degrades the favorable environment for bacteria, such as the rhizobia, earthworms, and other soil organisms, reducing soil carbon pools. This type of soil state most often results in a rise in the accessibility of metals to toxic levels, specifically aluminum and manganese (Figure 1b). There is sufficient genetic diversity for acidic soil tolerance in wheat (Tang et al., 2003). High concentrations of aluminum (Al) primarily affect the root growth and lead to a weaker root system in sensitive wheat, whereas tolerant wheat grows longer, deeper roots and secretes organic ligands from its roots to complex with Al in the soil, reducing Al take-up by plant systems (Tang et al., 2001).

Sodic-dispersive soils/sodicity are formed by a high amount of sodium and clay-forming massive soils. These soils have poor soil structure, pH (>8), and a harmful subsurface element ionic strength, predominantly sodium ions, which hinder wheat development (Sharma et al., 2022) (Figure 1c). About 70% of Australia's rangelands are arid and semiarid lands, making it the world's driest inhabited part of the planet, where rainfall is low, and temperature is high (DPIRD Report, 2018) (Figure 1c). In sodic soil, highly hydrated sodium ions replace divalent cations (like calcium and magnesium ions) at the surface of negatively charged clay particles and form cation shells around clay particles keeping soil particles separated from each other, causing a loss of soil integrity, and poor aeration and water infiltration (Figure 1c). Sodic-diffusive loams possess higher pH (above 7), bulk density, dispersion index, and metal ion concentration and are saline-rich in chlorides (NaCl, $CaCl_2$, and $MgCl_2$) and sulfates (Na_2SO_4) (Table 1) (DPIRD Report, 2018). From an agricultural perspective, sodic soil is associated with a high exchangeable sodium percentage >15 and pH > 8. This decrease in soil porosity makes the soil duplex and rigid, which significantly impacts seed germination rate, root development, water use efficiency (WUE), and uptake of nutrients. Therefore, sodicity has compound effects on agricultural productivity.

Salinity is a major soil limitation that hinders crop advancement and progression in growth by initiating ionic and oxidative stresses in the cytoplasm, brought on by reactive oxygen species, and this leads to a steady increase in phytotoxic ions. A nutritional imbalance results from the elevated concentrations of Na^+ and Cl^- that are subsequently accumulated, together with a loss in K^+ within the plant cell. The increased Na^+/K^+ ratios in the above and below plant parts disrupt effective water uptake and other essential nutrients such as Ca^{2+} and K^+/N^+ disequilibrium (Zörb et al., 2019). Photosynthetic activity and water use efficiency are the most significantly impacted components, which eventually slow down plant development and the production of secondary metabolites. The tolerance mechanisms to salinity for the improved productivity are brought about in two ways: plants with the ability to impair the root system's ability to absorb salt, and/or an effective acclimation process to regulate the salts percentage and its distribution in the plant system (Xiong et al., 2017).

Advances in genomics and cutting-edge technologies hold greater solutions for quantitative traits. The association of genetic sources along with desired characteristics, genetic and genomic knowledge with a proper understanding of mechanisms for improved tolerance to soil constraints is vital to improve the targeted varieties or lines. There is considerable genetic variability for sodicity (Sharma et al., 2022) and salinity (James et al., 2008; Rahnama et al., 2019). Advanced genomic sequencing and the discovery of tolerant factors have offered intensive pre-breeding knowledge that could be effectively used to breed elite wheats with greater stability and fitness for varying climatic conditions.

TABLE 1 Abiotic soil constraints, potential of hydrogen (pH), climatic conditions, basic exchangeable cations, and soil management practices.

Soil constraint	Soil pH	ECe (mS cm⁻¹)	ESP (%)	Characteristics/toxicity	Deficiency	Climatic conditions	Soil management
Acid	<6.0	–	–	Predominance of H^+, Al^{3+}, and Mn^{2+}	P, K, Ca, Mg, Mo, and B	Variable and changing climate; increased temperature and/or rainfall cause increased oxidizable sulfide materials causing soil acidification	Application of lime, dolomite, basic slag, flue dust, wood ash, pulp mill lime
High pH	>7.8	<4	<15	Higher amount of water-soluble salt, $CaCO_3$	Micronutrient cation: Zn, Cu, Mn, and Fe Trace elements: As, Se, F, and B	Climate change and low rainfall events	Elemental sulfur or aluminum sulfate
Saline	<8.5	>4	<15	Higher amount of water-soluble salt. The common soluble salts are sulfates, chlorides and carbonates of sodium, calcium, and magnesium	Micronutrient cation: Zn, Cu, Mn, and Fe Trace elements: As, Se, F, and B	Climate change: Rising air temperature and atmospheric greenhouse gases (GHGs) concentration, prolonged drought, and floods, decline in relative humidity with extreme rainfall events	Leaching of soluble salts; lowering down the water table depth through subsurface drainage; application of farmyard manure at 5 t ha⁻¹ at 10–15 days before sowing
Saline–sodic	<8.5	>4	≥15	Higher amount of water-soluble salt, exchangeable Na^+. The clay fraction is flocculated, and soils have a stable structure	Zn	Arid/semiarid; low rainfall	Application of gypsum
Sodic	>8.5	<4	≥15	Predominance of highly hydrated monovalent Na^+. Poor soil structure and waterlogged	Zn	Arid/semiarid; low rainfall	Application of gypsum

