













REVIEW

Temperature-smart plants: A new horizon with omics-driven plant breeding

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Abstract

The adverse effects of mounting environmental challenges, including extreme temperatures, threaten the global food supply due to their impact on plant growth and productivity. Temperature extremes disrupt plant genetics, leading to significant growth issues and eventually damaging phenotypes. Plants have developed complex signaling networks to respond and tolerate temperature stimuli, including genetic, physiological, biochemical, and molecular adaptations. In recent decades, omics tools and other molecular strategies have rapidly advanced, offering crucial insights and a wealth of information about how plants respond and adapt to stress. This review explores the potential of an integrated omics-driven approach to understanding how plants adapt and tolerate extreme temperatures. By leveraging cutting-edge omics methods, including genomics, transcriptomics, proteomics, metabolomics, miRNAomics, epigenomics, phenomics, and ionomics, alongside the power of machine learning and speed breeding data, we can revolutionize plant breeding practices. These

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advanced techniques offer a promising pathway to developing climate-proof plant varieties that can withstand temperature fluctuations, addressing the increasing global demand for high-quality food in the face of a changing climate.

1 | INTRODUCTION

Climate change has resulted in significant temperature fluctuations worldwide, posing a critical challenge to plant growth, yield, and distribution (Raza et al., 2019; Zandalinas et al., 2021; Farooq et al., 2022; Rivero et al., 2022; Zandalinas et al., 2023). Crops in field environments experience a wide range of temperature stress, including heat stress (HS; >25°C), chilling stress (CS; 0–15°C), and freezing stress (FS; <0°C), which seriously threaten agricultural food production (Zhang et al., 2019; Raza et al., 2021c; Zandalinas and Mittler, 2022; Raza et al., 2023e; Raza et al., 2024; Saeed et al., 2023). In response to these extreme temperatures, plants use a range of morphological, physiological, biochemical, molecular and cellular adaptations, which have been reviewed extensively in recent literature (Zhang et al., 2019; Raza et al., 2021c; Zandalinas and Mittler, 2022; Sharma et al., 2022; Ding and Yang, 2022; Djalovic et al., 2023; Raza et al., 2023c; Raza et al., 2023e; Saeed et al., 2023). Temperature stress, whether in isolation or combined with other stressors, can induce oxidative damage in plants (Zandalinas et al., 2018; Mittler et al., 2022; Zandalinas and Mittler, 2022). Consequently, HS and CS impede plant development by causing cellular injury or even cell death, leading to reduced membrane fluidity, decreased antioxidant enzyme activities, altered biosynthesis of various proteins and secondary metabolites, and changes in hormonal signaling and source–sink relationships after prolonged exposure (Zhang et al., 2019; Abdelrahman et al., 2020; Raza et al., 2021c; Sharma et al., 2022; Ding and Yang, 2022; Kumar et al., 2022; Raza, 2022; Raza et al., 2023c; Djalovic et al., 2023; Raza et al., 2023e; Raza et al., 2024; Saeed et al., 2023). Understanding how plants adapt to, respond to, and tolerate temperature fluctuations is crucial for enhancing plant productivity under changing climatic conditions. Investigating how plants have developed stress tolerance and survival strategies to mitigate the adverse effects of temperature stress can provide insights for innovative approaches in breeding temperature-smart crops.

In response to external and internal stimuli, plants must autonomously regulate their growth and development. Over the past few decades, various biotechnological techniques have been harnessed to understand the mechanisms and pathways underpinning plant responses and tolerance to temperature stress. Among these tools, omics approaches (e.g., genomics, transcriptomics, proteomics, metabolomics, miRNAomics, epigenomics, phenomics, and ionomics) at tissue or single-cell levels have emerged as cutting-edge methods with the potential to advance crop improvement and ensure global food security (Figure 1) (Varshney et al., 2018; Esposito et al., 2019; Varshney et al., 2020; Varshney et al., 2021b; Varshney et al., 2021a; Sinha et al., 2021; Raza et al., 2021c; Raza et al., 2021a; Shen et al., 2022; Derbyshire et al., 2022; Raza, 2022; Raza et al., 2022b;

Yan and Wang, 2023; Benitez-Alfonso et al., 2023; Jan et al., 2023c; Raza et al., 2023a; Raza et al., 2023b). These revolutionary omics approaches play a fundamental role in stress-smart breeding programs, offering significant insights into genetic, molecular, and physiological aspects shaping plant responses to temperature stress. By unraveling complex molecular systems, these approaches aid in designing temperature-smart plants with enhanced tolerance and yield, contributing to sustainable agriculture and addressing global food security challenges.

Similarly, machine learning (ML) (Singh et al., 2016; Yoosefzadeh Najafabadi et al., 2023; Yan and Wang, 2023) and speed breeding (SB) (Watson et al., 2018; Hickey et al., 2019; Alahmad et al., 2022) methods have gained widespread use to expedite breeding programs and develop new cultivars within shortened timeframes (Figure 1). Notably, ML can explore extensive datasets and forecast complex traits, enhancing cultivar productivity and enabling informed decisions for trait advancement, such as temperature-smart plants (Singh et al., 2016; Yoosefzadeh Najafabadi et al., 2023; Yan and Wang, 2023). In contrast, SB accelerates plant growth and shortens breeding cycles, facilitating the rapid generation of new cultivars. Moreover, SB significantly expedites traditional breeding timelines and influences the swift development of stress-smart and high-yielding plant varieties (Watson et al., 2018; Hickey et al., 2019; Alahmad et al., 2022).

This review comprehensively discusses the impacts of climate change and extreme temperatures on crop production. It also elucidates recent advances in various omics approaches with the potential to enhance the breeding and development of temperature-smart plants. Moreover, it explores the potential of single-cell omics-assisted breeding, ML, and SB in accelerating the creation of climate-smart plants. Ultimately, this review offers an up-to-date overview of fast-track breeding methods that could be pivotal in developing temperature-smart crop plants to meet future challenges.

2 | IMPACT OF CLIMATE CHANGE AND EXTREME TEMPERATURE ON CROP PRODUCTION

Climate change presents a constant and profound threat, exerting substantial pressure on various global economic sectors. The agricultural sector, heavily reliant on stable climate conditions, is particularly vulnerable, resulting in widespread yield losses on a global scale (Zandalinas et al., 2021; Farooq et al., 2022; Rivero et al., 2022; Benitez-Alfonso et al., 2023). Climate change contributes to the increase in the frequency and severity of various abiotic stresses, including temperature, salinity, drought, and flooding, which adversely affect crop production (Figure 2A) (Raza et al., 2019;

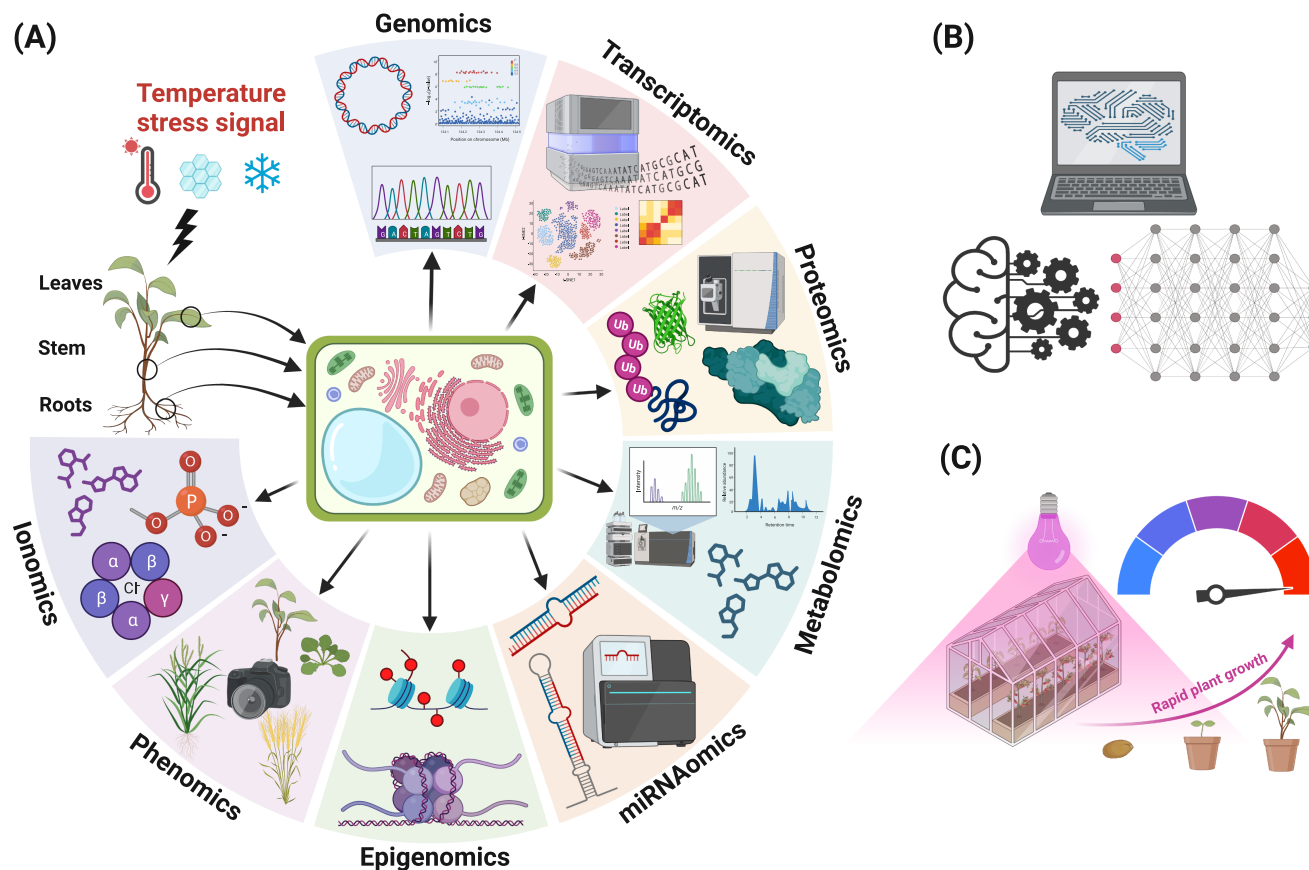


FIGURE 1 Systems biology approach to studying plant responses to temperature stress and enhancing tolerance mechanisms. (A) Integrated omics analysis involves merging two, three, or multiple omics approaches in a single study under the same or different stress conditions and plant tissues. This integration generates a comprehensive omics dataset for future breeding programs focused on developing temperature-smart plants. (B, C) Leveraging multi-omics data from integrated studies (shown in A) with machine learning algorithms and speed breeding methods to fast-track breeding processes to develop improved temperature-smart cultivars. (B) Machine learning processes these datasets to assess plant responses to temperature stress and discover key factors, such as markers, genes, metabolites, and proteins. (C) Speed breeding accelerates breeding cycles, facilitating rapid introgression of desired traits and evaluation of temperature-smart traits. This integration of multi-omics data, machine learning, and speed breeding modernizes the breeding process to develop improved cultivars adapted to extreme temperature conditions. Created with [BioRender.com](https://www.biorender.com).

Zandalinas et al., 2021; Farooq et al., 2022; Gonzalez et al., 2022; Rivero et al., 2022; Benitez-Alfonso et al., 2023; Djalovic et al., 2023; Varshney and Bohra, 2023; Zandalinas et al., 2023). These repercussions of climate change are predicted to affect agricultural yields in the years ahead (Figure 2B). Recent reports on climate change highlight its origins in natural factors, human activities, and deforestation. Human consumption of fossil fuels, the accumulation of harmful greenhouse gasses (GHGs), and land use practices have led to a dangerous escalation in atmospheric carbon dioxide (CO₂) concentrations, increasing from 284–410 ppm since the Industrial Revolution. Projections indicate a further increase to 730–1,000 ppm by 2100. Anthropogenic activities have also contributed to increased methane (CH₄) and nitric oxide concentrations in the atmosphere, further exacerbating global warming (Raza et al., 2019; Morán-Ordóñez et al., 2020) (<https://www.wri.org/insights/2023-ipc-ar6-synthesis-report-climate-change-findings>; <https://www.ipcc.ch/ar6-syr/>; <https://www.un.org/en/climatechange/science/causes-effects-climate-change>).

Recent data suggests that abrupt changes driven by climate change will intensify the frequency and magnitude of precipitation, temperature fluctuations, and extreme events like heat waves. These changes pose a significant challenge to plant survival and crop yields (<https://www.un.org/en/climatechange/science/causes-effects-climate-change>). The global mean temperature has increased by 0.8–1.5°C since the early 19th century (Li et al., 2023b; Saeed et al., 2023), with the heightened levels of GHGs forecast to increase global annual temperatures by 0.3–4.8°C by 2100 (Zandalinas et al., 2021). Climate change has triggered changes in temperature, rainfall patterns, and atmospheric conditions, negatively affecting the morphological, cellular, and metabolic processes in plants (Zhang et al., 2019; Zandalinas et al., 2021; Farooq et al., 2022; Rivero et al., 2022; Zandalinas et al., 2023). Extreme weather events resulting from global climate change indicate that low and high temperatures could adversely impact the productivity of major crops (Zhang et al., 2019; Zandalinas et al., 2021; Rivero et al., 2022).

