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Utilizing modern techniques and omics technologies to enhance stress tolerance in finger millet, with recent findings: A review

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ABSTRACT

Finger millet (Eleusine coracana) is an important food security crop because of its nutritional properties and powerful antioxidants, which enable the plant to withstand harsh environmental conditions. In addition, research should be done on sustainable agriculture development systems for poverty eradication through finger millet production and using its genomic resources as a strategy for other crop improvements. This review focuses on the Clustered Regularly Interspaced Short Palindromic Repeats and CRISPR-associated protein (CRISPR/Cas) systems, advanced breeding such as speed breeding, omics technologies, and how they all combined for the crop improvement strategy. CRISPR/Cas is a method used for altering genomes, specifically those of finger millets, to create cereals that can survive various environments. Also, the review discussed the genes associated with salt tolerance applied in the CRISPR/Cas genome editing technique, since salinity stress poses a great risk in agriculture fields. Plant breeding technology has contributed greatly to these achievements, such as speed breeding, genomic selection, genome editing, and high-throughput phenotyping, among others, which have improved various aspects of crops, including their yield potential and quality traits like faster growth rates, disease resistance levels, etc. High-throughput omics technologies, such as genomics, transcriptomics, and metabolomics, give molecular information for studying finger millet development.

1. Introduction

Finger millet is a highly nutritious and versatile crop with many health benefits. This means it's very important for food security and nutrition in places with abiotic stresses because of its high nutritional content and potential for value addition among other crops. Additionally, it can help human beings fight diseases caused by environmental factors like anti-diabetic, anti-inflammatory, and antioxidant properties, which are sourced from ragi (Kalsi et al., 2023; Premkumar, 2023). Extreme weather events such as burning heat waves or scorching droughts pose great threats to cultivated plants as they often lead to a fifty percent loss in production. In the last two decades, there have been numerous reports on the identification and characterization of differentially expressed genes under various abiotic stresses across plant species (Ajeesh et al., 2021). But Finger millet exhibits maximum resistance among cereals since it harbors several stress-responsive genes and it can survive under harsh conditions like floods where other crops fail. The name "climate resilient" came after the realization that this grain could be used as one of the model systems for functional genomics research work aimed at developing climate change-resistant crops. The crop Finger millet has been grown in the dry areas of Africa, India, and South Asia for a long time because no other crop can live there due to the low rainfall every year (Ajeesh et al., 2021; Shivhare et al., 2022). The robust antioxidant defense system which works together with increased signal perception to bring about unique physiological changes including osmotic adjustment required at low Na+/K+ ratio in saline soils should