Abbreviations: ECe, electrical conductivity; ESP, exchangeable sodium percentage.
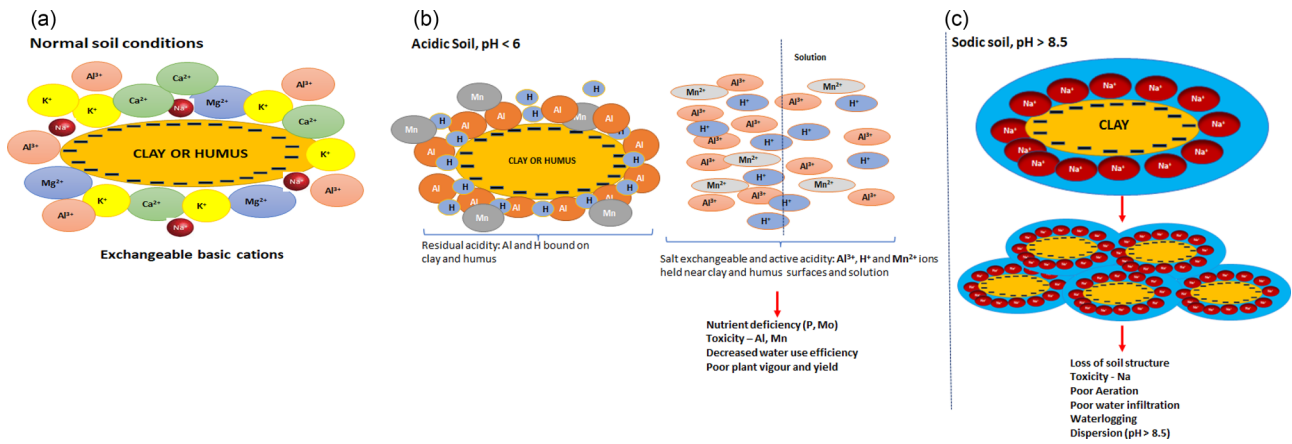
FIGURE 1 (a) Exchangeable basic cations in normal soil conditions, (b) pictorial representation of scenarios in acidic (pH < 6), (c) saline and sodic soils (pH ≥ 8.0), metal toxicities, with change in soil characteristics. pH, potential of hydrogen.

3 | PHENOTYPIC PLASTICITY IN RESPONSE TO CLIMATE CHANGE

Plasticity is the ability of a genotype to express different phenotypes under different environmental conditions. Climate change poses new agricultural challenges and presents extreme and unpredictable environmental conditions. Plant species tackle unfavorable environmental conditions through physiological response mechanisms. There have been earlier efforts to comprehend plasticity through ecological and evolutionary theory and transfer the knowledge to crop breeding. Understanding the molecular basis of plant responses in key primary and secondary functional traits that influence "fitness" in changing conditions is vital to harness agricultural adaptive plasticity (Brooker et al., 2022). In cereal production, agricultural fitness correlates with yield and/or quality-related characteristics, which is dependent on the enhancement of plasticity traits (Tables 2 and 3). Selection of lines is dependent on the fitness and commercial longevity of the variety that reflects on consistency for high yield, given the context of variable conditions (Stockinger, 2021). The genetic resources that exhibit high fitness could be effectively used to mitigate challenges faced by climate change (Fischer & Edmeades, 2010). Adaptive traits and underlying molecular changes are studied through primary and secondary traits (Table 2). The quantitative trait locus mapping studies and chromosomal locations that influence phenotypic plasticity and agricultural fitness, such as root traits, height, phenology and spike characteristics, photosynthesis efficiency, biomass and transpiration, sugar, and secondary metabolites in wheat, are presented in Table 3. These genomic locations can be well integrated in breeding programs to enhance plasticity and resilience in wheat productivity on constrained soils.

3.1 | Major mechanisms contributing to adaptation of plants to variable environments

Crops possess a sequence of adaptive methods for acclimatizing to varying ecological cues. Wheat exhibits varied mechanisms against changing conditions and stresses that were introduced during wild domestication and evolution (Dubcovsky & Dvorak, 2007). Plasticity is linked to "molecular adaptive machinery," which is a channel with several degrees of gene expression, regulation, and temporal and spatial controls at the cell stage (Shao et al., 2007). These responses are based on the integration of many transduced events of cell signal paths. Hormones dominate a principal place in such transduction systems, which coordinate with other hormones to control molecular pathways like cell division, expansion, and differentiation, which seem to be crucial for plant development amidst abiotic stress.

Different "physiological and biochemical functions" bring out adaptive mechanisms that help wheats cope with soil constraints. The major adaptive mechanisms include ionic balance and compartmentalization, activation and modulation of antioxidant enzymes and hormones, and biosynthesis of osmoprotectants and solutes. For instance, soil salinity and sodicity disrupt ionic homeostasis causing weaker root system, hyperosmotic stress, and oxidative damage, inhibiting overall crop growth and development. To counterbalance ionic stresses, plants have developed enhanced gene expressions of a class of kinases. An example is Ca^{2+}–calcineurin B-like protein (CBL)-CBL interacting protein kinase (CIPK) module that performs a critical function in controlling the cellular ion homeostatic balance (Sharma et al., 2022; Zhu, 2016). High Na^+, low K^+, excess Mg^{2+}, and high pH cause cytosolic Ca^{2+} signals activating CIPK family proteins increasing intracellular favorable Ca^{2+} ion concentration, and

TABLE 2 Wheat primary and secondary functional traits for investigating plasticity amidst changing soil conditions.

Priority	Traits	Biological significance
Primary adaptive traits	Stomatal size and density	Stomata control water loss and uptake of CO_2
	Height at maturity	Indication of competitive position in a stand
	Flowering time, phenology, size at reproduction, and pollen viability	Plasticity in these traits determine the ability to respond to a changing climate
	Seed size and number	Determines fitness
	Leaf mass per unit area	Measure of relative growth rate, photosynthesis capacity, and leaf nitrogen content
Secondary adaptive traits	Root-to-shoot ratio	The relative allocation of total plant mass to roots and shoots
	Specific root length	Root length per unit mass
	Water use efficiency	Carbon gain as a function of water loss. Can be measured as an integrated measure using isotopes or by instantaneous measures
	Leaf size, shape, and thickness	Leaf is the site of photosynthesis and is crucial for growth and carbon balance. Therefore, size and morphology are important
	Plant chemical defenses	Concentration of secondary metabolites is important in defense mechanism
	Leaf pigmentation	Pigmentation (e.g., anthocyanin) contribute to leaf longevity during senescence caused by abiotic stress

promoting vacuolar sequestration of excess Na^+ ions, thus maintaining ionic homeostasis to confer salt tolerance.