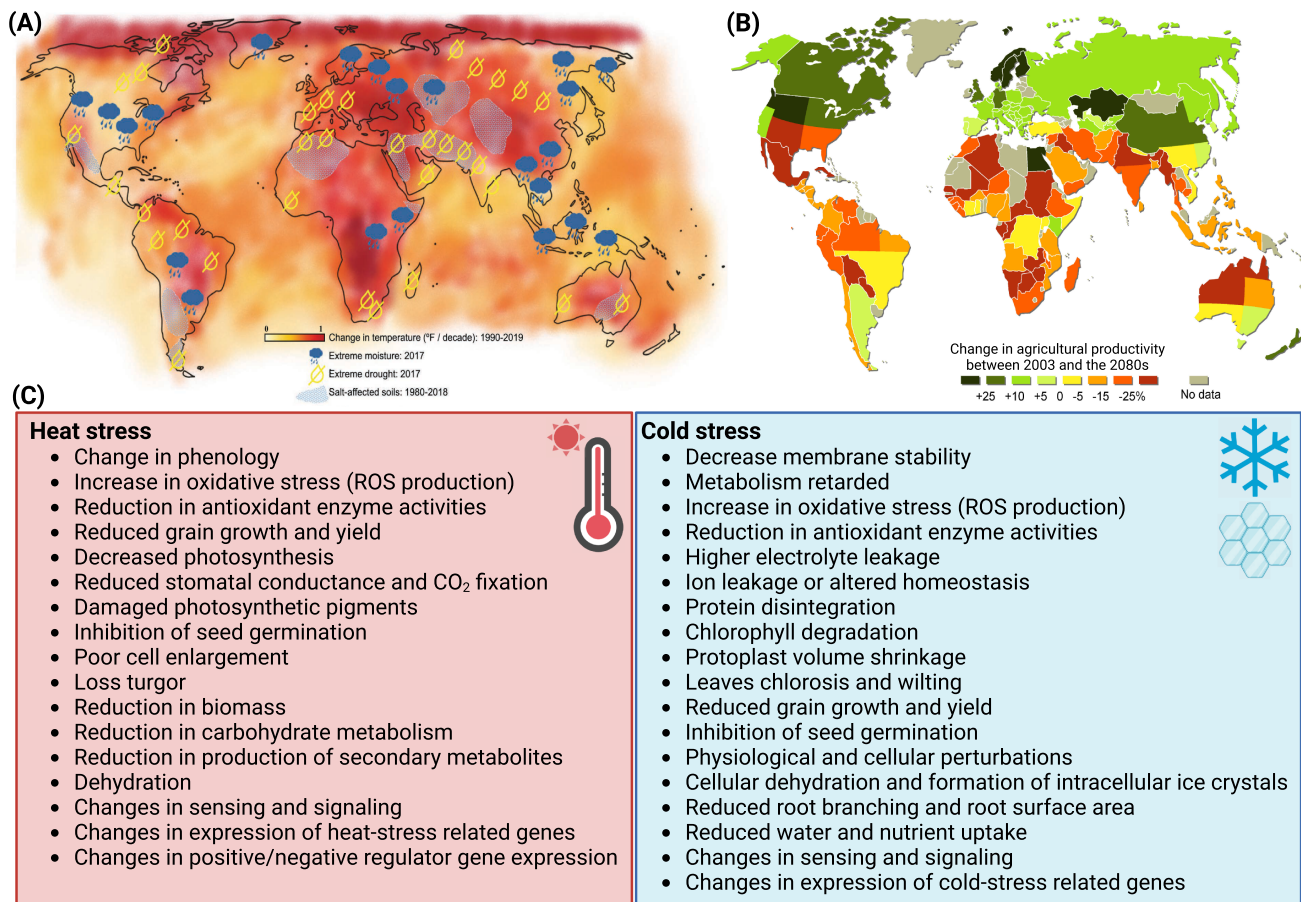


FIGURE 2 Impact of climate change on agricultural productivity. (A) Climate change manifestation varies across regions globally. It can entail synchronized or chronological events of two or more diverse stresses, including extreme temperatures, flooding, drought, and soil salinity. Data obtained from www.climate.gov and NOAA. Map adapted from Rivero et al. (2022). (B) Projected impact of climate change on agricultural yields by the 2080s, compared to 2003 levels, due to the multifaceted processes illustrated in (A). Source: <https://www.eea.europa.eu/en>. (C) Overview of the impact of extreme temperatures (heat and cold stress) on plant morphological, physiological, biochemical, molecular, and cellular processes. Modified from Raza et al. (2022a). Created with [BioRender.com](https://www.biorender.com).

Extreme weather conditions significantly disrupt various metabolic processes in plants (Figure 2C) (Raza et al., 2021c; Zandalinas and Mittler, 2022; Djalovic et al., 2023; Raza et al., 2023e; Raza et al., 2024; Saeed et al., 2023). The phenological phase of plants has an optimum temperature range for normal growth and development, and temperature fluctuations significantly impact growth, leading to crop loss and food shortages (Raza et al., 2021c; Raza et al., 2022a; Djalovic et al., 2023; Raza et al., 2023c; Raza et al., 2023e; Saeed et al., 2023). Recent data indicates that for every 1°C increase in the global average temperature, maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and soybean (*Glycine max* L.) production is projected to decrease by 7.4, 6.0, 3.2 and 3.1%, respectively, on average (Ding and Yang, 2022).

Crop plants encounter varying temperature conditions during growth, including high and low temperatures, posing significant risks to agricultural food production (Zandalinas et al., 2018; Zhang et al., 2019; Raza et al., 2022a; Huang et al., 2023; Raza et al., 2023c). Factors like temperature intensity, fluctuation frequency, and exposure duration impact the molecular mechanisms governing normal

plant growth and reproduction, significantly reducing morpho-physiological traits (Ding et al., 2020b; Zhang et al., 2021). Different crop species exhibit distinct temperature thresholds at various developmental stages, significantly impacting their growth (Ding and Yang, 2022). The plant photosynthetic system is particularly sensitive to HS, and cellular damage can occur due to disrupted leaf cellular organization (Allakhverdiev et al., 2008; Sun et al., 2023a; Zahra et al., 2023). Heat stress can significantly decrease chlorophyll (Chl) biosynthesis due to Chl synthase degradation (Sharma et al., 2022; Zahra et al., 2023), induce protein denaturation and aggregation, and enhance lipid membrane fluidity (Zhang et al., 2019; Ding et al., 2020b; Raza et al., 2022a; Raza et al., 2023c). Indirect impacts include enzyme denaturation in mitochondria and chloroplasts, protein synthesis inactivation, and disrupted cellular membrane integrity (Ding et al., 2020b; Wu et al., 2022; Sharma et al., 2022). Furthermore, HS affects microtubule organization (critical for cell division) and disrupts microtubule aster formation in mitotic cells (Mareri and Cai, 2022; Kumar et al., 2023b). Heat stress disrupts the reproductive phase of crop plants more than the vegetative stage, resulting in yield

loss due to pollen infertility and subsequent reduced fruit or seed development (Aghamolki et al., 2014; Cheabu et al., 2018; Ahmad et al., 2023). Recent data indicates that HS is linked to the inhibition of ribulose biphosphate carboxylase (RuBisCo) and RuBisCo activase, damaging the C3 cycle. This reduction in carbon fixation produces excessive reactive oxygen species (ROS) in plant photosystems, impeding plant repair mechanisms (Perdomo et al., 2017; Li et al., 2021b; Sharma et al., 2022; Qu et al., 2023).

Heat stress adversely affects various plant growth stages, decreasing germination percentage, seed vigor, and radicle growth, often associated with decreased relative water content, inhibiting overall plant growth (Zhang et al., 2019; Ding et al., 2020b; Wu et al., 2022). Wheat plants exposed to HS at pre-anthesis exhibited reduced dry weight due to alterations in net assimilation rate, decreasing seed nutritional value (Degen et al., 2021). This stress disrupts the balance between sucrose introduction and consumption within tissues, impacting the optimal growth of reproductive structures (Abdelrahman et al., 2020; Kumar et al., 2022). Temperatures above 30°C inhibits the translocation of resources to emerging grain, shorten the grain-filling period, and reduce starch accumulation due to diminished flag leaf assimilatory efficiency, impairing the reproductive physiology of wheat plants (Ullah et al., 2022). Managing the source–sink balance, by facilitating the passage of photoassimilates to sink tissues and adjusting their consumption is essential to enhance wheat grain yields under HS (Kumar et al., 2017; Hütsch et al., 2019; Abdelrahman et al., 2020). However, interruptions in these interactions significantly affect final grain yields under HS. For example, HS at 45°C adversely affected crop physiology and caused 80–90% seedling mortality in wheat plants (Abd El-Daim et al., 2014). Extreme temperatures accelerate the aging process in plants, triggering premature senescence, characterized by early yellowing and shedding of leaves, ultimately reducing photosynthetic capacity and crop productivity (Guo et al., 2022; Ahmad et al., 2023; Zahra et al., 2023). Heat stress also reduces root and shoot lengths, plant height, and biomass production in various field crops (Zhang et al., 2019; Ding et al., 2020b; Wu et al., 2022; Raza et al., 2023c). For instance, HS at 39°C decreased rice shoot length by 16.67% (Kilasi et al., 2018), while HS at 42 °C decreased shoot length and biomass of tomato (*Solanum lycopersicum* L.) (Mukhtar et al., 2023).

Reproductive tissues are particularly vulnerable to HS and CS. For instance, when crop development reaches the anther differentiation stage, CS can lead to production losses of up to 30–50% (Liu et al., 2019; Hassan et al., 2021). Recent data revealed that CS adversely impacts critical crop growth stages in cereals, resulting in carbohydrate accumulation that alters hormone contents (Xu et al., 2022a). Furthermore, CS significantly affects proteins involved in carbohydrate metabolism, protein folding, dilapidation, and stress, and the synthesis of compatible solutes (Raza et al., 2021b; Mehmood et al., 2021; Raza et al., 2021c; He et al., 2023; Seydel et al., 2022). Moreover, FS can cause cellular desiccation and disruptions in cell membranes in crop plants, resulting in damaged membrane structures that disturb osmotic homeostasis and affect metabolic activities (Liu et al., 2019; Ding et al., 2020b; Hassan et al., 2021).

Another significant effect of temperature stress is the associated reduction in water use efficiency (WUE) (Li et al., 2021b), such that CS and HS adversely affect the plant root–shoot system, which regulates nutrient and water uptake and their transport to above-ground plant tissues (Kummerow and Ellis, 1984; Caldwell and Richards, 1989; Jackson et al., 2000). Moreover, temperature fluctuations often increase respiration rates in plants, resulting in a higher energy demand, which can deplete plant resources and negatively impact overall growth and yield (Debnath et al., 2022; Sharma et al., 2022). It has been well-documented that CS decreases grain yield in various crop plants (Rane et al., 2021; Ullah et al., 2022; Kuczyński et al., 2022; Li et al., 2022b; Bhat et al., 2022; Hernández et al., 2023), significantly impacting future food security for the growing population. For instance, CS at 13/8°C decreased maize yield by 21.87% (Waqas et al., 2017), while CS at 4°C decreased wheat yield by 40% (Li et al., 2017).

3 | OMICS-DRIVEN BREEDING FOR TEMPERATURE-SMART PLANTS

Plant responses to temperature stress depend on the regulation of genes, proteins, metabolites, miRNAs, and epigenetic markers, collectively shaping plant phenotype. Integrated omics approaches have been explored extensively to elucidate stress responses and tolerance mechanisms, enabling the expedited development of temperature-resilient crop plants (Figure 1). Despite remarkable advances in genomics (Varshney et al., 2005; Varshney et al., 2018; Bohra et al., 2020; Varshney et al., 2020; Varshney et al., 2021b; Varshney et al., 2021a; Sinha et al., 2021), there is a pressing need to explore other omics approaches, including transcriptomics, proteomics, metabolomics, miRNAomics, epigenomics, phenomics, and ionomics profiling, to enhance our understanding of gene–phenotype interactions, or more precisely, genotype–environment interactions (see Figure 1). Before embarking on large-scale omics integration, it is essential to investigate diverse germplasm to determine the relationship between temperature-stressed and stress-free plants (Figure 3A). This knowledge will help identify the best germplasm, cultivars, or wild relatives with superior performance under temperature stress. In the subsequent sections, we have comprehensively reviewed the literature to explore the mechanisms underpinning temperature stress tolerance in various plant species to help fast-track breeding processes (e.g., genetic engineering) to design temperature-smart crop plants and ensure future food safety (Figure 3).