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have been included (Keerthana et al., 2022; Mahadik & Satyan, 2023). Amomg cereal crops, finger millet (*Eleusine coracana*) demonstrates distinctive advantages compared to major grains like rice, wheat, maize, and other millets. While rice (*Oryza sativa*) struggles with salinity stress and wheat (*Triticum aestivum*) shows limited heat tolerance, finger millet exhibits superior resistance to multiple abiotic stresses (Ajeesh et al., 2021). Unlike rice and wheat, which typically follow C_3 photosynthesis, finger millet utilizes the more efficient C_4 pathway shared with maize (Zea mays), enabling better water use efficiency and adaptation to high temperatures (Goyal et al., 2023; Pardo & VanBuren, 2021). Compared to pearl millet (Pennisetum glaucum) with its basic genome size of 1.7 Gb, finger millet's unique AABB genome (1.2 Gb) with 9 chromosomes ($2n = 4x = 36$) provides a robust foundation for stress tolerance (Hittalmani et al., 2017; Varshney et al., 2017). In stress response studies, finger millet outperforms barnyard millet (Echinochloa frumentacea) in accumulating protective compounds like proline, MDA, CAT, phenols, and flavonoids (Assefa et al., 2013). Nutritionally, finger millet surpasses rice, wheat, and even other millets, particularly in calcium content, with some genotypes accumulating up to 450 mg/100 g compared to rice (10 mg/100 g) and wheat (30 mg/100 g) (Singh et al., 2015b). Its ability to thrive in regions where maize, rice, and wheat fail, especially in the dry areas of Africa and South Asia, establishes finger millet as a crucial crop for food security in challenging environments (Ajeesh et al., 2021; Shivhare et al., 2022). Additionally, while foxtail millet (Setaria italica) shows some drought tolerance, finger millet demonstrates broader adaptability to various abiotic stresses, including both drought and salinity (Mbinda & Mukami, 2021). It can tolerate high levels of alkalinity that are beyond the limits of most plants yet; within the same sodium chloride concentration under different accessions, there is a wide range of genetic diversity for grain yield. This implies that finger millet could serve as an alternative sustainable crop in the face of increasing global environmental challenges especially those related to soil degradation caused by rising salinization within such habitats (Kalyana et al., 2022). Ragi's ability to adapt across diverse ecological zones coupled with its nutritional richness and health benefits throughout different stages of human life including pregnancy periods makes it one among many key factors towards achieving food security under abiotic stress-prone regions. Therefore these attributes need further exploration to enable people to live healthy lives regardless of their environments (Maitra et al., 2024). There is limited knowledge in agricultural research regarding the genetic basis behind plants' ability to withstand adverse conditions like floods or droughts leading to poor harvests thereby threatening world food supplies (Nair & Devi, 2024). Water use efficiency is higher in C_4 photosynthesis than any other system hence making it suitable for adaptation under limited moisture availability and higher temperatures since it utilizes carbon more effectively where there is little water but high-temperature forces plants into such conditions (Goyal et al., 2023; Pardo & VanBuren, 2021). This shows that the plant should be able to use the C_4 pathway effectively where there is efficient acquisition of CO_2 leading to continuous growth even when climatic conditions become unfavourable. With modern genomics tools, it will be possible to reveal the structure controlling carbon assimilation via the C_4 pathway during different stages using the mentioned model organism. Some studies aim to identify genes responsible for controlling or influencing such pathways through rigorous sequencing efforts undertaken so far (Li et al., 2021; Saleem et al., 2021). Both MDA (malondialdehyde), proline, CAT (catalase), phenol, and flavonoids showed significant increases whenever finger millet and barnyard millet were subjected to stressful conditions (Assefa et al., 2013). Additionally, these crops exhibited a great reduction in protein, and carbohydrate amylase levels when they encountered stress situations like those reported by Debieu et al., (2018). For instance, when exposed to abiotic stresses like droughts some researchers have observed incremental values for proline content together with other parameters including MDA, H_2O_2, antioxidant activity electrolyte leakage. Furthermore, levels of proline, glycine betaine, TSS (total soluble sugars), and antioxidant enzymes like SOD (superoxide dismutase), CAT, APX (ascorbate peroxidase), and GPX (glutathione peroxidase) rise (Mundada et al., 2020). Fig. 1 shows the impact of some abiotic stress in finger millet.

2. Finger millet component purification, detection, and profiling

Numerous nutrients and bioactive substances found in finger millet (*Eleusine coracana*) enhance its nutritional value and capacity to withstand stress. These components can now be thoroughly characterized using a variety of detection and profiling techniques thanks to recent developments in analytical techniques.

2.1. Metabolite profiling

Metabolite profiling in finger millet has emerged as a crucial approach for understanding the biochemical basis of stress tolerance and nutritional quality. Analyses using Gas Chromatography-Mass Spectrometry (GC–MS) have shown that both conventional and innovative food processing techniques significantly alter metabolite profiles. These assessments aid in comprehending the ways in which various processing methods impact finger millet's functional and nutritional qualities (Singh et al., 2024). Finger millet's metabolomic profiling has also revealed differences in key metabolites that are essential to stress response mechanisms, including sugars, organic acids, and amino acids (Li et al., 2021).

High-resolution mass spectrometry (HRMS) techniques have increased the possibility to detect and characterize metabolites with unprecedented precision (Li et al., 2021). These advanced analytical methods have enabled comprehensive profiling of both primary and secondary metabolites that play vital roles in stress response mechanisms. Integration of metabolomics with other omics approaches has provided deeper insights into finger millet's stress adaptation mechanisms. Mass spectrometry-based metabolomics, particularly when combined with liquid chromatography (LC-MS) and gas chromatography (GC–MS), has revealed complex metabolic networks involved in stress response (Singh et al., 2024b). Recent studies using HRMS have identified key metabolites associated with drought and salinity tolerance, including proline, glycine betaine, and various flavonoids (Mundada et al., 2020).HRMS analysis has enabled the identification of metabolites that accumulate during various abiotic stresses, particularly drought and salinity conditions. These include osmolytes, antioxidants, and specialized defensive compounds (Mundada et al., 2020). Advanced metabolite profiling has helped characterize bioactive compounds that contribute to the nutritional value of finger millet, including phenolic acids and flavonoids (Muthamilarasan et al., 2016). Time-course studies using HRMS have revealed dynamic changes in metabolite profiles during different developmental stages and stress conditions (Singh et al., 2024).