There are also a few critical "morphogenic responses" like increased lateral root development (Arif et al., 2019; Kaashyap et al., 2018). Besides this, there lies a powerful systematic action and interaction among antioxidant level, auxin metabolism, and lateral root formation. Metal toxicity in acid and alkaline soils in 60% of the world's arable land modifies root system architecture and cell division as an adaptive strategy in crops (Liang et al., 2023; Sun et al., 2020). Root exudation of organic acids, phenolics, amino acids, and extracellular enzymes helps in alleviating stress caused due to soil metal toxicities (Arif et al., 2019; Kaashyap et al., 2018). A deeper understanding of molecular processes, physiological and biochemical roles, and crucial "morphogenic responses" and interlink of the physiological understanding of tolerance processes from molecular methods is significant for enhancing the wheat yield potential in arid and semiarid regions.

3.2 | Epigenetic regulation for stress adaptation on constrained soils

Epigenetics is the investigation on hereditary variations in chromatin function without changing the DNA structure or genetic code. Epigenetic codes include DNA methylation, modifications of histones including their variants, and certain long noncoding RNAs, which impact the construction and accessibility of chromatin and chromatin's genetic or biological role (Duan et al., 2018). Besides DNA and histone methylation, it has been observed that the control of stress responses for adaptation to challenging environmental conditions involves other histone marks, such as "methylation, acetylation, phosphorylation, ubiquitination, glycosylation, and ADP-ribosylation" (Chang et al., 2020; Kim et al., 2015). There are inevitably associations between the reaction to environmental change, particularly adaptations to soil salinity and other abiotic stress, and stimulation of epigenetic regulatory systems (Konate et al., 2018).

Epigenetic pathways are engaged in the development of stress memory, which is later passed down to the progeny of pressured parent plants (Friedrich et al., 2019). Consequently, decoding the epigenetics of these stress responses generated by the plants may be put to greater use for breeding stress-tolerant crops (Chang et al., 2020). There have been several attempts to investigate the epigenetic mechanisms underlying abiotic stress reactions. The levels of epigenetic marks and cross-talks between epigenetic mechanisms are stimulated or suppressed following abiotic stress management (Figure 2). DNA methylation is essential for controlling how genes are expressed in response to environmental cues. As an epigenetic mark, DNA methylation adds to epiallelic diversification and modifications in the regulation of gene expression (Kimatu, 2015).

To select fitness and stable features while breeding robust wheats in crop improvement programs, it is necessary to conduct extensive investigations on the variations in DNA

TABLE 3 Quantitative trait locus (QTL) mapping studies conducted for plasticity traits—root, height, phenology, spike characteristics, photosynthesis efficiency, biomass, transpiration rate, sugar, and metabolite production in wheat.

Plasticity traits	QTL chromosomal location	References
Root traits		
Root development	7AS	Merchuk-Ovnat et al. (2017)
Root length	1BL, 2DS, 5AL, 6AL, 7BL, 3AL	Ayalew et al. (2017)
Seedling root traits	4B, 7A, 7B	Ma et al. (2017)
Root traits	2B, 5B, 7B, 6D	Ahmad et al. (2017)
Root and shoot traits	4B	Iannucci et al. (2017)
Root morphology and yield	1A, 1B, 4B, 6B	Lucas et al. (2017)
Root length	1BL, 2DS, 5AL, 6AL, 7BL, 3AL	Ayalew et al. (2017)
Root elongation rate	5D, 7D	Hamada et al. (2012)
Maximum root length	2A, 4D, 5A, 6A, 7B, 3B, 5B; 2B, 7B	Ren et al. (2012) and Kabir et al. (2015)
Primary root length	2B, 7B; 2A, 4D	Ren et al. (2012) and Kabir et al. (2015)
Lateral root length	1A, 2B, 4B, 6A, 6B	Ren et al. (2012)
Total root length	2B, 4B, 6A, 6B, 6D, 2A, 2B, 3A, 5A, 3B, 4A, 4D, 6D	Kabir et al. (2015)
Seminal root angle	6A	Alahmad et al. (2019)
Root angle, length, number	2A, 1A, 1B, 2B, 3B, 4B, 6A	Soriano and Alvaro (2019)
Root: shoot ratio	2A	Soriano and Alvaro (2019)
Shallow root weight	3A, 2A, 2D, 4A	Ehdaie et al. (2016)
Deep root weight	4B, 2D, 3A, 4A	Ehdaie et al. (2016)
Root biomass	3A	Ehdaie et al. (2016)
Height, phenology, and spike characteristics		
Plant height, days to heading, spike length, seeds per spike, number of spikes per plant	5A, 5B, 6B, 2D, 2B, 6B, 7A, 1B, 4B	Mwadzingeni et al. (2017)
Plant height	1B, 2D, 4D, 6B, 6A, 3A, 2D	Wu et al. (2012) and Würschum et al. (2017)
Spike fertility	4B	Wurschum et al. (2018)
Plant height, days to heading, spike length, TKW, grain yield	1B, 2B, 3B, 4B, 5B, 6B, 7B	Soriano et al. (2017)
Days to anthesis, grain filling period, TKW	5A, 7A	Gahlaut et al. (2017)
Days to flowering and maturity	1B, 5B, 4A	Kamran et al. (2013)
Seeds per spike, number of spikes per plant, TKW, grain yield	3A, 1A, 7A	Xu et al. (2017)
Photosynthesis efficiency, biomass and transpiration		
Stay-green	3A, 7B, 1B, 2A, 3B, 4A, 4B, 4D, 5B	Christopher et al. (2018)
Chlorophyll content	7A, 5A, 1A, 5A	Yang et al. (2007)
Photosynthetic capacity	3B, 6A, 7D, 1B	Yang et al. (2007)
Normal vegetation index	3A, 1B, 5B, 4B, 4D, 5A, 3A, 2D, 5A, 4B, 5B, 6B, 4D	Gao et al. (2015)
Harvest index and biomass	2B, 2D, 7D, 2D, 3A, 6B, 2A, 7D, 4A, 6B, 1B	Ehdaie et al. (2016)
Photosynthesis, TKW, grain yield	5D, 6D, 7D	Saeed et al. (2017)
Leaf water content, leaf dry weight, chlorophyll fluorescence	1,2,3	Jiang et al. (2017)