3.1 | Genomics innovations

Genomics is a classic omics approach, providing comprehensive data on the entire genome rather than just a single gene or its product (Varshney et al., 2018; Varshney et al., 2021b). Genomics focuses on complete hereditary material information, including essential data on the three critical interactions (heterosis, pleiotropy, and epistasis),

(A) Germplasm

- Temperature-tolerant
- Temperature-sensitive
- Landraces
- Wild relatives

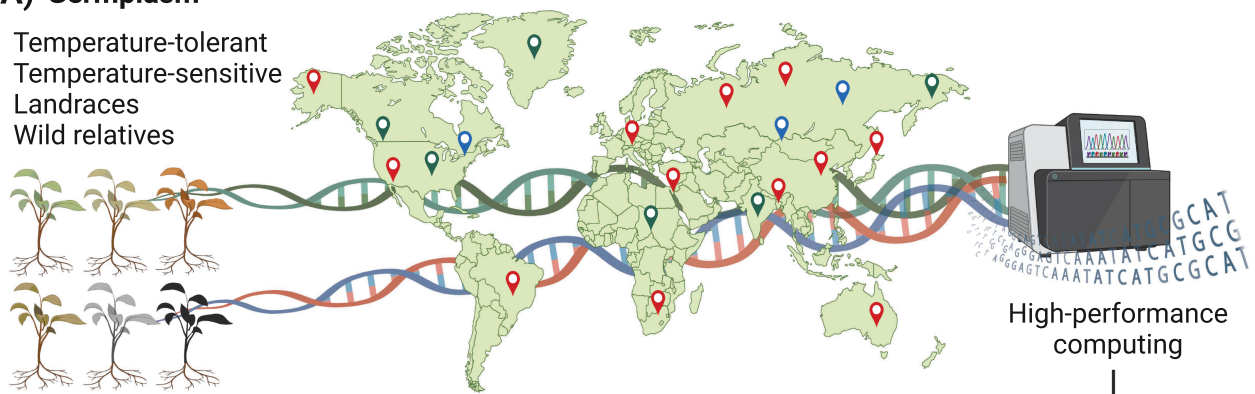
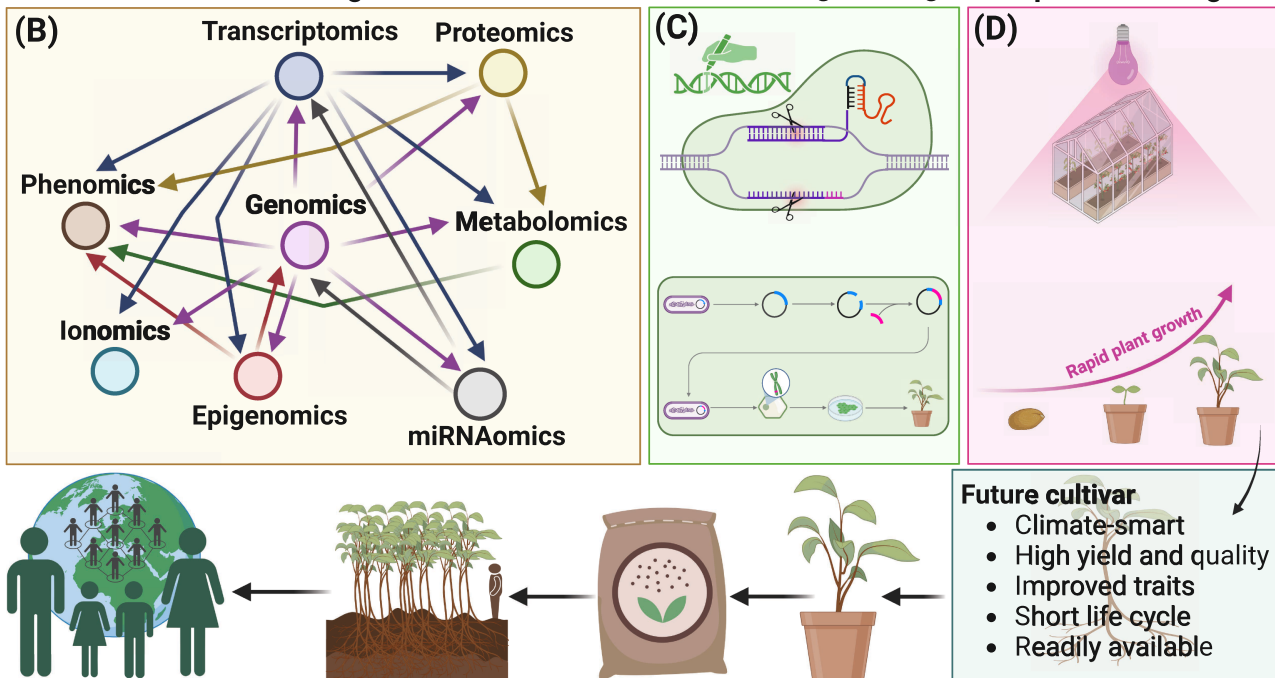
**Omics integration****Genetic engineering****Speed breeding**

FIGURE 3 Omics-mediated proposed strategies for designing temperature-smart cultivars. **(A)** collecting and screening germplasm, **(B)** omics integration, **(C)** genetic engineering, and **(D)** speed breeding. **(A)** Collecting and screening diverse germplasm from various gene banks and regions worldwide, including temperature-tolerant and -sensitive lines/cultivars, landraces, and their wild relatives. Recent advances in high-performance computing, including the use of multi-omics-level data, have greatly enhanced crop genetic exploration. **(B)** Integrating diverse omics tools can help uncover stress-associated key players, such as genes, proteins, metabolites, miRNAs, and metabolic pathways, that are pivotal in understanding temperature stress responses and tolerance mechanisms. **(C)** Genetic engineering methods, including gene editing and transgenic breeding, offer immense potential in designing climate-smart future crops to address global food security challenges. Technologies like the CRISPR/Cas system have revolutionized modern agricultural biotechnology (Tariq et al., 2023; Yaqoob et al., 2023; Zaman et al., 2023a; Zaman et al., 2023b). Key players revealed through integrated omics can be genetically engineered to modulate gene expression and the abundance of metabolites/proteins associated with stress tolerance. The CRISPR system and introgression can be used to transfer favorable loci/genes isolated from wild relatives into cultivated/domesticated plants. **(D)** Speed breeding involves the manipulation of environmental conditions under which crop genotypes are cultivated, with the objective of fast-tracking the breeding cycle and advancing to the next breeding generation as quickly as possible (Watson et al., 2018; Hickey et al., 2019; Alahmad et al., 2022). This method is instrumental in rapidly developing numerous generations of modern climate-smart crop plants. In conclusion, integrating these tools could empower plant scientists to develop future-ready cultivars for farmers and growers that are poised to help feed the ever-growing global population (<https://www.un.org/development/desa/en/news/population/world-population-prospects-2017.html>) and ensuring future food safety. Created with BioRender.com.

enabling the identification of a consortium of genes that can be subsequently used in crop improvement programs (Varshney et al., 2005; Varshney et al., 2018; Varshney et al., 2020; Varshney et al., 2021b; Sinha et al., 2021; Shen et al., 2022). Advances in high-throughput next-generation sequencing platforms, robust computational biology tools, and database management practices for sequence analysis have significantly enhanced genomics capabilities (Varshney et al., 2018; Bohra et al., 2020; Varshney et al., 2021b). Genomics can identify single and multiple genes specific to stress responses and quantitative trait loci (QTL) using techniques like polymerase chain reaction and hybridization-based molecular markers, which can be subsequently used in agricultural breeding programs like genomics-assisted breeding (GAB) and marker-assisted selection (MAS) to develop superior cultivars (Varshney et al., 2018; Varshney et al., 2020; Bohra et al., 2020; Varshney et al., 2021b).

Genome-wide association (GWAS) and QTL mapping studies are instrumental in identifying key elements (e.g., genes, QTL, molecular markers, genomic regions) associated with temperature stress responses in plants. For instance, under HS (45°C), GWAS and linkage analysis uncovered two QTLs (*qDW7* and *qFW6*) associated with rice seedling development (Wei et al., 2021). Heat stress significantly affects rice grain quality, often leading to chalkiness. Fine mapping identified two QTLs associated with chalkiness in single-segment substitution lines for all 12 chromosomes: HP67-11 from *Oryza glaberrima* and 11-09 from *Oryza sativa* (Yang et al., 2021). Reproductive stages in rice are highly sensitive to HS and crucial for rice quality and yield. A QTL analysis of the genetics underlying HS sensitivity identified a QTL on chromosome 5 in *O. rufipogon* Griff (*qHTH5*) coding the *HTH5* gene—which affects the pyridoxal phosphate-binding protein PLPBP—with differential expression patterns in the HS (38 ± 0.5°C from 8:30 am to 3:00 pm) and CS (~30 ± 0.5°C from 3:00 pm to 8:30 am) treatments (Cao et al., 2022). More recently, a genomics study used 113 segment substitution lines derived from heat-sensitive (9311) and heat-resistant (N22) indica varieties at the heading stage (38 ± 2°C) (Nguyen et al., 2022). Five QTL associated with HS tolerance were detected based on a seed-setting rate evaluation: *qSSR6-1*, *qSSR7-1*, *qSSR8-1*, *qSSR9-1*, and *qSSR11-1* located on chromosomes 6, 7, 8, 9, and 11, respectively (Nguyen et al., 2022).

A GWAS study involving 96 wheat genotypes was conducted to elucidate the genetic basis of HS tolerance (Ahmed et al., 2022a). Using single nucleotide polymorphisms (SNPs) array and assessing various physiological and yield indices, the study investigated the response of these genotypes under normal and HS environments (>40°C). A structure analysis identified 320 significant ($-\log_{10}P \geq 3$) marker-trait associations (MTAs), with 169 MTAs recorded under normal conditions and 151 MTAs under HS conditions across chromosomes 4B, 6B, 7B, 5A, 1B, and 3D. The candidate SNPs identified in this study could be used to develop HS-tolerant wheat genotypes (Ahmed et al., 2022a). Another GWAS study identified seven QTL associated with the response to post-anthesis HS (daytime maximum 21°C/night-time minimum 15°C) for two weeks in 199 European winter wheat varieties (Touzy et al., 2022). Two main QTLs associated with HS tolerance for thousand-kernel weight were identified

on chromosomes 4B and 6B, offering valuable tools for breeders to improve grain yield in the face of rising temperatures (Touzy et al., 2022).

Heat-tolerant association mapping was used to investigate genomic regions associated with HS in 543 tropical maize plants in various locations, with temperatures ranging from 35–40°C (Seetharam et al., 2021). The study identified 269 novel significant SNPs linked to grain yield, with another 175 SNPs found within 140 unique gene models involved in various biological pathways responding to different abiotic stresses, including HS (Seetharam et al., 2021). In another GWAS study, 375 maize inbred lines were sown at the end of May, experiencing temperatures ranging from 29–35°C (Ahmed et al., 2022b). The stressed plants flowered from early to mid-July, encountering temperatures ranging from 38–45°C. The study assessed the effect of HS on pollen germination percentage (PGP), identifying 10 SNPs associated with PGP35°C ($p \leq 10^{-5}$), nine associated with PGP45°C ($p \leq 10^{-6}$ to 10^{-8}), and 10 SNPs associated with the PGP ratio ($p \leq 10^{-5}$). The genetic mapping of yield (adjusted weight per plant, AWP^{-1}) and flowering time (anthesis–silking interval ASI) revealed five common SNPs: three shared for AWP^{-1} between normal and HS conditions, one for ASI between conditions, and one associated with ASI and AWP^{-1} (Ahmed et al., 2022b). In another GWAS mapping study involving 162 early-maturing inbred maize lines sourced from the International Institute of Tropical Agriculture, Ibadan, Nigeria, researchers identified four SNP markers exhibiting pleiotropic effects for days to 50% anthesis and days to silking under HS combined with drought (Osuman et al., 2022).

An integrated omics investigation explored important agricultural traits using non-reference sequences within the rice genome (Woldegiorgis et al., 2022). The genomic variation analysis detected 76,435 SNPs, identified SNPs related to HS tolerance, and mapped 1,677 differentially expressed genes (DEGs) to 46 HS-resistant QTL regions. Two DEGs, calmodulin-binding protein 60 A-like (*maker_00000041*) and cysteine-rich receptor-like protein kinase 6 (*maker_00001878*), were up-regulated and harbored SNPs linked to HS tolerance in the non-reference rice sequences (Woldegiorgis et al., 2022). Anthesis is a critical phase in the rice development cycle, significantly influencing grain yield and quality. A recent study identified five QTL associated with relative spikelet fertility (RSF) rate, one of which (*qRSF9.2*) contained 16 candidate genes for HS tolerance (Hu et al., 2022). One specific gene (*LOC_Os09g38500*) contained non-synonymous SNPs significantly associated with RSF (Hu et al., 2022). A meta-QTL analysis was conducted to identify potential candidate genes associated with the rice grain chalkiness trait, retrieving 64 meta-QTL from a pool of 403 previously identified QTL comprising 5,262 non-redundant genes (Kumar et al., 2023a). Further investigations revealed 39 candidate genes associated with non-synonymous allelic variations under HS conditions (38–41°C) (Kumar et al., 2023a). The study also screened 185 F12 recombinant inbred lines derived from two US rice cultivars to identify genomic regions associated with grain quality traits under HS conditions (30 ± 1°C day/22.2 ± 1°C night, at the booting stage) (Kumar et al., 2023a). These efforts identified 15 QTLs (nine

associated with night-time HS) containing 6,160 SNPs and 149 DEGs. Eleven potential candidate genes were significantly linked to SNP associations and HS tolerance in rice (Kumar et al., 2023a).

In response to CS, a GWAS involving 370 rice accessions was conducted using the rice diversity panel to explore correlations among cold-stressed phenotypes (Phan and Schläppi, 2021). The study identified 20 novel QTLs associated with antioxidant activity, including membrane damage, seed survivability, catalase, and anthocyanin, under CS (10°C, 7 days) (Phan and Schläppi, 2021). Another GWAS analysis in rice focused on the seedling stage response to CS and chilling acclimation identified 235 SNPs (120 and 88 for relative shoot fresh weight under CS and chilling acclimation, respectively) and 11 and 12 QTL for CS and chilling acclimation, respectively (Li et al., 2022a). A GWAS study investigated phenotypic and physiological parameters at the seedling emergence stage in 200 cotton accessions from five ecological distributions under constant chilling (CC) and diurnal variation in chilling (DVC) identified 575 significantly associated SNPs and 35 stable QTL, with five each associated with traits under CC and DVC stress and 25 co-associated (Shen et al., 2023a). Another recent GWAS study coupled with RNA-seq in 351 core rice germplasm under three temperature conditions detected 54, 59, and 21 QTL (total 134 QTL) associated with normal, CS, and chilling acclimation conditions, respectively (Khatib et al., 2022). Furthermore, the integrated SNP analysis of these 134 QTL identified 116 QTL for three temperature conditions (53, 43, and 18 QTL linked to normal, CS, and chilling acclimation, respectively), with two QTL colocalized for CS and chilling acclimation (Khatib et al., 2022).