The integration of metabolome data with transcriptome and proteome analyses has provided a systems-level understanding of finger millet's stress response mechanisms (Kayastha et al., 2023). This multi-omics approach has been particularly valuable in Identifying key metabolic pathways involved in stress tolerance and understanding metabolite-protein interactions during stress response. It also helps in elucidating the regulation of metabolic networks under different environmental conditions

Modern metabolomics approaches using HRMS have also contributed to crop improvement strategies by identifying metabolic markers for stress tolerance, guiding breeding programs through metabolite-assisted selection and helps in evaluating the impact of genetic modifications on metabolic profiles. The application of high-resolution metabolomics continues to expand our understanding of finger millet's biochemical responses to environmental stresses, providing valuable insights for crop improvement strategies (Devos et al., 2023). These

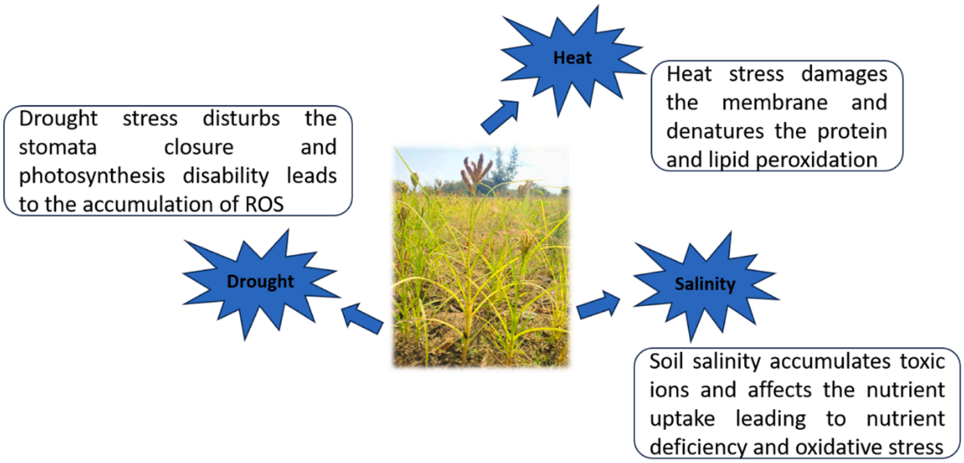

Fig. 1. Impact of a few abiotic stresses on finger millet.

advanced analytical approaches are particularly important for developing stress-tolerant varieties while maintaining or enhancing nutritional quality.

2.2. Protein and peptide analysis

Recent studies have identified novel antioxidant peptides through protein hydrolysis of finger millet. These peptides have been purified and characterized using various chromatographic techniques, demonstrating significant antioxidant properties that contribute to both nutritional value and stress tolerance (Kumar et al., 2019). The protein content analysis reveals variations during hydrothermal processing, with significant changes in protein structure and functionality (Dharmaraj et al., 2011).

2.3. Carbohydrate and lipid characterization

Hydrothermal processing significantly affects the carbohydrate and lipid profiles of finger millet. Studies have shown alterations in starch properties and lipid compositions, which influence both nutritional quality and functional properties (Dharmaraj et al., 2011). These changes are particularly relevant for understanding the crop's stress response mechanisms, as carbohydrates play crucial roles in osmotic adjustment during abiotic stress (Mundada et al., 2020).

2.4. Polyphenol content and bioaccessibility

Research has demonstrated that domestic processing methods significantly impact polyphenol content and bioaccessibility in finger millet. Various processing techniques can either enhance or reduce the availability of these beneficial compounds (Pradeep & Sreerama, 2024). The presence of these polyphenols contributes to the plant's antioxidant defense system, which is crucial for stress tolerance (Keerthana et al., 2021).