(Continues)

TABLE 3 (Continued)

Plasticity traits	QTL chromosomal location	References
Canopy temperature	4A, 7D	Lopes et al. (2013)
Sugar and metabolites		
Stem water soluble carbohydrates	4A, 2D	Nadia et al. (2017)
Water-soluble carbohydrates	1A, 4B, 1D, 4A, 1A, 2D, 7B, 7D, 6B, 4A	Gao et al. (2015)
Water-soluble carbohydrates	1A, 1B,1D, 4A	Ovenden et al. (2017)
Cell wall bound phenolics	4B, 6R	Hura et al. (2017)

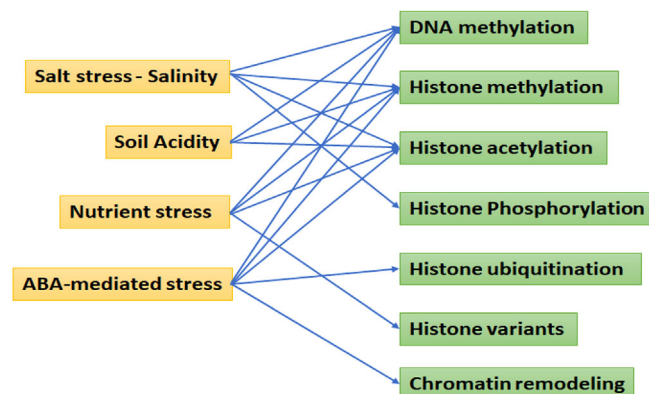Abbreviation: TKW, 1000 kernel weight.

FIGURE 2 Cross-talks between epigenetic mechanisms and soil constraints.

methylation within and between genotypes. High-affinity potassium transporters (HKTs) are important for maintaining the balance of Na$^+$ and K$^+$ in wheat when it is exposed to high concentrations of salt (Munns et al., 2012). Under salt stress, methylation in wheat and its consequences on the expression of HKT genes have been addressed. NaCl stress caused a genotype- and tissue-specific spike in cytosine methylation, which in turn decreased the expression of TaHKT2;1 and TaHKT2;3 in the root and shoot sections of tolerant wheat, enhancing its ability toward salinity tolerance (Kumar et al., 2017). Abscisic acid (ABA) is necessary to regulate plant response to stress. High salinity is one among the many environmental conditions that cause the biogenesis of ABA, which controls crucial primary and secondary characteristics like seed germination rate, stomatal conductance, and root development (Table 2). The primary ABA signaling regulatory mechanism for stressful adaption has now been uncovered. Whilst under pressure, ABA interacts with a regulatory pyrabactin resistance1 (PYR1)/PYR1-like (PYL) elements of ABA receptors, inhibiting clade A protein phosphatase type 2Cs (PP2Cs) and releasing SNF1-Related Protein Kinase 2s (SnRK2s) (Zhu, 2016). To control several biological activities, including transcription, RNA translation, epigenetic regulation, and flowering time adjustment, the stimulated SnRK2s phosphorylate downstream effectors (Wang et al., 2013).

Besides transcription factors, RNA-directed DNA methylation (RdDM) is a critical regulator of gene activation in plants under abiotic stress. In a regular state, the RdDM mechanism significantly methylates the MYB74 promoter. The low level of transcription of MYB74 is an indication against tolerance for salinity in wheat (Xu et al., 2015). Besides DNA methylation, histone methylation, and histone variants, the upregulation of bHLH- and MYB-related transcription factors activate ABA-inducible gene expression, which promotes progression, advancements of plant, and ionic homeostasis (Abe et al., 2003; Fan et al., 2014). The appropriate nutrient intake is completely essential for the overall progression and growth of the crop.

Crops have sophisticated systems for adapting to changes in pH and the accessibility of nutrients within the soil, which they have developed throughout the course of evolution. In addition, the process by which epigenetic modifications could be passed down to offspring as a form of stress memory is not completely understood. The swift development of high-throughput genotyping and a variety of tools for chromatin profiling will significantly contribute to a greater comprehension of the epigenetic changes underlying stress responses in wheat.

4 | GENOMIC SELECTION TO ENHANCE PLASTICITY AMIDST CHANGING CLIMATIC CONDITIONS

Genomic selection (GS) predicts quantitative traits and has the capability to accommodate numerous quantitative characteristics in a breeding pipeline by combining pedigree information and high-density genotypic data (Crossa et al., 2017). Advances in sequencing technology have enabled the identification of genome-wide single-nucleotide polymorphisms (SNPs) that could be successfully imputed in the GS models. Recently exome-capture for wheat was enabled using a genotype by sequencing platform that captures population-wide variation in gene-rich regions (He et al., 2019), and these variants represent functional variations that are protein modifier impact types that significantly alter gene expressions for

quantitative traits. Quantitative traits like soil constraint tolerance are governed by many minor effect genes (Bhat et al., 2016). These complex traits normally have low heritability and are environmentally sensitive. Many direct and indirect selection indices (Table 2) are created for effectively choosing the genotypes for target traits. Prediction accuracy for complex traits could be further improved by incorporating gene-rich alleles and comprehensive primary and secondary functional traits (Table 2) (Hickey et al., 2019; Li et al., 2021). Implementing primary and secondary traits in the multivariate pedigree and high-density SNP information has closed the large genotype–phenotype and improved the prediction accuracy of GS for complex traits, such as yield, drought, and heat (Mason & Singh, 2014; Sun et al., 2017). In recent times, with the advent of cost-effective advanced sequencing technologies, the incorporation of quantitative environmental measurements measuring $G \times E$ and research into phenotypic plasticity have gained revived attention to enable GS for complex traits (Fan et al., 2016; Gage et al., 2017; Kusmec et al., 2017).