A GWAS study investigating 96 barley spring cultivars to understand cold acclimation (20 /15°C, 14 days) at different time intervals using Chl fluorescence-related traits identified three major and putative genomic regions, with 52 significant quantitative trait nucleotides (QTNs) on chromosomes 1H, 3H, and 6H (Elakhdar et al., 2023). The QTN annotation identified metabolites like hydrolase activity, ABA signaling, protein kinase, and some signal transduction players (Elakhdar et al., 2023). A novel GWAS study detected CS tolerance-related QTL (*qPSR7-2*) on chromosome 7 in 173 *japonica* rice germplasm (Xiao et al., 2023). Fine mapping identified Os07g0541800 as a candidate gene associated with *qPSR7-2*, encoding cysteine-rich receptor-like kinase (Xiao et al., 2023). Another study exploring the impact of CS (13°C, 14 days) on the germination rate of 151 cucumber (*Cucumis sativus* L.) accessions from seven diverse ecotypes identified 1,522,847 SNPs, with seven loci (*gLTG1.1*, *gLTG1.2*, *gLTG1.3*, *gLTG4.1*, *gLTG5.1*, *gLTG5.2*, and *gLTG6.1*) associated with low-temperature germination (LTG) (Li et al., 2023a). *gLTG1.2*, *gLTG4.1*, and *gLTG5.2* exhibited strong signals for four germination indices across two years. Moreover, eight candidate genes associated with abiotic stresses were reported, with three significantly linked to LTG: *CsaV3_1G044080* (pentatricopeptide repeat-containing protein) for *gLTG1.2*, *CsaV3_4G013480* (RING-type E3 ubiquitin transferase) for *gLTG4.1*, and *CsaV3_5G029350* (serine/threonine-protein kinase) for *gLTG5.2* (Li et al., 2023a). Frost tolerance (FroT) QTL were identified in 276 winter wheat genotypes

previously phenotyped at field locations in Germany and Russia (Soleimani et al., 2022). From a pool of 17,566 SNPs, 53 were significantly associated with FroT, corresponding to 23 QTL regions on 11 chromosomes (1A, 1B, 2A, 2B, 2D, 3A, 3D, 4A, 5A, 5B, and 7D). The QTL regions on chromosome 5A were strongly responsible for FroT (Soleimani et al., 2022).

The availability of genome sequences for numerous crop plants has facilitated the exploration of novel gene family members in different species in response to various stress conditions. For instance, an exploration of the NAC (*NAM*, *ATAF1/2*, and *CUC2*) gene family in *Kandelia obovata* revealed expression patterns of different members in response to CS at 4°C over various time points (0, 6, 12, and 24 h) (Sun et al., 2021). Among the identified genes, 12 were up-regulated, and one was down-regulated under CS. Promoter analysis of these *KoNAC* genes revealed the presence of stress-related elements like ABRE (abscisic acid response element), LTR (low-temperature response), WUN (wound-responsive element), and STRE (stress response element) (Sun et al., 2021). In maize, the hyperosmolality-gated calcium-permeable channels (*OSCA*) gene family was explored in response to temperature stress, identifying *ZmOSCA2.2* and *ZmOSCA2.3* genes as key responders to temperature stress stimuli (Li et al., 2022d). Another study investigated the cellulose synthase-like gene (*Csl*) gene family in contrasting cultivars of *Musa acuminata* in response to CS, identifying 42 *MaCsls*, with *MaCslA4/12*, *MaCslD4*, and *MaCslE2* promising candidate genes for chilling tolerance (Yuan et al., 2021). A study on *Prunus persica* identified 17 calcium-dependent protein kinase (*CDPK*) family genes, with the sequence analysis revealing *PpCDPK2*, *PpCDPK7*, *PpCDPK10*, and *PpCDPK13* genes related to CS tolerance during postharvest (Zhao et al., 2022a).

These genomics studies have significantly advanced our understanding of temperature stress adaptation in different plant species. High-throughput sequencing tools and pioneering computational analysis have led to the documentation of key genes, QTL, and SNPs crucial for stress adaptation and tolerance in crops like rice, wheat, and maize. These outcomes have informed the genetic basis of stress responses and specified new insights for precision plant breeding plans. Harnessing this learning provides scientists with robust tools to design climate-smart crop varieties, confirming food security in the face of rapidly shifting climatic conditions.

3.2 | Transcriptomics

Transcriptomics is a powerful tool for analyzing gene expression profiles, regulatory pathways, related transcripts, and post-translational modifications in organisms (Raza et al., 2021a; Raza et al., 2021c; Raza et al., 2021b). It plays a crucial role in deciphering how plants swiftly reprogram transcription networks in response to external stimuli (Bhardwaj et al., 2021). High-throughput transcriptomic tools lay the foundation for gene discovery, molecular marker development, and marker-assisted breeding (Varshney et al., 2020), ultimately contributing to temperature-smart plant breeding (Raza et al., 2021a; Raza et al., 2021c; Raza et al., 2021b). Here are some examples of how

transcriptomic studies have enhanced our understanding of plant responses to HS. A study on lentil (*Lens culinaris* L.) exposed to HS (40°C) for 4 h identified 4,327 DEGs (1,959 up-regulated and 2,368 down-regulated) (Hosseini et al., 2021). Up-regulated genes were predominantly related to cell cycle and division, protein binding, and microtubule binding, while down-regulated genes were associated with membrane and transport (Hosseini et al., 2021). In coffee (*Coffea arabica* L. (polyploid) and *Coffea canephora* (diploid)), exposure to HS at 42°C altered the expression of 667 DEGs in both species (Marques et al., 2021). Photosynthesis and other biochemical processes, including photosystems I and II, Chl a/b binding, and RuBisCo activity, were notably down-regulated in *Coffea arabica* (Marques et al., 2021). The comparison of heat-tolerant and heat-sensitive rose varieties (*Rosa multiflora* and *Rosa chinensis*, respectively) exposed to 45°C for 6 h exhibited up-regulation (3,849 and 3,453) and down-regulation (3,483 and 2,944) of DEGs, respectively, in *R. chinensis* (Qi et al., 2021). Variability in gene expression patterns in response to HS was observed between a self-root grafting line (XX) and a heterogeneous grafting line (XW) (Qi et al., 2021). In rice, Wei et al. (2021) identified eight genes significantly regulated in response to HS (45°C for 52 h), including *LOC_Os06g10790*, *LOC_Os06g10860*, *LOC_Os07g30330*, *LOC_Os06g10810*, *LOC_Os01g09450*, *LOC_Os03g59040*, *LOC_Os12g42980*, and *LOC_Os02g12890*.

Potato (*Solanum tuberosum* L.) variety ‘Hezuo 88’ exposed to HS for 6 h exhibited up-regulation of 160 DEGs enriched in various processes, including amino acid production, cell wall degradation, protein degradation, hormone metabolism, secondary metabolism, and heat shock proteins (HSPs) and down-regulation of 538 DEGs related to signal transduction, RNA regulation, fatty acid desaturation (lipid metabolism), and cytokinin metabolism (Liu et al., 2021a). A comparative transcriptomic analysis of two Chinese cabbage cultivars (‘268’ and ‘334’) revealed significant differences in their response to HS, with ‘268’ up-regulating 11,055 DEGs involved in ribosome biosynthesis, autophagy pathways, and glutathione metabolism and down-regulating photosynthesis-related genes, and ‘334’ exhibiting changes in endoplasmic reticulum protein processing and hormonal signal transduction (Yue et al., 2021). In rice, elevated night-time temperatures (by 2–3°C) resulted in the down-regulation of 695 DEGs related to HS, photosynthesis, and protein folding and up-regulation of 415 DEGs associated with signaling, carbohydrate metabolism, RNA processing, kaurene synthesis, and post-translational protein modifications (Desai et al., 2021). A comparative review of lentil plants exposed to HS and stemphylium blight stress highlighted the expression of DEGs associated with cell cycle and division, cell wall synthesis, photosynthesis, phytohormones (auxin and ABA), kinases (LRR-RLKs and serine/threonine kinases), transcription factors, and HSPs among others (Tiwari et al., 2022).

Ren et al. (2023) observed CS responses in grapevines (*Vitis vinifera* L.), noting the regulation of various metabolites, phytohormones, and specified proteins, controlled by the up- and down-regulation of cold-regulated genes (COR). The authors identified significant transcription factors in the AP2, RAV1, and ERF gene families that regulate the CS response in grapevine. Moreover, Cheng et al. (2023)

highlighted the role of the CBF (C-repeat-binding factor)-COR pathway in managing CS in two tea cultivars: cold-tolerant Shuchazao (SCZ) and cold-sensitive Yinghong 9 (YH9). SCZ exhibited enhanced amino acid and arginine biosynthesis under CS compared to YH9. Waititu et al. (2021) reported increased expression of 779 DEGs in a cold-tolerant maize variety under CS (<10°C), with many related to antioxidation, transport, hormone signaling, glutathione, and lipid, carbon, and amino acid metabolism, and increased expression of 877 DEGs in cold-sensitive maize varieties, with many associated with proteolysis, peroxisomes, ribosomes, MAPK signaling, and carbon metabolism. Tian et al. (2021) explored the response of cold-tolerant and cold-sensitive Rutaceae (*Zanthoxylum bungeanum*) varieties exposed to CS (4°C), revealing the expression of 3,513 and 25,157 DEGs, respectively. Among these DEGs, pivotal hub genes like *ERD7*, *PP2C*, *LEA D-29*, *ZB01477*, and *pp34* played significant roles in regulating the CS response in these plants. In another study, wild apple (*Malus sieversii* L.) exhibited 4,410 DEGs under FS (–4°C) related to the regulation of hormone signal transduction, starch and sucrose metabolism, peroxisome function, and photosynthesis pathways (Zhou et al., 2021). Transcription factors, including *DREB1/CBF*, *MYC2*, *WRKY70*, *WRKY71*, *MYB4*, and *MYB88*, played prominent roles in the FS response (Zhou et al., 2021).

Comparative transcriptomic analysis of cold-tolerant (C18) and cold-sensitive (C6) rapeseed varieties under CS (4°C for 0, 1, and 7 days) unveiled 3,358 and 2,819 DEGs on days 1 and 7 of CS exposure, respectively, related to secondary metabolism, amino acids, lipids, and cell wall pathways (Raza et al., 2021b). Key genes, including *Bn4CL3*, *BnCEL5*, *BnFRUCT4*, *BnUGP1*, *BnAXS1*, and *BnBAM2/9*, were instrumental in conferring CS tolerance in rapeseed (Raza et al., 2021b). Yan et al. (2022a) investigated the role of inositol, a cyclic polyol-inositol, in managing CS in a cold-tolerant rapeseed cultivar (C18) compared to a cold-sensitive cultivar (C20). The authors reported that C18 increased inositol concentration with decreasing temperature and increased expression of 35 inositol enzyme-encoding DEGs. Inositol regulated CS by enhancing calcium (Ca²⁺) influx and inhibiting the *CBL1* (calcineurin B-like) gene. Exogenous application of inositol induced the expression of CBF-COR genes, contributing to cold tolerance (Yan et al., 2022a). Luo et al. (2023) reported that the down-regulation of *BnaMYBL17* (MYB-like gene) adversely impacted CS tolerance in Zhongshuang 6 (ZS6) rapeseed cultivar exposed to CS (–4°C for 4 h). Transcriptomic analysis of *BnaMYBL17* revealed 14,298 DEGs and 1,321 candidate target genes. Up-regulation of genes like *BnaPLC1*, *BnaFLZ8*, and *BnaKOIN* was associated with increased freezing sensitivity in ZS6 (Luo et al., 2023).

Luo et al. (2022) conducted a comparative transcriptomic analysis using two tobacco cultivars—cold-tolerant ‘Yanyan97 tobacco (YT)’ and cold-sensitive ‘Taiyan8 tobacco (TT)’—exposed to CS (4°C) at the five-leaf stage for varying durations, reporting distinct DEG expression patterns between TT and YT, which were closely associated with their CS response and explained their differential cold tolerance (Luo et al., 2022). Moso bamboo (*Phyllostachys edulis*) exposed to CS (0°C) for 2 or 4 h exhibited 2,322 (1,418 up-regulated and 904 down-regulated) and 661 (565 up-regulated and 96 down-regulated) DEGs,

respectively, mainly involved in dehydration responses (Huang et al., 2022). A study on centipede grass (*Eremochloa ophiuroides*) exposed to CS (4 °C) for varying durations identified 129, 398, and 477 DEGs after 3, 6, and 9 h of CS exposure, which were associated with various cellular and molecular processes, including transcription regulation, redox mechanisms, phosphorylation, and DNA-templated processes (Liu et al., 2023). Two passionfruit (*Passiflora edulis*) varieties—cold-tolerant Tainong 1 (TN1) and cold-sensitive Huangjinguo (HJG)—exposed to CS (7 °C) exhibited a 33.6% increase in DEGs compared to normal temperature conditions (Wu et al. (2021).

These examples illustrate the power of transcriptomics in uncovering the molecular responses of plants to temperature stress, offering valuable insights into the genes and pathways involved in their adaptation to extreme temperatures. Transcriptomic studies contribute to understanding temperature stress responses in various plant species, facilitating the development of temperature-smart crops through breeding and genetic engineering.