2.5. Nutraceutical profiling

Comprehensive nutraceutical profiling of finger millet genotypes has revealed significant variations in bioactive compounds across different varieties. These studies have identified key compounds that contribute to both nutritional value and stress tolerance mechanisms (Kumar et al., 2021). Methanolic extraction techniques have been particularly useful in detecting and assessing nutraceutical compounds in finger millet, providing insights into their potential health benefits and stress-protective roles (Sharma et al., 2016). The characterization of these components has significant implications for both crop improvement and nutritional enhancement. Understanding the biochemical profiles helps in identifying stress-responsive compounds that can be targeted for enhancing stress tolerance and to develop improved processing methods to enhance nutrient availability in selecting genotypes with superior nutritional and stress-tolerance profiles

3. Salinity stress

Even though millets are generally considered glycophytes, different genetic profiles determine the variance in salt tolerance among various genotypes of finger millet, according to researchers (Choudhary et al., 2023; Kheya et al., 2023). Thus, given its resistance against many abiotic stress factors like salts (Premkumar, 2023; Mahadik & Satyan, 2023), finger millet seems like a good alternative crop. Modern biotechnological methods are being used to create varieties that can tolerate high levels of salts in finger millet (Mbinda & Mukami, 2021). This is because saline conditions affect growth negatively especially during germination stages up to the early vegetative phase hence resulting in slowly growing plants with increased electrolyte leakage accompanied by changes in physiological and biochemical properties. In any case, it should be noted that different types or breeds of finger millets respond differently when exposed to salty environments some displaying higher levels of tolerance than others (Mukami et al., 2020). New ideas which may comprise using fluorescent *Pseudomonas aeruginosa* SPF-33 and SPF-37 strains for mitigation of soil salinity; these two rhizobacteria species found beneficial in promoting growth among plants have been found effective at enhancing overall performance including salt stress tolerance amongst finger millet seedlings (Mahadik & Kumudini, 2020). These findings point out how important biotechnological approaches and plant-promoting rhizobacteria could become towards achieving this revolution in agriculture they also show that it can be done thus bringing forth salt-resistant varieties of finger millets.

3.1. Mechanism of salinity tolerance

Halophytes can live in salty environments, while glycophytes cannot tolerate high levels of salt. This is a major issue for global agriculture, as most crops are glycophytes and die when exposed to too much sodium chloride (Shahzad et al., 2022). When plants take up salt ions from the soil, it disrupts their growth by causing ion toxicity. This type of stress affects the roots by reducing water intake but increases water loss through leaves. In plants under high-salt conditions, the accumulation of sodium (Na^+) and chloride (Cl^-) ions in tissues is very harmful, high levels of sodium inhibit the absorption of necessary potassium ions required for healthy plants. Hydrogen peroxide (H_2O_2), hydroxyl radicals, and other reactive oxygen species (ROS) are produced by salt-stressed plants. Such reactive compounds oxidatively damage various biological components including proteins, nucleic acids, membrane lipids, and chlorophyll. To counteract oxidative stress, enzymatic as well as non-enzymatic defense systems are employed by plants (S. Singh et al., 2021). Many genes involved in environmental responses such as giving salt tolerance or avoidance have altered their RNA and protein synthesis rates, and multiple genes and transcription factors are upregulated by salt stress in different plant species. Therefore genetic factors play a crucial role in determining their salinity resistance (Zhao et al., 2020; Amirbakhtiar et al.,2019). Different genes get activated upon exposure to salinity stress in plants, finger millet genotype was sequenced whose leaf transcriptomes showed transporters, vacuolar ATP synthase, transcription factors signaling molecules, etc., (Rahman et al., 2014). According to a study, two brassinosteroid-related genes were identified as playing critical roles in stress response and adaptation mediated by phytohormones such as abscisic acid and jasmonic acid (Wang et al., 2020). Fig. 2 shows molecular level changes during salinity stress.