4.1 | Capturing $G \times E$ interactions to enhance plasticity

There are a variety of interlinked controlling mechanisms contributing to wheat plasticity in changing environments (Dornbusch et al., 2011). Understanding how populations adapt to changing environment is critical for predicting resilience to climate change. Reaction norms offer data that may be compared across genotypes, populations, or species on the direction and amount of phenotypic change to maximize fitness in response to environmental variation. They also address plasticity with respect to changing environments by incorporating population-level response (average response across all individuals in a population) and the variation among individuals in a population.

The structure of plant canopies is an important part of using arithmetic models to describe how crops interact with their surroundings. Reaction norms could be established by defining the structure of wheat typically defined by roots, stems, and leaves, and intrinsic variables. For example, leaf size controlled by water, nitrogen and carbon availability, physical factors (e.g., temperature and water vapor pressure deficit), plant hormone, and more metabolic compounds facilitates reactions to developmental (e.g., floral transition) and ecological signals (e.g., red: far-red light). Normally, primary traits presented in Table 2 are influenced by secondary traits and reaction norms can be established to define the plasticity of traits on constrained soils. There are few quantitative studies on plasticity in wheat on dimensions of phytomers (leaf blades, sheaths, and internodes) on tillers (Evers et al., 2005; Fournier et al., 2003; Tivet, 2001) and first juvenile leaves or main stem alone (Equiza & Tognetti, 2002). Size-mediated effects are often influenced by growth responses to environmental conditions. The length of a cereal leaf influences the length of the consecutive one, which is termed size-mediated effect by Louarn et al. (2010), and a direct relationship between the size of the shoot apical meristem and leaf blade width was proposed by Kirby (1977).

Phenotypic stability would be the result of low stomatal conductance, high photosynthetic activity, drought tolerance, improved plant architecture, and many more trait improvement listed in Table 2, which renders stability in changing environment. The complex plasticity traits have been previously mapped for drought tolerance, root morphology (Kadam et al., 2017; Lucas et al., 2017), and yield plasticity (Mangin et al., 2017). Phenotypic plasticity for several traits was analyzed using nested association mapping under multiple environment (Kusmec et al., 2017). WUE is an important adaptive trait in changing environmental conditions. WUE is the quantity of dry matter produced per unit of water transpired by the crop. WUE is positively associated with yield because the seed yield is dependent on total crop mass (Chamarthi et al., 2023; Chen et al., 2011; Sinclair, 2012). In conclusion, it is also important to understand the regulatory mechanisms of the observed patterns in the changing environment to enhance plasticity. This integrated strategy will make it easier to describe plasticity as an interaction between the environment and the genotype ($G \times E$) and interpret prediction accuracy for complex trait in commercial breeding.

5 | FUNCTIONAL ALLELES TO ENHANCE QUANTITATIVE TOLERANCE

5.1 | Variant characterization

Modern plant breeding methods are focused on identifying the genetic causes of phenotypic differences to create and comprehend adaptive mechanisms. Genome-wide association studies detect variants for trait enhancements by assessing genotypic and phenotypic associations (SNPs and InDels) (Bhoite et al., 2019; Prasad et al., 2012; Sharma et al., 2022). Even though these kinds of studies are quite widespread, the biological interpretation of the results is still difficult, particularly when it comes to quantitative traits expressed at different growth stages with many minor genes contributing to trait expression. The low heritability and genetic gain of minor genes throughout the genome make practical breeding challenging. In this case, tracking functional alleles and high linkage disequilibrium haplotypes closely linked to the genes offers better resolution in breeding programs. Genotype by sequencing platforms enables tagging new and functional alleles, which could be successfully harnessed to improve genetic gain in breeding programs. Additionally,
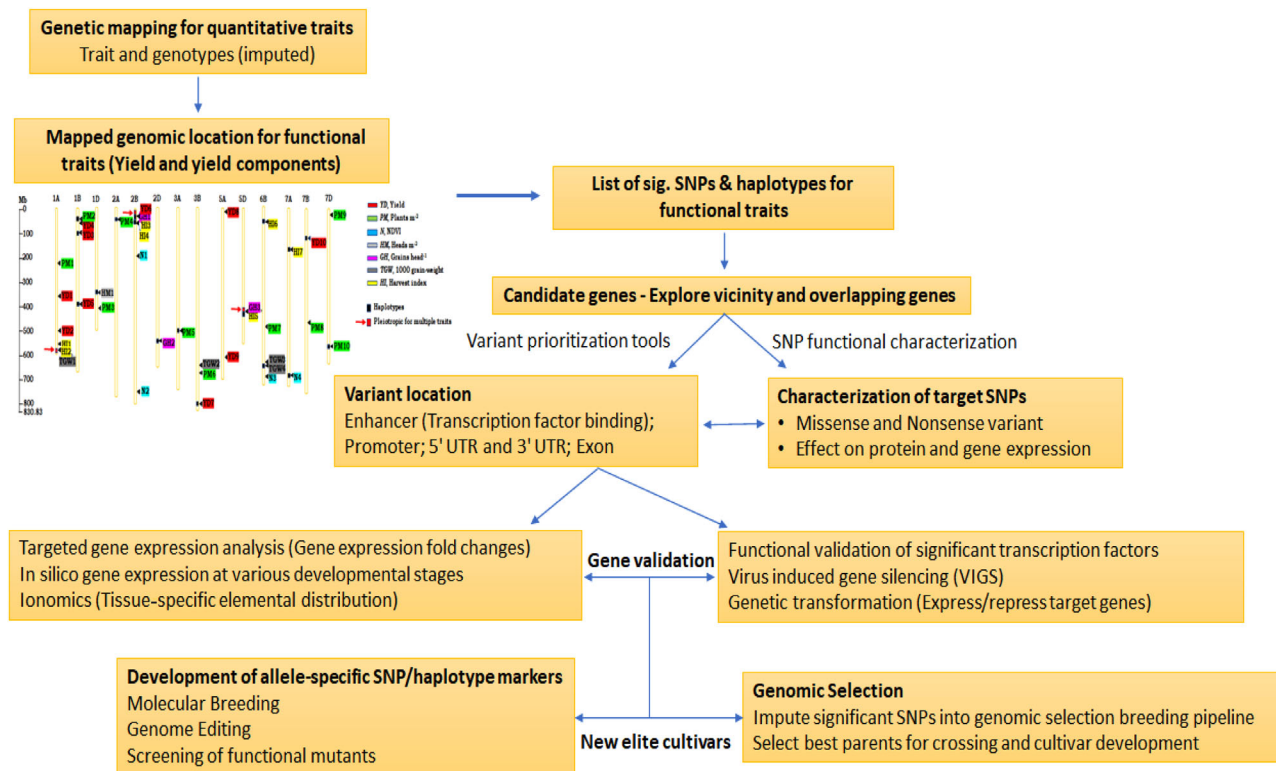
FIGURE 3 Proposed pre-breeding pipeline for enhancing quantitative tolerance on constrained soils—association mapping for functional traits, variant characterization, validation of genes and transcription factor, and allele-specific marker development for single-nucleotide polymorphisms (SNPs) and haplotypes. *Source*: Chromosome mapping illustration sourced from Sharma et al. (2022).