3.3 | Proteomics

Proteomics examines the protein constituents in an organism at a specific point in time, serving as a vital link between the transcriptome and the metabolome (Yan et al., 2022b; Jan et al., 2023b). In recent decades, proteomic approaches as a powerful next-generation research tool have significantly advanced, especially with the establishment of instruments with high resolution and mass accuracy (Raza et al., 2021a; Jan et al., 2023b; Yan et al., 2022b). These techniques have been instrumental in unraveling plant responses to changing temperatures at the protein level (Raza et al., 2021a; Raza et al., 2021c). For example, HS disrupts plant protein balance and regulatory mechanisms (Xu et al., 2021; Raza et al., 2021c). In a study on Monterey pine (*Pinus radiata*) embryos exposed to two HS conditions (40 °C for 4 h, 60 °C for 5 min), proteomic analysis revealed the up-regulation of ribosomes, cell wall carbohydrates, transmembrane transport proteins, HSPs and chaperones, post-transcriptional regulation proteins, and fatty acid biosynthesis proteins and the down-regulation of adenosylhomocysteinase protein, glycolytic pathway enzymes, nitrogen assimilation enzymes, oxidative stress enzymes, and methionine-tRNA ligase (Castander-Olarieta et al., 2021). Similarly, in chickpea (*Cicer arietinum* L.), HS led to the differential expression of various proteins, including HSP70, ribulose bisphosphate carboxylase/oxygenase activase, plastocyanin oxidase and protoporphyrinogen oxidase, alongside the up-regulation of proteins related to defense, transport, intracellular traffic, and protein biosynthesis (Makonya et al., 2021).

Wang et al. (2021) reported 1,591 differentially abundant proteins (DAPs) related to stimuli response, structural molecule activity and transporter activity, catalytic activity, energy production and conversion, and carbohydrate transport and metabolism in two pepper varieties (heat-tolerant 17CL30 and heat-sensitive 05S180) upon HS exposure (40 °C). In wheat under HS, Chunduri et al. (2021) reported enhanced expression of DAPs involved in translation, gliadins, and

low-molecular-weight glutenins and decreased expression of defense-related, photosynthesis, glycolysis, and high-molecular-weight glutenins DAPs. Lettuce plants suffered early bolting within 8 days of HS (33 °C), resulting in 93 DAPs, with 38 up-regulated, such as HSP-like proteins (XP_023757207.1, XP_023740399.1, and PLY74879.1), thaumatin-like protein, rRNA 2'-O-methyl-transferase fibrillar-like protein, GA-related protein14-like protein, and aldehyde dehydrogenase family 2 member B4, and 55 down-regulated, such as the Calvin cycle protein CP12-3 and TsetseEP-like protein (Hao et al., 2021). Furthermore, proteomic characterization of *Brachypodium distachyon* cell walls under HS (40 °C) revealed decreased cell wall expansion, lignification, and protease activity associated with 46 DAPs (4 up-regulated and 42 down-regulated) (Pinski et al., 2021). In strawberries, HS (37 °C) resulted in 1,138 DAPs (490 up-regulated and 648 down-regulated) enriched in binding functions, catalytic activity, and cellular and organelle processes (Lv et al., 2022a).

Potato plants exposed to CS (4/2 °C day/night) for 7 days exhibited 52 DAPs related to ribosome formation, cell movement, photosynthesis, signal transduction, nitrogen metabolism, energy metabolism, protein synthesis and degradation, defense response, and other physiological processes (Li et al., 2021a). In rapeseed exposed to CS (8/4 °C day/night) for 0, 1, and 7 days, Mehmood et al. (2021) reported 8, 25, and 43 up-regulated and 2, 20, and 30 down-regulated DAPs in cold-tolerant 'C18' and 18, 25, and 25 up-regulated, and 5, 54, and 127 down-regulated DAPs in cold-sensitive 'C6', respectively. The DAPs in C18 were related to photosynthesis-antenna proteins, thiamine metabolism, and anthocyanin biosynthesis, while those in C6 were associated with carbon, glyoxylate, and dicarboxylate metabolism (Mehmood et al., 2021). In another rapeseed study, a comparative proteomic analysis of cold-tolerant '17NTS57' and cold-sensitive 'NQF24' exposed to CS (−4 °C) revealed 1,235 DAPs after 12 h and 1,543 DAPs after 24 h in the cold-tolerant variety associated with the biosynthesis of flavonoids, phenylalanine, tyrosine, and tryptophan, and ubiquinone and other terpenoid-quinones, and lysine degradation (Mi et al., 2021). An iTRAQ-based proteomic analysis of cold-tolerant rice 'Kongyu131' under CS (8 °C) unveiled 289 DAPs (169 up-regulated and 125 down-regulated) enriched in antioxidant activity, photosynthesis, binding, molecular functions, carbon metabolism, and secondary metabolite biosynthesis (Qing et al., 2022).

Cold-tolerant *Citrus junos* produced 6,678 distinct protein species upon exposure to FS (−7 °C for 36 h), with 413 classified as DAPs and associated with the secondary metabolite biosynthesis, phenylpropanoid biosynthesis, and starch and glucose metabolism (Jiang et al., 2021). Cold acclimation of wheat seedlings (4 °C for 28 days) resulted in 668 DAPs involved in defense responses, signal transduction, protein regulation, carbohydrate metabolism, and phenylpropanoid biosynthesis (Xu et al., 2022b). Exposure of *Calendula officinalis* to CS (4 °C for 24 h) revealed 24 DAPs, with up-regulation observed in proteins related to stress resistance, antioxidant defense, signal transduction, respiration, photosynthesis, fatty acid metabolism, and other plant development-related proteins (Jan et al., 2023a). Cold acclimation improved cold tolerance in *Sonneratia apetala* by up-regulating proteins related to ROS scavenging, photosynthesis, energy

and carbohydrate metabolism, protein folding, and cofactor biosynthesis and down-regulating proteins related to stress response and growth, including VHA, OEE2, CSD, ELIP, and EIF5A (Shen et al., 2021). Liu et al. (2022a) reported that parental salt priming enhanced cold tolerance in wheat seeds [wild-type Novosibirskaya 67 (WT) and its Chl b-deficient mutant (ANK)], with expression changes in DAPs associated with photosynthesis, electron transfer activity, carbohydrate metabolism, and redox homeostasis, including 17 and 4 up-regulated and down-regulated DAPs in WT and nine and 27 up-regulated and down-regulated DAPs in ANK compared to the non-primed test group (Liu et al., 2022a).

Proteomic studies have revealed intricate protein-level responses and adaptation to temperature stress in various crop plants. These analyses revealed changes in key pathways such as photosynthesis and defense mechanisms. In short, discovering key proteins offers new insights for targeted breeding, promoting the development of temperature-smart crop plants.

3.4 | Metabolomics

Metabolomics, an advanced computational tool in systems biology, offers a comprehensive profile of primary and secondary metabolites and hormones produced by single cells or organisms during cellular mechanisms (Raza, 2022; Shen et al., 2023b). It plays a crucial role in deciphering the mechanisms underlying plant–environment interactions, especially in changing climate conditions (Raza, 2022; Yan et al., 2022b; Shen et al., 2023b). Various metabolites indicate stress-adaptive mechanisms by modulating plant signaling cascade networks, growth patterns, and physiological conditions (Raza, 2022; Hall et al., 2022; Yan et al., 2022b; Shen et al., 2023b).

In recent years, research efforts have focused on identifying temperature stress-responsive metabolites and associated pathways. For instance, metabolomic profiling of tomato was conducted to understand the HS response (38°C for 1 h) by suppressing or overexpressing *HsfB1* in WT and transgenic plants (Paupière et al., 2020). Knock-down plants accumulated metabolites (glucose, sucrose, and polyamine putrescine), whereas *HsfB1* overexpressing plants accumulated products from the flavonoid and phenylpropanoid pathways and some caffeoyl quinic acid isomers, contributing to HS tolerance (Paupière et al., 2020). Cucumber exposed to HS (38/30°C light/ dark 12/12 h) and normal conditions (Chen et al., 2023) exhibited 125 differential accumulated metabolites (DAMs) (99 up-regulated and 26 down-regulated), with significant changes in four metabolic pathways associated with HS: plant hormone signal transduction, amino sugar and nucleotide sugar metabolism, porphyrin and Chl metabolism, and glycine, serine, and threonine metabolism (Chen et al., 2023).

Metabolite profiling of rice leaf segments from six cultivars sensitive to high-night temperatures revealed the accumulation of several metabolites, including sugars, organic acids, amino acids, and unknown analytes, in response to HS (Schaarschmidt et al., 2021). In another study, intermediates of the lignin biosynthetic pathway, including caffeate and coniferaldehyde, increased in *Populus* spp. after exposure

to HS (35°C) for 3 days (Zhao et al., 2022b). A study on tobacco revealed increased levels of sugars (sedoheptulose and sucrose) and non-codogenic amino acids (pipecolate and c-amino butyrate) at 22 and 37 °C, respectively (Krawczyk et al., 2022). A metabolomic analysis of 304 lettuce (*Lactuca sativa* L.) accessions exposed to 21, 28, or 35°C for 40 h revealed significant decreases in the average germination rate with increasing temperature, and sensitive accessions accumulated more amino acids, sugars, sterols, organic acids, phenolic compounds, and terpenoids than tolerant accessions (Wei et al., 2020).

To gain insights into the relationship between yield-growth traits and metabolic dynamics within source and sink structures, a study conducted on the impact of HS on single mature pollen grains in two contrasting rice cultivars—N22 (heat-tolerant) and Koshihikari (heat-sensitive)—revealed contrasting varietal differences in phosphatidylinositol (PI) and 106 other metabolites in mature pollen (Wada et al., 2020). N22 and Koshihikari exposed to HS (34°C for 48 h after the heading stage) exhibited 90.0 and 46.8% spikelet fertility, respectively (Wada et al., 2020). Similarly, in winter wheat, a study examined the impact of post-heading high-night temperature (HNT; 23°C) on sink–source metabolic dynamics, reporting elevated proteinogenic amino acids like glycine, methionine, and some carbohydrates, i.e., sucrose, glucose, fructose, myo-inositol, raffinose, and maltose, in the spikes (sinks) during HNT (Impa et al., 2019). Contrasting responses were observed between the heat-tolerant genotype ‘Tascosa’ and the heat-sensitive genotype ‘TX86A5606’. Tascosa exhibited reduced TCA intermediate compounds, such as isocitrate and fumarate, and amino acids like lysine, leucine, and tyrosine in the leaves (sources) compared to TX86A5606 under HNT (Impa et al., 2019), suggesting alterations in carbohydrate and amino acid metabolism/accumulation to sustain improved respiratory load under HNT. These changes potentially aided Tascosa in maintaining cell turgor, stabilizing cell membranes, and protecting the photosynthetic electron transport chain during HNT (Impa et al., 2019). A metabolic profiling study in bread wheat cultivars responding to post-anthesis HS (35:28 ± 0.08°C for 10 days) identified changes in 316 metabolites, with increased levels of tryptophan, arginine, histidine, pipecolate, and α -amino adipate and decreased levels of anthranilate, dimethylmaleate, guanine, glycerone, and galactosylglycerol in heat-stressed plants (sources) compared to control plants (Thomason et al. (2018). Interestingly, metabolites like arginine and pipecolate, which increased under HS, exhibited strong negative correlations with yield, PSII efficiency, and Chl content. Conversely, metabolites decreasing under HS, like dimethylmaleate and galactosylglycerol, exhibited positive correlations with yield, SPAD values, and PSII efficiency. These findings suggest potential roles for certain metabolites as stress markers, offering insights for targeted wheat breeding strategies to enhance yields (Thomason et al., 2018).

Metabolomic profiling of wheat under FS identified 88 DAMs, including alkaloids, amino acids, and some phenolic acids, with 13 metabolites closely associated with CS tolerance (Lv et al., 2022b). The dynamics of metabolite accumulation were studied in six wheat genotypes to understand the impact of CS (2°C) and prolonged CS

(28 days at 10°C, followed by 2°C to day 49) (Vaitkevičiūtė et al., 2022). The genotypes exhibited varying glucose, protein, and amino acid concentrations between CS treatments (Vaitkevičiūtė et al., 2022). In another metabolic study, two rice varieties—O2428 (Japonica) and YZX (Indica)—subjected to low temperature (LT, 15°C for 4 days), normal temperature (NT, 30°C), and a transition from LT to NT identified 730 metabolites, with 35 related to the LT stress response and involved in phenylpropanoid, amino acid, inositol phosphate, and glutathione biosynthesis (Yang et al., 2019). An eco-metabolomics analysis of four *Nepenthes* species—highlander (*N. minima*) with CS tolerance and lowland species (*N. ampullaria*, *N. rafesiana*, and *N. northiana*) with HS tolerance—showed increased levels of various phytohormones (e.g., jasmonic acid, auxin, and trigonelline), nitrogen storage, polyamide synthesis, norbergenin and lignin production (Wong et al., 2020).