4. Heat stress

Ramakrishna et al. discovered a gene in the finger millet's genome called EcHSP17.8 and further found out that this particular gene becomes more active at abnormal temperatures; from which it can be assumed that plants recognize their molecular vulnerability to heat as well as provides hints for further study (Ramakrishna et al., 2018). On the other hand, Opole et al noted that during its reproductive phase finger millet is more vulnerable to high temperatures than any other stage of its life cycle. Besides these findings also revealed some interesting variations in grain yield under such conditions between different genotypes and the number of seeds per panicle produced thus calling for consideration of genetic diversity when looking for heat adaptation (Opole et al., 2018). During a transcriptome analysis, genes showed differential expression among heat-sensitive and tolerant varieties under heat stress in finger millet. This is important because it helps us know various genetic components involved with tolerance in this crop hence allowing more investigations and breeding efforts (Goyal et al.,2023). One of the methods involved creating transgenic plants using the mtlD gene. This genetic modification significantly improved drought and salinity resistance therefore demonstrating biotechnological approaches towards ensuring plants survive unfavorable environmental conditions (Hema et al., 2014). Fig. 2 shows molecular level changes during heat stress.

5. Drought stress

More frequent and severe droughts caused by global warming are the main limiting factor for agriculture. Many biochemical processes essential for growth in plants such as ion uptake, chlorophyll synthesis, respiration, or glucose metabolism among others are interrupted by dry spells that result in low productivity because they suppress photosynthesis (Zougmoré et al., 2018). Some of the ways through which plants respond to dryness include but are not limited to the activation of various enzymes; production of cell-permeant metabolites during metabolism; endogenous hormones like abscisic acid (ABA), reactive oxygen species (ROS) etc., (Anjum et al., 2017). This AtERF71/HRE2 acts as a mediator between ABA and hypoxia responses via transcription factors in arabidopsis where coordinated regulation between ABA- and ROS-mediated signaling pathways is important for improving drought tolerance (Park et al., 2011). Also, the upregulated genes that confer the ability of plants to survive under long-term water deficits like calcineurin B1(CBL1) which is highly conserved, not only serves as an obligatory item in the presence of salt stress but also gives tolerance to osmotic stress induced by high solute concentration which leads to cell dehydration hence closing stomata thereby reducing transpiration rate preventing wilting of leaflets during dry periods and promoting intracellular moisture retention for longer cell viability under drought condition especially when combined with ROS scavenging molecules that help keep redox balance at optimal conditions. Ren et al., (2010), carried out an extensive study focused on finger millet to unravel its intricate nature together with various components linked to traits

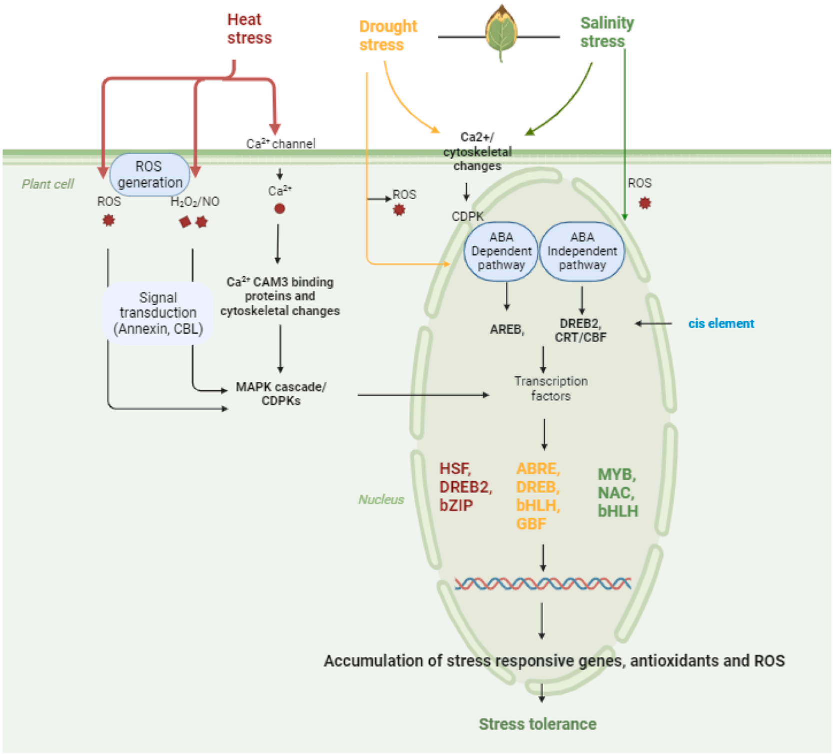

Fig. 2. Molecular mechanism behind the heat, drought, and salinity stress.