genome-wide variant annotation tools like snpEff (Cingolani et al., 2012) are useful resources to identify the role of alleles/variants in gene expression and protein coding. Analysis of the effect of SNPs for impacts on protein coding (high, moderate, low, and modifier), location of SNPs in open reading frames and intergenic regions determine the gene regulation. Functional SNPs were observed in mechanisms like amino acid, nucleotide biosynthesis, and cellulose and lignin metabolism, which control how carbon and energy are used (Cingolani et al., 2012; Sarkar & Maranas, 2020) and are major breeding targets to tackle abiotic stress. Therefore, gene-derived functional "SNP" markers (Bagge et al., 2007; Sharma et al., 2022) and functional alleles are valuable resources in the molecular breeding of complex traits (Figure 3).

5.2 | Functional quantitative genes validation

Quantitative trait expression is regulated by numerous major/minor/modifier genes at various developmental stages. Gene effects in quantitative trait expression do not produce clear distinct phenotypes and phenotyping minor gene effects is arduous and very challenging. The functional analysis tools, such as differential gene expression profiles (Bhoite et al.,

2021), group-segregant allelic analysis (Bhoite et al., 2019), in silico gene expressions at various developmental stages, virus-induced gene silencing (VIGS), and ionomics to recognize tissue-specific elemental composition (Figure 3), are effective to validate major/minor/modifier candidate gene effects for quantitative tolerance expression. This integrated approach helps in understanding the roles of genes and mechanisms involved in the acclimation process of abiotic stress tolerance.

Evidence regarding the role of abiotic stress-responsive genes in a variety of crops has been uncovered using computational (in silico) methods and comparative genomic methodologies (Gorantla et al., 2007; Soares-Cavalcanti et al., 2012; Tran & Mochida, 2010; Vij & Tyagi, 2007). The causal effect of candidate genes identified for herbicide tolerance in wheat was effectively validated by transcriptome sequencing by estimating differential expression profiles for candidate genes in tolerant and susceptible cultivars (Bhoite et al., 2021). Investigating phenotypes and in silico gene expression analysis for candidate genes at various developmental stages reveals a repertoire of genes involved in the abiotic stress response. The in silico gene expression profiles of candidate genes identified for sodic-dispersive soil tolerance were determined to validate the stage at which genes highly expressed matched the developmental stage of trait

measurement (Sharma et al., 2022). VIGS is a high-throughput functional genomic technique that has been shown to effectively validate transcription factors and a large number of genes contributing to abiotic stress tolerance and mechanisms (Manmathan et al., 2013; Senthil-Kumar & Udayakumar, 2006; Senthil-Kumar et al., 2008). VIGS is a posttranscriptional gene silencing–based technique that has been used for gene functional studies. VIGS has also been used as an effective tool to characterize genes associated with salt (Guo et al., 2010), nutrient deficiency (Ramegowda et al., 2014), and oxidative stress tolerance (Apel & Hirt, 2004; Pastori & Foyer, 2002).

High-throughput analysis of elemental compositions (ionome) is a potent approach for functional analysis and validation of its genes and gene networks. Analysis within the tissue-specific elemental composition is important to study the effects of salt, mechanisms of adaptation, and tolerance to osmotic effects caused by elemental toxicities in soil (Jiang et al., 2010; Xue et al., 2011). There are 13 required minerals for all plant life, some of which are macronutrients like nitrogen and phosphorus and others like sodium, potassium, manganese, boron, iron, and calcium (Shelden & Roessner, 2013). Several mineral deficiencies cause severe growth retardation and even possible death, but excessive levels of some minerals can also be poisonous in large doses. In the case of acidic soils, aluminum, manganese, and boron could be at toxic levels and in sodic environment sodium ions are at toxic levels. Both scenarios have a significant impact on metabolic processes; crops can develop mechanisms to cope with either deficiency or toxicity. Laser ablation inductively coupled plasma mass spectrometry, also known as LA-ICP-MS, is a technique that generates three-dimensional pictures of spatial element distributions. This technique is effective for achieving spatial element distributions in thin segments of biological material (Becker & Becker, 2010; Hare et al., 2012). The differential elemental composition in specific tissue through ionomics will serve as a validation tool for ion transporter candidate genes and the function of those transporters.