A study exposing the seeds of two quinoa (*Chenopodium quinoa*) variants (Quinoa 2324 and Dian Quinoa 281) to CS (−2, 5, and 22°C) for 11 h detected 794 metabolites, mainly soluble sugars and some involved in secondary metabolism, such as α -linolenic acid, phenolic acids, flavonoids, lipids, amino acids, nucleic acids, and organic acids (Xie et al., 2022). Cold-tolerant (C18) and cold-sensitive (C6) rapeseed genotypes subjected to CS (8/4°C day/night for 7 days) exhibited 31 metabolites related to carbohydrates, amino acids, secondary metabolites, lipids, membrane transport, cofactors and vitamins, nucleotides, and energy metabolism (Raza et al., 2021b). Another metabolic profiling study on cold-tolerant (GX74) and sensitive (XY15) rapeseed genotypes exposed to short CS treatments (−2°C for 2 h) detected 545 metabolites primarily involved in sugar metabolism, ROS scavenging, photosynthesis, phytohormone signaling, and MAPK signaling metabolism pathways (Liu et al., 2022b). *Camellia oleifera* flower buds subjected to CS (6°C) exhibited differential expression of metabolites associated with carbohydrate, phenylpropanoid, and hormone metabolism in two contrasting cultivars (Wang et al., 2023). In another study, *Camellia sinensis* var. ‘Shuchazao’ (cold-tolerant, SCZ) and *C. sinensis* var. *assamica* ‘Yinghong 9’ (cold-sensitive, YH9) subjected to CS (10/4°C day/night) for 7 days followed by freezing acclimation (4/0°C day/night) for another 7 days, and they identified 51 DAMs only in SCZ, involved mainly in amino acid pathways metabolism, particularly arginine and lysine metabolism (Cheng et al., 2023). A metabolome analysis of five spring and five winter rapeseed ecotypes exposed to CS (4°C for 12 h) identified 41 metabolites in spring ecotypes and 47 in winter ecotypes, with most involved in sugar, amino acid, and organic acid metabolism pathways (Jian et al., 2020).

Metabolomic profiling in rice highlighted the significance of oxylipins in stress adaptation, with one member (*OsHPL1*) of the cytochrome P450 (CYP74) family selected for metabolic profiling under cold stress (6°C for 24 and 48 h) (Wu et al., 2023). The study identified 597 metabolites, most involved in jasmonate metabolism and some related to sugar, secondary metabolite, and amino acid pathways (Wu et al., 2023). *Saussurea involucreata* (Sik.), an alpine plant, exhibited altered metabolic patterns under CS, with 360 of the 753 metabolites identified by Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway analysis associated with secondary

metabolism, amino acids, and sugars, including phenylpropane synthesis, glycolysis, pentose phosphate pathway, tricarboxylic acid cycle, glutamic acid-mediated proline biosynthesis, and purine metabolism (Sun et al., 2023b). An investigation to identify key metabolites involved in CS (4°C, 3 days) tolerance in common bean (*Phaseolus vulgaris* L.) reported that methionine, flavonoids, and malondialdehyde could serve as biomarkers for plant chilling injury (Yang et al., 2023).

Metabolomics studies have informed complex plant responses to temperature stress, revealing dynamic metabolic pathways and adaptive approaches. Identifying key markers increases our perception of stress adaptation and tolerance mechanisms in diverse plant species. These insights increase our knowledge of plant–environment interactions and pave the way for designing temperature-smart crop plants.

3.5 | miRNAomics

microRNAs (miRNAs), a distinct class of small, non-coding, regulatory RNAs typically single-stranded, usually 20–24 nucleotides in length, play a crucial role in regulating gene expression in plants (Bhogireddy et al., 2021; Raza et al., 2023d; Islam et al., 2024). They modulate the expression of target genes by inhibiting translation or cleaving target transcripts (Bhogireddy et al., 2021; Jamla et al., 2021; Raza et al., 2023d). These small regulators control the regulatory network of numerous metabolic pathways in plants, influencing processes such as protein re-folding, antioxidant machinery activation, photosystem efficiency, and reproductive events, facilitating plants to withstand HS and CS (Ding et al., 2020a; Das et al., 2021; Megha et al., 2018; Islam et al., 2024). Various studies have been conducted to identify temperature-responsive miRNAs in plants (Islam et al., 2024). For instance, deep sequencing and computational/molecular analysis of harvested bananas (*Musa acuminata*) conducted under CS (6°C) and HS (35°C) identified 113 known and 26 novel miRNAs, with 42 differentially expressed under HS and CS (Zhu et al., 2019). Target assessment of these miRNAs confirmed that 15 modulated the expression levels of genes specific to temperature responses, with miR156 and miR535 families exhibiting potential roles in modulating SPL gene expression levels (Zhu et al., 2019).

A study on sweet potato identified correlations between miRNA target modules and temperature stress (6°C CS, 47°C HS), with negative correlations for miR156, miR159, miR160, and miR167, and their targets, *lSPLs*, *lBMYB*, *lBARF10*, and *lBARF8*, and a positive correlation for miR162 and its target DCL1, indicating that complex regulatory gene networks are involved in temperature stress responses (Yu et al., 2020). A study on *Betula luminifera* exposed to HS (45°C) identified 206 miRNAs (84 novel and 115 known), of which 98 were HS-responsive (Pan et al., 2017). The subsequent degradome sequencing revealed 44 miRNAs and 71 target genes that regulated stress-responsive genes, transcription factors, and some functional protein enzymes. The functional assignment of these miRNA targets confirmed that the genes were related to protein synthesis/folding, transport, cell wall organization, defense, antioxidants, and overall cellular growth and development under HS (Pan et al., 2017).

In flowering Chinese cabbage, small RNA libraries generated after the HS treatment (38°C, 6 and 12 h) highlighted 43 known and 49 putative novel miRNAs that displayed differential expression in heat-susceptible and heat-tolerant varieties (Ahmed et al., 2020). Among these differentially expressed miRNAs, the nine known and 14 unknown miRNAs expressed exclusively in the heat-tolerant variety and their targets (RPS6, TOA1-like reticulon) were involved in HS tolerance (Ahmed et al., 2020). A genome-wide analysis in maize under CS (4°C, 48 h) identified 321 known miRNAs associated with leaf elongation (6), mature zones (20), and putative meristem (24) (Aydinoglu, 2020). The meristem-associated miRNAs were subjected to *in silico* target predictions, confirming the negative regulatory role of miR160, miR319, miR395, miR408, miR528, and miR1432 (Aydinoglu, 2020). A recent integrated small RNA sequence analysis in pea (*Pisum sativum* L.) under CS (8/2°C day/night, 16 days) identified 136 miRNAs and the modulatory network of 39 miRNA-mRNA targets with variable expression trends (Mazurier et al., 2022). The study also confirmed the involvement of 11 miRNA families and their target genes during CS responses, with the target genes associated with multi-stress defense mechanisms, antioxidants, and cell wall synthesis (Mazurier et al., 2022).

Numerous studies have identified and assigned specific functions to miRNA or miRNA families, including plant metabolism and development regulation under temperature stress. For instance, miR156 targeted the gene coding SQUAMOSA PROMOTER BINDING PROTEIN (SBP)-LIKE (SPL), an important factor binding to the promoter of the heat shock factor in soybean (Ding et al., 2023). The study also highlighted the significant role of the miR156-SPL module in regulating male fertility and HS in soybean (Ding et al., 2023). In other studies, miR156 enhanced CS tolerance in rice by targeting SPL genes that encode several transcription factors, such as MYB and WRKY, with a central role in CS tolerance (Zhou and Tang, 2019) and targeted the transcription factor MYB15 to positively regulate ABA-mediated CS tolerance in tomato (Zhang et al., 2022). The miRNA superfamily miR156-miR529-miR535 has a high sequence identity and is crucial for optimal plant growth and development. From this family, miR535 altered the expression levels of the C-repeat (CRT) binding factor (CBF) and influenced osmotic regulation under CS in rice (Sun et al., 2020b). miR169 (miR169/ Nuclear Factor YA (NF-YA) module) is an auxin-regulated miRNA with a key role in maintaining cellular signaling in *Arabidopsis* roots (Aslam et al., 2020). miR528 reduced the expression of the transcription factor MYB30 by targeting an F-box domain-containing protein gene (Os06g06050, positive regulator of MYB30) in rice under CS (Tang and Thompson, 2019). Dong et al. (2022) demonstrated that the miR164a-NAM4 module, with NAM as a member of the NAC transcription factor family and a target of miR164a, is responsible for CS tolerance in tomato. This module conferred CS tolerance by directly regulating genes encoding 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACS) and ACC oxidase (ACO) for ethylene synthesis induction. Sun et al. (2022a) reported that miR1320 targets the APETALA2/ethylene-responsive factor (ERF) transcription factor in rice, repressing the JA-mediated cold signaling pathway to provide CS tolerance.

According to Szaker et al. (2019), miR824 negatively regulates AGAMOUS LIKE 16 (AGL16), a MADS-box transcription factor that negatively regulates flowering time through *FLOWERING LOCUS T*. The authors suggested that the heat-mediated regulation of miR824/AGL16 is well-preserved within the *Brassicaceae* family, and miR824 acts as a post-translational memory factor for fine-tuning post-stress development in *Arabidopsis* (Szaker et al., 2019).

miRNAs have successfully improved crop temperature tolerance through overexpression. For example, in tomato, overexpression of miR319d from *Solanum habrochaites* conferred HS and CS tolerance by inhibiting *GAMYB-like1* and altering ROS signal transduction (Shi et al., 2019). The miR156/SPL13 module improved HS tolerance in alfalfa (*Medicago sativa* L.) in miR156 overexpressing lines and SPL13 RNAi knockout lines (Matthews et al., 2019). Transgenic creeping bentgrass plants overexpressing rice miR393 (*Osa-miR393a*) exhibited enhanced HS tolerance associated with induced expression levels of small HSPs (Zhao et al., 2020). Overexpression of soybean miR1508a in soybean itself conferred CS tolerance through possible cleavage of the miR1508a target gene xyloglucan endo-trans-glucosylase/hydrolase (Sun et al., 2020a). These promising findings underscore the significant role of miRNAs as vital molecular regulators for combating temperature variations in agriculture and the importance of exploring temperature-responsive miRNAs in various plant species to develop strategies for coping with temperature fluctuations.

3.6 | Epigenomics

Epigenomic investigations involve the study of epigenetic changes—changes in gene expression associated with DNA methylation and post-translational histone modifications, not changes in DNA sequence (Fortes and Gallusci, 2017; Saeed et al., 2022). Despite advances in various omics methodologies, epigenomic approaches are relatively underexplored, requiring further investigations of experimental designs and methodological frameworks (Fortes and Gallusci, 2017; Lempe et al., 2022). Epigenomic analysis principally examines epigenetic marks or epi-marks, including DNA methylation events and histone post-translational modifications. These epi-marks undergo dynamic changes in response to endogenous and/or external (environmental) stimuli, significantly shaping plant phenotypic plasticity (Fortes and Gallusci, 2017; Saeed et al., 2022). Epigenetic regulation in response to temperature fluctuations primarily encompasses changes in DNA methylation patterns, histone modifications, small and long non-coding RNAs, and chromatin remodeling, collectively influencing gene expression patterns and contributing to the epigenetic memory of plants (Liu et al., 2015; Zhao et al., 2020; Ueda and Seki, 2020).

DNA methylation patterns in various plants undergo alterations in response to temperature stress. For instance, 325 differentially methylated genes were identified in the leaves of maize seedlings subjected to HS (42°C, 8 h) and associated with carbon metabolism, RNA transport, spliceosomes, ubiquitin-mediated proteolysis, and homologous recombination (Qian et al., 2019). In *Arabidopsis*, a study

investigating the role of histone H1 in repressing heterochromatic transposable elements (TEs) in response to HS reported that H1 functions differently in TE repression depending on the specific location of TEs and confirmed that H1 and DNA methylation suppresses HS-mediated responses in plants (Liu et al., 2021c). DNA methylation changes in barley subjected to HS (25°C) during grain filling regulated seed germination, with the promoters of genes involved in ABA biosynthesis (9-cis-epoxycarotenoid dioxygenase, NCED) hypermethylated and those related to ABA catabolism (abscisic acid 8'-hydroxylase, ABA'8OH), gibberellic acid biosynthesis (gibberellin oxidase, GA20ox), and NADPH oxidase (Rboh) hypo-methylated in HS-treated seeds (Sakai et al., 2022).

Epigenomic interactions, particularly those related to epigenetic silencing mechanisms, play a critical role in regulating gene expression and maintaining genome stability in response to environmental stresses, including temperature. These interactions involve various epigenetic marks, such as DNA methylation and histone modifications, contributing to heritable changes in gene expression patterns. Some recent studies shed light on the epigenetic responses of plants to temperature stress. For example, Guo et al. (2021) demonstrated that histone modifications can maintain heritable gene silencing in maize under HS (42°C, 4 h) and suggested the involvement of H3 lysine 9 dimethylation (H3K9me2), histone H3 lysine 27 dimethylation (H3K27me2), and histone H3 lysine 27 trimethylation (H3K27me3) in the heritable silencing of MuDR transposon. Tong et al. (2021) reported significantly down-regulated expression levels of DNA methyltransferase genes (DNA METHYLTRANSFERASE1; MET1 and CHROMOMETHYLASE2/3; CMT2/3) and up-regulated expression levels of the three demethylase genes (DEMETER-LIKE3; DML3, REPRESSOR OF SILENCING 1; ROS1 and DEMETER; DME) in tea plants after CS treatment (4°C, 0 h) for 7 days, highlighting the crucial role of DNA methylation in the early CS response. Sicilia et al. (2020) demonstrated the vital role of DNA demethylases in the demethylation of promoter regions of genes (DFR and Ruby) involved in anthocyanin biosynthesis during CS. In another study, potato under CS (4°C for 14 d) exhibited improved chromatin accessibility and histone modifications of active genes (Zeng et al., 2019). The authors proposed that the bivalent H3K4me3-H3K27me3 epi-mark creates a distinct chromatin environment, enhancing accessibility for regulating CS-responsive proteins (Zeng et al., 2019). The above studies highlight that epigenomics is a promising tool for enhancing temperature stress tolerance in plants. Further exploration and research in this field are needed to uncover the full potential of epigenomic strategies for crop improvement in the face of changing environmental conditions.