associated with drought tolerance which can help in enhancing future crop yield. There are some varieties of finger millets that have shown response towards water constraints thus indicating the possibility of coming up with better breeds that are resistant or tolerant to dry conditions. Identification of genes/proteins involved in combating dryness remains elusive, to effectively deal with drought, it is important to gain deeper insights into regulatory systems controlling gene expression and protein-protein interactions during drought stress so that appropriate measures can be taken. Some of the results showed that Finger millet CaM (EcCaM) contributes to grain Ca^{2+} accumulation, among Ca^{2+}-rich genotypes, with EcCaM transcripts being highly expressed at the spike stage but localized within high calcium genotype GP-45 grains, where they occur more abundantly in embryos and aleurone layers than other tissues (Singh et al., 2015). Overexpression protects plants from salt and drought stress via an ABA-dependent pathway, whose synthesis may be regulated by overexpression during periods when there is limited availability of water due to osmotic stress caused by high-concentration salts soils, leading to cellular dehydration and evoking response(s) directed towards keeping moisture content within cells, resulting in stomatal closure so that transpiration rates can be reduced, thus preventing stress (Reddy et al.,2021). Fig. 2 shows molecular level changes during drought stress.

6. Plant stress signaling

To detect stress in plants, multiple plant sensors must detect a stressor, which then triggers nitric oxide (NO) and cyclic adenosine monophosphate (cAMP) secondary messengers. Cyclic adenosine monophosphate is an important signaling molecule involved in adaptation and physiological regulation within plants, but its complex structure and target proteins have not been identified yet. The researchers found that when they used genetic methods to lower cAMP levels, these plant cells became defective (Blanco et al., 2020; Keshan & Rather, 2021). These second messengers activate or deactivate many pathways including mitogen-activated protein kinases (MAPKs) pathway among others. Ultimately, these transcription factors' activity gets affected by those signaling routes around them that either activate or repress their functioning, particularly during various abiotic stresses like drought stress (Danquah et al., 2014). During the gene expression modulation step for stress-responsive genes within the promoter region where TFs bind with specific regulatory sites leading to changes in their expression levels (Dong et al., 2006; Mizoi et al., 2013). Transcription factors are proteins that bind to DNA sequences called enhancers or promoters thereby controlling the rate of transcription of genetic information from DNA to messenger RNA (mRNA). They have a DNA binding domain allowing them to recognize particular DNA sequences within the promoter region of genes. Depending on its transcription activation or repression domain a given TF can either enhance or reduce target gene expression levels accordingly (Keshan & Rather, 2021). Throughout time many different types have been discovered involved in responding to various abiotic stresses so far but some examples listed in Table 1

Table 1
Different transcription factor families associated with stress response in finger millet.

TF Family	References
bHLH (basic Helix-Loop-Helix)	(Xie et al., 2012; Zhao et al., 2016)
bZIP (basic region/leucine Zipper)	(Ramakrishna et al., 2018)
CBF/DREB (C-repeat Binding Factor/Dehydration Responsive Element-Binding Protein)	(Vera et al., 2023)
ZFP (Zinc Finger Protein)	(Mazumdar et al., 2023)
AREB/ARF (Abscisic acid-response Element-Binding Protein/Abscisic acid-Response Factor)	(Sakuraba et al., 2015)
MYB (Myeloblastosis)	(An et al., 2020)
NAC (no apical meristem), ATAF, and CUC2 (cup-shaped cotyledon)	(Premkumar, 2023; Prusty et al., 2024)

6.1. Gene expression towards abiotic stress

Thriving in the harsh conditions of semi-arid tropical regions, finger millet stands out for its exceptional ability to withstand drought. Researchers have conducted studies to understand the gene expression related to abiotic stress in finger millet and its potential for enhancing stress tolerance, similarly, the function of a few genes has been successfully studied in pearl millet, foxtail millet, and finger millet. The names of these genes and their traits have been listed in Table 2.