6 | PRECISE GENE EDITING IN WHEAT FOR TRAIT IMPROVEMENT

In wheat, "clustered regularly interspaced short palindromic repeats" (CRISPR)/CRISPR-associated endonuclease (Cas) and "transcription activator-like effector nuclease" based gene editing have been implemented to generate novel functional gene mutations. The created alleles have displayed great potential for targeted trait improvement and successful applications have been accomplished in a variety of agronomic traits in wheat, such as powdery mildew resistance (Li et al., 2022; Wang et al., 2014), preharvest sprouting (Abe et al., 2019), and grain weight (Zhang et al., 2018). The current editing strategy in wheat is mainly through the knockout of a single-candidate gene. However, more considerations and efforts are required to address quantitative traits, including tolerance to soil constraints and the signaling/inducible genes for plant plasticity.

6.1 | Multiplex gene editing

Using site-directed nucleases to simultaneously and precisely induce two or more DNA breaks within a single genome in one mutagenesis incident is called multiplex genome editing (Cong et al., 2013). CRISPR/Cas9 is versatile and can be reprogrammed to target different genes across chromosomes, multiple copies of the same gene, and multiple gene variants of gene families in a genome. It can be facilitated by the expression of multiple single-guide RNAs (sgRNA) driven by small RNA polymerase III, polycistronic Cys4 system, polycistronic HH-gRNA-HDV, polycistronic tRNA-gRNA, and the CRISPR/Cas12a (Cpf1) system with a smaller size for construction and multiplexing (Abdelrahman et al., 2021). Previous studies have used *Agrobacterium* strains transformed with a pooled vector library carrying sgRNA cassettes to develop a population-scale mutant library in rice (Meng et al., 2017), tomato (Jacobs et al., 2017), and barley (Nejat, 2022). Such genome- or gene family–wide targeted mutations greatly improved the efficiency in functional gene screening and development of advanced crop lines for breeding programs. For more specific trait improvement through multiplex editing, herbicide resistance, yield potential, disease resistance, and grain/fruit quality are the major focuses in rice and tomato (Abdelrahman et al., 2021), and such outperforming materials have great commercialization value.

Notably, mutation alleles resulting from multiple targets can be across wheat genomes and chromosomes and are segregated independently; therefore, a larger segregation population is required for the selection of homozygous mutants, and high-throughput genotyping approaches should be employed to identify the gene variants. In another important cereal crop maize, a gene discovery pipeline BREEDIT that combines multiplex genome editing of whole gene families with crossing schemes to improve complex traits such as yield and drought tolerance has been proposed recently (Lorenzo et al., 2022). In wheat, Sánchez-León et al. (2018) edited a conserved region adjacent to the coding sequence of 45 α-gliadin genes in both bread and durum wheat. Gene editing frequencies in the complex genomic background varied in mutant lines, but edited wheat plants exhibited a significant reduction in immunoreactivity induced by gluten. The reported technical platforms provide a reference for multiple gRNA designs and construction and serve as invaluable resources for wheat editing practices. Along with the

identification of key genes and regulators responsible for wheat adaptation to soil constraints, multiplex gene editing is capable to alter multiple gene targets simultaneously to create new plant lines with plasticity and combined tolerance. For instance, an overexpression of *TaALMT1* (*aluminum-activated malate transporter 1* (Pereira et al., 2010) and *TaHKT1;5-D* (Byrt et al., 2014) contributes to aluminum and salinity tolerance in bread wheat, respectively. Editing both genes to upregulate expression levels can enhance wheat acid soil and salinity tolerance simultaneously.

Apart from the direct editing of genes controlling wheat response to stress, using wild relatives as a genetic source for cultivated wheat improvement is another pathway. Crop wild relatives are widely recognized as a valuable resource of genetic divergence for the development of domesticated crops (Bohra et al., 2022; Brozynska et al., 2016), tolerant to all kinds of stresses. For wheat, progenitor species hold untapped diversity for potential climate-responsive traits for breeding and advancement, including wide flowering time variation, drought tolerance, and root system architecture (Leigh et al., 2022). However, wild relatives often have unfavorable behaviors for gene introgression, such as shattering, seed dormancy, small grains, and short life cycles. A recent de novo domestication of wild species through the targeted improvement of various traits with genome editing has been proposed in crops (Yu et al., 2021). In wild allotetraploid rice (*Oryza alta*), for example, multiplex editing improved several important traits, including seed shattering, grain size, plant height, and flowering time (Yu et al., 2021). The domesticated crop can not only be developed into a new cereal but also used as a gene donor for the cultivated crop with improved traits for efficient and effective crossing and gene exchange (Table 2). Therefore, a multiplex gene editing system is robust and essential for rapid de novo domestication to capitalize on desirable traits of wild plants.

6.2 | Novel alleles for smart control of gene expression

Plant plasticity is an adaptive strategy driven by epigenetic regulation, signaling, and gene networking. Numerous research studies have illustrated a key tolerance mechanism that enhances the uptake of essential minerals and/or the unloading of toxic ions for plant survival through the activation or repression of functional genes (Han et al., 2014, 2018; Huang et al., 2020). However, a simple gene switch on or off is not a smart strategy for plants dealing with seasonal and variable stresses, such as drought, waterlogging, or frost. Indeed, the transcriptional regulation of responsible genes for adaptive/inducible expression is a more energy-smart and effective solution (Munns et al., 2020). Although wheat pan-genomes (Walkowiak et al., 2020) reveal the structural variations in

the genes of interest (promoters in particular) identified from mapping populations (Figure 3) and can partially link with the expression profiles in pan-transcriptomes, the diverse genetic backgrounds reduce the confidence of causal polymorphisms for gene expression. The natural variations in the pan-genome accessions are also relatively limited for the screening of trait expression.