3.7 | Ionomics

Ionomics is an important approach for understanding how plants absorb, distribute, and accumulate nutrients from the soil, especially in response to external stimuli like temperature stress. The ionome represents the pool of essential inorganic nutrients, required in relatively small quantities, that are vital for plant metabolism and stress

adaptation (Huang and Salt, 2016; Ali et al., 2021). Ionomics approaches include the high-throughput profiling of elemental composition and deviations in response to various stimuli and/or stressful environments (Huang and Salt, 2016; Ali et al., 2021). While ionomics is more commonly associated with studying responses to metal stress, salinity, and drought, relatively few studies have explored the ionome of plants under temperature stress. A study by Ardini et al. (2016) profiled the ionome of wild-type and mutant *Nicotiana langsdorffii* plants subjected to HS (50 ± 1°C, 2 h), noting significant decreases in iron (Fe) and zinc (Zn) concentrations and increases in calcium (Ca) and magnesium (Mg) concentrations, which varied significantly in roots and aerial parts, suggesting altered efficiency in uptake and transport processes. Tovar et al. (2022) investigated the ionome of quinoa seeds under HS applied during anthesis to the roots (30°C) with shoots growing at 22°C, to shoots (35°C) with roots growing at 22°C, and to roots and shoots growing at 30 or 35°C. The seed ionome significantly altered after the 11-day HS treatment, indicating long-lasting effects of HS on seed development and the role of short heat exposure in changing the nutritional quality of quinoa seeds. While these studies provide valuable insights into the ionic responses of plants to temperature stress, the ionomics approach is relatively underexplored in temperature stress studies.

3.8 | Phenomics

Phenomics—the study of the plant phenotype—has become increasingly important in the post-genomic era for understanding how plants respond to various environmental factors, including temperature stress (Singh et al., 2018). Plant phenomics focuses on acquiring high-dimensional phenotypic information on a whole-plant scale, complementing the insights from genomics. Understanding these phenomic characteristics can provide mechanistic insights into the pathways connecting genotypes to specific phenotypes (Houle et al., 2010). Several approaches are typically used to explore plant phenomes: visible light, infrared, thermal-based, fluorescence, spectroscopic, and integrated imaging (Singh et al., 2018). Several studies have successfully applied phenomics in addressing plant responses to temperature stress.

For instance, Dingkuhn et al. (2017) studied the phenotypes of 203 *indica* rice accessions to decipher thermal stress and spikelet sterility. The study used the RIDEV model to successfully capture 64% of variations when cold acclimation was applied during the vegetative stage. Gao et al. (2020) used high-throughput phenotyping to assess HS-induced alterations in *Arabidopsis*, confirming that a low quantum yield of PSII increased the leaf angle. They also demonstrated that exposure to HS (45°C) for 6 h provided more precise differentiation between heat-treated and control plants compared to other long-term exposures (Gao et al., 2020). Marla et al. (2022) used an unmanned aircraft system (UAS) high-throughput phenotyping platform to analyze sorghum phenotypes for chilling tolerance. The UAS-derived normalized difference vegetation index values obtained from phenomic mapping were correlated with QTL related to CS tolerance identified in the same study (Marla et al., 2022).

Despite significant progress in high-throughput genotyping in recent decades, the development of rapid and efficient phenotyping methods has lagged. Consequently, reliable plant phenotyping under environmental stress conditions has become crucial for crop improvement (Chen et al., 2019). For instance, using non-destructive phenomics tools to understand HS (35°C) tolerance during anthesis in *Brassica* species revealed that floral volume is a critical phenomic trait for HS tolerance (Chen et al. 2019). Furthermore, whole-plant measurements were strongly correlated with variations in fresh weight, highlighting the importance of whole-plant imaging (Chen et al., 2019). While phenomics is in its infancy in elucidating the impact of temperature stress on crops, it has shown promise for accelerating crop breeding efforts to improve HS tolerance (Basavaraj and Rane, 2020). Combining high-throughput genomics with phenomics can provide valuable insights and facilitate the development of climate-smart crops (Marsh et al., 2021).

Integrating genomics and phenomics data using bioinformatic tools can create comprehensive clade-specific datasets, making it easier to select climate-adaptive traits for breeding purposes (Marsh et al., 2021). While integrating different omics strategies can be highly beneficial, establishing such systems can be challenging. Emerging technologies, such as rapid genomics cycling, high-throughput phenomics, and historical descriptions of environmental relatedness (enviromics), may be crucial for improving conventional breeding methods and achieving genetic gain (Crossa et al., 2021). Thus, integrating appropriate omics approaches to identify and improve climate-resilient traits, including temperature-responsive traits, is the key to developing climate-smart crops for the future.

4 | ERA OF SINGLE-CELL OMICS-ASSISTED BREEDING FOR CROP IMPROVEMENT

Recent technological advances have enabled researchers to use single cells (sc) to explore various molecular dimensions, including genome, transcriptome, proteome, ionome, metabolome, and epigenetic modifications, at high resolution and across thousands of cells (Libault et al., 2017; Macaulay et al., 2017; Hu et al., 2018; Shaw et al., 2021; Chen et al., 2020; Rich-Griffin et al., 2020; Argelaguet et al., 2021). Moreover, several databases have been developed to facilitate the use of sc in plant biology, including PlantscRNAdb (Chen et al., 2021a), Single-Cell Portal (Svensson et al., 2020), PsctH (Xu et al., 2022d), PCMDB (Jin et al., 2022), IonFlow (Iacovacci et al., 2021), scDEC (Liu et al., 2021b), RA3 (Chen et al., 2021b), epiAnno (Chen et al., 2022), and PlantCADB (Ke et al., 2022). When combined with computational biology, these databases have provided opportunities for sc-genome-wide approaches to assess different molecules, such as DNA, RNA, protein, and chromatin, with the highest resolution in many organisms, including plants (Libault et al., 2017; Hu et al., 2018; Argelaguet et al., 2021). For instance, Argelaguet et al. (2021) alluded to using genomic DNA to analyze the sc-genome, methylome, or chromatin accessibility. In the same cell, RNA can be used to profile the transcriptome, and proteins can be studied for the proteome.

Serrano-Ron et al. (2021) conducted sc-RNA-seq to investigate the order of tissue initiation in *Arabidopsis*. They discovered the ontological hierarchy of lateral root formation, involving an early and sequential differentiation of main root tissues and stem cells. In another study, 3D-sc-shape analysis and sc-mRNA sequencing were used to characterize root meristems and mature root segments in brassinosteroid-binding mutants and wild-type *Arabidopsis* (Graeff et al., 2021). Han et al. (2017) developed an sc-RNA-seq protocol for rice to assess allelic expression patterns in mesophyll cells of *indica* (93–11), *japonica* (Nipponbare) inbred lines, and F1 reciprocal hybrids. They observed widespread monoallelic gene expression in individual mesophyll cells. Thibivilliers and Libault (2021) have reported several other recent examples.

In addition to sc-RNA-seq, several studies have explored metabolome profiling at subcellular, sc- and sc-type levels in crops like soybean, *Arabidopsis*, and cotton, as reviewed by Misra et al. (2014). For example, Brechenmacher et al. (2010) conducted sc-type metabolomics on soybean root hairs before and after inoculation with *Bradyrhizobium japonicum*, identifying 2,610 metabolites, with 166 altered in response to *B. japonicum*. Trehalose was identified as one of the most induced metabolites following inoculation. Guo et al. (2007) used gene expression and metabolome profiling to investigate cotton fiber during cell elongation and secondary cell wall synthesis, offering insights into the active role of cellulose and its synthesis.

Several sc-RNA-seq studies have been conducted in *Arabidopsis* (Brennecke et al., 2013; Efroni et al., 2015; Efroni et al., 2016; Denyer et al., 2019; Ryu et al., 2019; Jean-Baptiste et al., 2019). Jean-Baptiste et al. (2019) reported that 752 of the 1,783 identified HS-responsive genes were differentially expressed following heat shock treatment, highlighting the significant role of HSPs in gene expression across diverse cell types under HS. Moreover, sc-RNA-seq was used to study gene expression patterns during Chinese cabbage (A03) leaf development, particularly in response to HS (40°C for 12 h), revealing that the least fractioned subgenome expressed more genes than the medium and most fractioned subgenomes in different cell types (Sun et al., 2022b). Furthermore, HS affected gene expression in a cell type-specific manner and influenced subgenome dominance. Notably, key meristem development genes, including *SHOOT MERISTEMLESS (STM)*, *KNOTTED 1-LIKE HOMEBOXs KNAT1*, *KNAT2* and *KNAT6*, *CYTOCHROME P450 (CYP78A5)*, and *LIGHT SENSITIVE HYPOCOTYL 3 (LSH3)* were detected in specific clusters (Sun et al., 2022b). These genes and several others are involved in shoot meristematic cells (Zondlo and Irish, 1999; Cho and Zambryski, 2011; Luo et al., 2019). Comparing the results from these studies suggests that sc-omics analysis could be used to identify genes, metabolites, proteins, ions, and epigenetic factors at the sc-level. Additionally, sc-omics holds great promise for future crop breeding, genetic research, and pathway engineering.

5 | CONTRIBUTION OF MACHINE LEARNING TO FAST-TRACK BREEDING EFFORTS

The generation of phenotypic data for crops is a critical step in categorizing crops as sensitive or tolerant to the specific stress under

investigation (Rahaman et al., 2015; Song et al., 2021; Oteng-Frimpong et al., 2023; Yoosefzadeh Najafabadi et al., 2023). The labor-intensive, time-consuming, potentially destructive, subjective, costly, inefficient, and lack of inter- or intra-rate repeatability of manual phenotyping (Araus et al., 2018) has prompted the need for efficient, automatic, and accurate technologies capable of capturing phenotypic data across all growth stages and correlating it with genomics information (Song et al., 2021; Xu et al., 2022c; Li et al., 2022c). The advent of high-throughput phenotyping, coupled with artificial intelligence (AI) and ML, has successfully addressed the major bottleneck hindering crop breeding efforts (Singh et al., 2016; Yoosefzadeh Najafabadi et al., 2023; Yan and Wang, 2023; Hayes et al., 2023).

Machine learning has been increasingly integrated into sc-RNA-seq (Denyer et al., 2019; Jean-Baptiste et al., 2019), particularly in the analysis of unsupervised sc-transcriptomes to reconstruct sc-developmental trajectories over pseudotime, identifying hundreds of genes with cell-type-specific expression (Jean-Baptiste et al., 2019). The clustering of hundreds to millions of sc-genes reported in most sc-RNA-seq and metabolomics studies has mainly used unsupervised ML approaches (Brechenmacher et al., 2010; Jean-Baptiste et al., 2019; Denyer et al., 2019; Luecken and Theis, 2019; Sun et al., 2022b). Machine learning is also instrumental in constructing pan-genomes (Golicz et al., 2016; Song et al., 2020; Bayer et al., 2021; Danilevicz et al., 2020; Torkamaneh et al., 2021; Jha et al., 2022; Ebler et al., 2022), enabling the identification of core, dispensable, and specific genes that expedite functional validation and reveal regulatory roles in genomics (Khan et al., 2020; Tay Fernandez et al., 2022; Zanini et al., 2022; Shi et al., 2023).

Furthermore, ML algorithms have found applications in crop yield and complex traits prediction, crop growth monitoring, precision agriculture, and automated irrigation (Yoosefzadeh-Najafabadi et al., 2021; Yoosefzadeh-Najafabadi et al., 2022b; Jeyaraj et al., 2022; Li et al., 2022c; Croci et al., 2023). Machine learning is also used to identify genomic regions associated with specific traits (Yoosefzadeh-Najafabadi et al., 2022a) and select superior genotypes through genomic selection (Tong and Nikoloski, 2021; Yoosefzadeh-Najafabadi et al., 2022a; Jubair and Domaratzki, 2023). It can also translate biological knowledge and data into precision-designed plant breeding by facilitating omics sciences in plant biology, expediting the discovery of agronomically usable genes, mutations, and metabolites for knowledge-driven molecular breeding (van Dijk et al., 2021; Yan and Wang, 2023). In commercial breeding programs, ML techniques have been applied to develop predictive models for data-driven genomic design breeding (Yan and Wang, 2023). Its ability to identify predictive patterns complements traditional comparative genomics approaches in plant science (van Dijk et al., 2021). For example, ML-enabled phenotyping of 869 field-grown sorghum accessions for WUE traits generated data used for GWAS and transcriptome-wide association studies (TWAS) (Ferguson et al., 2021), leading to the discovery of multiple candidate genes with known and putative roles in key WUE traits.

Machine learning has been used to understand and predict gene expression in plants under biotic and abiotic stresses (Zou et al., 2011; Sartor et al., 2019; Washburn et al., 2019; Azodi et al., 2020;

Wang et al., 2020) and regulatory architecture (Mejía-Guerra and Buckler, 2019; Zhou et al., 2022). Zhou et al. (2022) studied transcriptome changes in response to heat or cold stress in maize seedlings from three genotypes (B73, Mo17, and W22) and their F1 hybrids. They used motifs enriched near transcription start sites for thermal stress-responsive genes to develop predictive models of gene expression responses, identifying known and novel cis-regulatory elements involved in heat or cold stress and offering potential applications for designing stress-responsive promoters using biotechnology approaches. Other studies have applied ML in breeding temperature-smart crops, particularly in freezing injury assessment (Wang et al., 2016; Cogato et al., 2020; Fu et al., 2021; Sanaeifar et al., 2023). For example, Li et al. (2022c) used five deep learning networks and unmanned aerial vehicle images to predict freezing-tolerant rapeseed lines among more than 3,000 pure lines, reporting greater than 92% accuracy in recognizing freezing-tolerant rapeseed.