Targeted editing in the promoters of protein-coding or noncoding genes (microRNA) has been conducted in Arabidopsis and rice (Gong et al., 2020; Lowder et al., 2015) to control gene expression. Simultaneous gene activation has been achieved by targeting different regions in the promoter upstream of these genes. CRISPR/Cas9 introduced random mutations that can alter *cis*-regulatory elements, such as promoter enhancers and silencer sequences that regulate gene transcription, which could result in a range of quantitative transcriptional and phenotypic changes (Abdelrahman et al., 2021). In tomato, novel *cis*-regulatory alleles have been created by CRISPR/Cas9-mediated mutagenesis in the *SlCLV3* promoter (Rodríguez-Leal et al., 2017). Notably, the phenotypic effect on yield components was not predictable from allele type or transcriptional change and was determined only after a comprehensive screening of a continuum of variation. Such streamlined trait improvement can directly develop and select the most desirable regulatory variant in the context of targeting loci and epistatic environments in specific genetic backgrounds, which is a prime example for wheat improvement. The combination of gene editing and speed breeding systems (Ghosh et al., 2018) could greatly save breeding time.

We hypothesize that editing *TaALMT1* has great potential to enhance wheat acid and alkaline soil tolerance, as the extruded malate anions can not only bind to Al^{3+} under low soil pH but also can acidify the rhizosphere under alkaline conditions (Kamran et al., 2020). Although the upstream regulator(s) of *TaALMT1* is yet identified, it has been demonstrated that increasing *TaALMT1* expression can promote malate secretion and thus enhance plant Al^{3+} resistance (Pereira et al., 2010). Therefore, designing multiple CRISPR targets in the gene promoter region could induce novel *cis*-regulatory elements that have not been detected in natural germplasms (Rodríguez-Leal et al., 2017), which may upregulate gene transcription and contribute to superior plant tolerance to both acid and alkaline soil after the functional screening.

Nevertheless, the hexaploid complex genome and genotype dependency on in vitro tissue culture and plant regeneration are some of the hurdles facing current gene editing practices in elite wheat varieties. Some reports demonstrated that a complete knockout of all three homoeologous copies (AA, BB, and DD) is essential for the trait expression, such as the *mlo* gene mutation for powdery mildew resistance (Wang et al., 2014) and the *qsd1* for seed dormancy (Sato et al., 2016). Chopping out a single copy or two homoeologous copies could not lead to a desired phenotype. In this scenario,

identifying conserved regions between three homoeologs is required to design a sgRNA to facilitate full coverage. However, it would limit the selection of target locations within the genes and conflict with primer design for the subsequent mutation genotyping that needs specific amplification to differentiate the three homoeologs. On the other hand, there are a handful of wheat transformation reference varieties, including two spring types of Bobwhite and Fielder, and another winter type Kenong 199 (Wang et al., 2022; Zhang et al., 2018). Recalcitrance against tissue culture and transformation is universal in grain crops, including wheat and barley (Han et al., 2021); therefore, new protocols are being developed to counteract the bottleneck. For example, an in planta particle bombardment of shoot apical meristem has been optimized to bypass culture steps and to create stably genome-edited wheat plants (Liu et al., 2021). Han et al. (2021) modified another culture process for highly efficient gene editing in commercial barley varieties and may shed some light on wheat research. A recent breakthrough is that co-expressing the *TaWOX5* gene promotes wheat transformation and regeneration efficiency and is also evident in *Triticum monococcum*, triticale, rye, barley, and maize (Wang et al., 2022). Gene editing technology is opening the window to more elite and commercial wheat varieties, to generate certain gain-of-function, loss-of-function, or smart transcriptional regulation alleles for plant climate resilience.

7 | CONCLUSIONS

Understanding soil constraint responsive network, identification of key genes, and their inclusion to improve wheat performance is exceedingly complicated and challenging especially because the inheritance of abiotic stress reaction is polygenic. In addition, reaction against any abiotic stress is genotype-dependent due to background genetic differences. Systematic and concerted efforts of employing efficient genetic and genomic tools to determine the genetics underpinning plasticity for such complex traits are prerequisites for wheat improvement on constrained soils. Elite germplasm screening, large-scale and high-throughput phenotyping, high-quality genotype data, and state-of-the-art biotechnologies can boost the mining of invaluable genetic resources for wheat improvement and should be effectively connected as a system framework. The role of proteomics, metabolomics, and crop management strategies are promising supplementary research areas in understanding trait, soil constraints, and gene expression. Identification of significant alleles, candidate genes, and epigenetic regulation pathways for plasticity remains a challenge in wheat due to the complex genome but would maximize the genetic gain for plant performance. Although the gene editing process and mutant genotyping need refinement for both simplicity and efficiency, the cutting-edge technology provides opportunities to create novel and targeted alleles to counteract soil constraints. The modern genetic tools further provide opportunities for stacking multiple gene-related alleles and favorable alleles of network genes regulating and connecting multiple pathways for a much shorter breeding time.

AUTHOR CONTRIBUTIONS
Roopali Bhoite: Conceptualization; investigation; methodology; visualization; writing-original draft; writing-review & editing. **Yong Han**: Investigation; methodology; writing-original draft. **Alamuru Krishna Chaitanya**: Investigation; writing-original draft; writing-review & editing. **Rajeev K. Varshney**: Supervision; writing-review & editing. **Darshan Lal Sharma**: Conceptualization; methodology; supervision; writing-review & editing.

CONFLICT OF INTEREST STATEMENT
The authors report no conflict of interest.

DATA AVAILABILITY STATEMENT
The comprehensive review about soil constraints, advances in genomic tools, plasticity traits, and mapping studies is publicly available as per citation.

ORCID
Roopali Bhoite https://orcid.org/0000-0002-0512-8084
Yong Han https://orcid.org/0000-0001-6480-0398
Rajeev K. Varshney https://orcid.org/0000-0002-4562-9131
Darshan Lal Sharma https://orcid.org/0000-0001-5826-3258

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