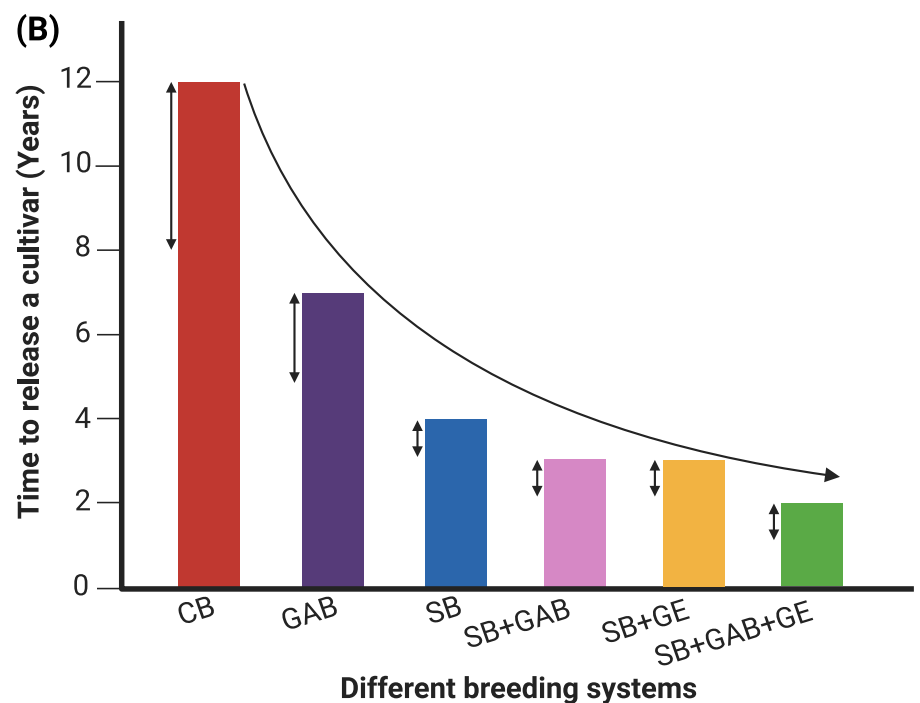
Machine learning is anticipated to continue playing a pivotal role in harnessing the rapidly accumulating multi-omics data in plant biology to breed temperature-smart and stress-resilient crops (Yan and Wang, 2023). Automated phenotyping systems incorporating ML and AI can address current plant stress research challenges, particularly in temperature-related phenotyping (Xu et al., 2022c).

However, within the realm of climate-smart agriculture, the Internet of Things, and big data applications, it is important to acknowledge that the widespread adoption of ML is not without its challenges (Sharma et al., 2020; Cravero et al., 2022). Despite ML significantly accelerating breeding programs and contributing to innovations in crop improvement, several fundamental issues need careful consideration (Singh et al., 2016; Yoosefzadeh Najafabadi et al., 2023; Yan and Wang, 2023; Hayes et al., 2023). Challenges such as ensuring data privacy, interpreting complex ML models accurately, and the need for large and diverse datasets for precise predictions pose substantial hurdles. Furthermore, integrating ML into precision agriculture and computerized systems demands robust cybersecurity measures to safeguard sensitive agricultural data (Sharma et al., 2020; Shaikh et al., 2022; Cravero et al., 2022). Hence, it is vital to balance the advantages of ML and address these challenges for the responsible and efficient exploitation of expertise within agricultural sectors.

6 | CONTRIBUTION OF SPEED BREEDING TO FAST-TRACK THE GROWTH OF NEW CULTIVARS

The concept of SB has emerged as a valuable tool to expedite the development of new cultivars for various purposes, including research, human consumption, and industrial use (Watson et al., 2018; Hickey et al., 2019; Alahmad et al., 2022). Speed breeding involves techniques that manipulate the environmental conditions in which crop genotypes are grown to accelerate flowering and seed set to advance to the next breeding generation as quickly as possible (Figures 3, 4) (Wanga et al., 2021; Chiurugwi et al., 2019). Conventional breeding for annual crops like maize, barley, wheat, and soybean typically takes

FIGURE 4 Contribution of speed breeding (SB) to fast-track the growth and release of new cultivars. **(A)** Multiplication and advancement of rice generations in SB chamber. It is particularly relevant for regions like northern South Asia with seasonal restraints, such as low temperatures during the dry season. Therefore, the International Rice Research Institute (IRRI)-South Asia Regional Centre (ISARC) in Varanasi is working to develop temperature-smart rice cultivars that can survive and deliver higher yields during the dry season. Source: <https://www.irri.org/news-and-events/news/speedbreed-crop-breeding-center-built-speed>. **(B)** Integration of SB with different breeding systems. The graph demonstrates how different breeding systems adjust in terms of the time required to develop and release advanced cultivars. Arrows with color bars indicate the average variation in time required to release a variety, which can also vary from species to species. From top to bottom, the curved arrow indicates how integrating different breeding systems helps release a variety quickly. Abbreviations: Conventional breeding (CB); genome editing (GE); genomics-assisted breeding (GAB); speed breeding (SB)



8–12 years from crossing parental lines to the commercial release of new cultivars (Jähne et al., 2020). Speed breeding can potentially reduce the time needed for breeding by more than half (Figure 4) (Hickey et al., 2019; Wanga et al., 2021).

Ghosh et al. (2018) proposed three SB methods: SB I, II, and III, with the choice of method depending on specific needs and resource availability, as detailed in Ghosh et al. (2018) and Abdul Fiyaz et al. (2020). Specific SB protocols have been developed and tested for various crops (Watson et al., 2018; Hickey et al., 2019; Abdul Fiyaz et al., 2020; Cazzola et al., 2021; Wanga et al., 2021).

Speed breeding can be used independently or with advanced accelerated breeding methods like omics-assisted selection, genome editing, and genomic prediction to develop advanced cultivars (Jähne

et al., 2020). For example, Rana et al. (2019) applied a biotron-based SB technique to transfer the *hst1* (*O_sRR22*) gene from Kaijin rice cultivar, known for its salt tolerance, into high-yielding Yukinko-mai background using MAS within 17 months. Hickey et al. (2017) successfully introgressed multiple resistance traits to leaf rust, net and spot forms of net blotch, and spot blotch from four donor parents into scarlet cultivars within two years and eight generations. Katiyar-Agarwal et al. (2003) successfully overexpressed the *hsp101* gene in basmati rice, improving its HS tolerance. Therefore, SB offers a promising approach to fast-track breeding temperature-smart cultivars in rice and other essential food security crops.

In addition to multi-omics-assisted breeding approaches, such as MAS and metabolite-assisted selection, SB can reduce the cost and

space required to breed numerous cultivars. It can expedite the early registration of new cultivars by generating distinctness, uniformity, and stability (DUS) data within a shorter timeframe, a requirement for plant breeders' rights (Saccomanno et al., 2020). Combining SB with other technologies like GAB, ML, genome editing, and phenomics can further accelerate the phenotyping of large accessions for temperature-related traits and facilitate fast-track breeding (Figure 4B) (Rai, 2022; Xu et al., 2022c).

7 | OUTSTANDING QUESTIONS

1. Which developmental phases and plant tissues should be targeted for comprehensive omics analysis to gain insights into the key mechanisms that drive temperature stress responses in plants, and how do these responses fluctuate across different developmental phases, especially in light of potential variations among plant species?
2. How can we enhance the integration of multi-omics approaches to provide a more comprehensive understanding of the genetic and molecular mechanisms governing plant responses to extreme temperatures, ultimately facilitating the breeding of temperature-smart plants?
3. What are the key genomics, transcriptomic, proteomic, and metabolic regulatory networks and pathways involved in plant responses/tolerance to extreme temperatures, and how can we manipulate them to uncover targeted breeding strategies for designing temperature-smart crops?
4. Are there omics technologies and methodologies that hold promise for advancing our understanding of temperature stress responses in plants and fast-tracking the breeding of smart future cultivars?
5. Can we identify and develop MAB and GAB tools (mainly MAS) that facilitate more precise and efficient trait introgression for temperature hardiness in different plant species?
6. How can ML algorithms be refined and fitted to predict plant responses to temperature stress with higher precision and proficiency by integrating real-time environmental data?
7. What are the most effective strategies for integrating ML predictions with conventional breeding methods to fast-track the development of temperature-smart cultivars that are robust and adjustable?
8. How can we ensure the accessibility and affordability of omics and ML tools for plant researchers and breeders in developing countries where climate change severely impacts agricultural production?
9. Can non-model plant-based omics investigations provide deeper insights into temperature stress tolerance mechanisms, and to what extent can findings from model plant-based research be correlated?
10. How can realistic climate simulation facilities be developed to mimic the omics-assisted breeding crop responses in natural field environments?
11. What are the potential environmental implications and safety concerns associated with SB techniques, and how can these be mitigated or minimized in the quest for expedited crop development?
12. What potential environmental, ethical and/or safety concerns are linked to genetic engineering tools (mainly genome-edited crops) used to manipulate omics-derived data in plant breeding, and how can these concerns be addressed for future breeding?
13. How can we optimize the use of fast-forward breeding techniques, such as GAB, gene editing, and transgenic breeding, in combination with omics approaches to design temperature-smart plants with improved traits?
14. What are the long-term effects and adaptability of temperature-smart plants in changing climates (i.e., real-world agricultural systems), and how can we anticipate and manage these potential consequences?
15. How can interdisciplinary collaboration between plant biologists, geneticists, data scientists, and agronomists be fostered to successfully tackle the multifaceted challenges of breeding temperature-smart plants?
16. What strategies and policies can be enacted at the national and international levels to ensure the widespread adoption of temperature-smart plants and contribute to achieving global food security goals, including the Food and Agriculture Organization's (FAO) 'zero hunger' goal?

8 | CONCLUDING REMARKS AND FUTURE OUTLOOKS

The ongoing and unpredictable shifts in the global climate have raised concerns within communities, with food security issues becoming an alarming challenge due to the ever-increasing world population. Extreme temperatures, a consequence of climate change, significantly jeopardize overall crop health and yield. These temperature extremes trigger various morphological, physiological, biochemical, and molecular disruptions in plants, disturbing their homeostasis (Figure 2). Understanding and engineering specific and non-specific plant stress responses, enabling plants to withstand current and future changing environmental conditions, is essential to address and prevent these escalating food security challenges.

Applying cutting-edge biotechnological tools, such as omics approaches and modern breeding techniques, has emerged as an extraordinary means of advancing breeding methodologies to create temperature-smart future cultivars (Figure 3). Advanced genomics, transcriptomics, proteomics, metabolomics, miRNAomics, epigenomics, phenomics, ionomics, ML, and SB are used widely to decipher complex mechanisms and their components in response to temperature stress (Figure 1). These high-throughput and rapid technologies lay the foundation for a deeper understanding of tolerance mechanisms by revealing key molecular, genetic, transcriptomic, proteomic, and metabolic factors responsible for these responses. Genomics innovations such as GAB, MAS, QTL mapping, and GWAS have made

remarkable strides in this endeavor. It is time for similar advances in other omics fields to expedite the journey toward temperature-smart plants. Recent developments in sc-omics have further enabled the establishment of coherent connections between various omics disciplines, consolidating them at a sc-level. Integrating ML and SB makes the goal of creating temperature-smart plants increasingly attainable (Figure 1). These tools offer a framework for constructing a multi-dimensional database to bridge the knowledge gaps in plant research.

Numerous plant species, such as *Arabidopsis*, wheat, rice, maize, soybean, tomato, and rapeseed, have been extensively assessed using various omics platforms under extreme temperatures. These species serve as a valuable source of large omics datasets that can be translated into other major food crops to develop ready-to-grow, temperature-smart future crop plants. Moreover, the data derived from omics integration can be manipulated using genetic engineering tools, such as gene editing and transgenic breeding, to develop temperature-smart plants. While there have been many successful outcomes in breeding temperature-smart cultivars through genetic engineering, we advocate for omics-mediated genetic engineering of newly identified key players to further advance the field and maximize the utility of omics data. Finally, the modern cultivars generated could be subjected to SB methods to accelerate their growth within a shorter timeframe (Figures 3, 4). However, numerous pivotal questions and bottlenecks still require more attention and concerted efforts from the scientific community to design climate-smart future crop plants (see **outstanding questions**). In summary, integrated omics approaches are key to breeding plants that are adaptable and resilient to the ever-evolving environmental and climatic conditions, in turn, paving the way to fulfilling the FAO's 'zero hunger' goal and the United Nations Sustainability Development Goals, and ultimately fostering sustainable agribusiness and improved quality and security.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

AUTHORS' CONTRIBUTION

AR, KHMS, and RKV conceived the idea. AR, SB, TK, BK, MJ, SA, RGRC, SC, RMR, and KHMS participated in writing the original draft and literature search. AR designed the figures. KHMS and RKV

supervised the work. AR, RGRC, SNN, ID, RMR, KHMS, and RKV proofread and edited the manuscript. All authors have read and approved the final version of the manuscript.

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