6.2. Functional characterization of key genes

Researchers are investigating important genes (Table 3) in millet species to better understand their stress tolerance mechanisms. Pearl millet, foxtail millet, and finger millet all include genes that protect against drought, heat, salt, and nutritional deficiency. Various genes play important roles in modulating water transport, lipid metabolism, heat shock response, and transcriptional regulation, all of which contribute to the overall stress tolerance of millet species. Each gene serves as a genetic tool, directing researchers toward the creation of stress-tolerant millet varieties, which are critical for ensuring food security in the face of climate change and environmental instability.

7. CRISPR/Cas system in genome editing

The Clustered Regularly Interspaced Short Palindromic Repeats and CRISPR-associated protein (CRISPR/Cas) system is an excellent technique for modifying plant genomes, particularly finger millet crops. It can recognize and cleave specific DNA sequences inside the genome. The idea behind this targeted genome modification technology came from a naturally occurring gene-editing system in bacteria that protects them from viruses. The CAS enzymes and CRISPR are part of an adaptive defense mechanism, which is now known as the CRISPR/Cas9 system (Ma et al., 2016). This method can help speed up the production and sale of genetically modified crops and food products by addressing fears about “foreign DNAs” found in these items. Different nations have shown different reactions towards genome-edited crops; for example, Argentina has previously welcomed them while some countries are still debating how they should be regulated. In Japan, a CRISPR/Cas9 edited tomato with higher levels of γ-aminobutyric acid (GABA) than its non-edited counterparts was recently introduced into the market (Waltz, 2022). Many see this as being able to make edited genomes widely accepted throughout many parts of the world where they may not have

Table 2
Genes associated with drought and salt stress responses in various millet and plant species.

Gene	Function	Reference
EcDehydrin7	Confers drought resistance in tobacco	(Singh, et al., 2015)
Metallothionein	Responsive to drought in GPU-28 genotype	(Parvathi et al., 2013)
Farnesylated protein ATFP6	Responsive to drought in GPU-28 genotype	(Parvathi et al., 2013)
EcTAF6	Drought response regulating gene	(Parvath & Nataraja, 2017)
Salt stress response genes	Found in Co-12 and Trichy 1 finger millet genotypes	(Rahman et al., 2014)
EcNAC67 TF	Increased salinity and drought resistance in rice	(Rahman et al., 2016)
EcCIPK31-like	Confers drought tolerance in finger millet	(Nagarjuna et al., 2016)
EcbZIP17	Confers resistance to heat and salty stressors in tobacco	(Ramakrishna et al., 2018)

Table 3
Functional characterization of key genes in stress tolerance pathways across various millet species.

Millet	Gene	Function	Reference
Pearl Millet	PgPIP2;6	Aquaporin facilitates water transport under drought and heat stress	(Palakolanu et al., 2022)
	PgTAGLip1 and PgTAGLip2	Triacylglycerol lipases combating rancidity in flour	(Aher et al., 2022)
	PgHSP10	Heat shock protein (small subunit) 10, a promoter of heat stress tolerance	(Kummari et al., 2020)
	PgNAC21	NAC transcription factor 21 orchestrating salinity stress tolerance	(Shinde et al., 2019)
Foxtail Millet	SiCBL5	Calcineurin B-like protein 5, a safeguard against salt stress	(Yan et al., 2022)
	SiMYB3	MYB transcription factor gene 3, guiding through low-nitrogen stress	(Ge et al., 2019)
	SiMYB42	MYB transcription factor gene 42, battling low nitrogen stress	(Ding et al., 2018)
Finger Millet	EcNAC67	NAC transcription factor 67, a commander of drought and salinity stress tolerance	(Rahman et al., 2016)
	EcbZIP17	Leucine zipper transcription factor, enhancing growth and abiotic stress tolerance	(Ramakrishna et al., 2018)
	EcDREB2A	Dehydration-responsive element-binding protein 2A, leading the fight against heat stress through ROS scavenging	(M. Singh et al., 2021)
	EcCaM	Calmodulin, a guardian of drought and salinity tolerance	(Jamra et al., 2021)

been otherwise adopted because people would not know what exactly is being changed about an organism's DNA. One such use case could involve making cereal plants more resistant to harsh climates using CRISPR / Cas9 editing techniques. For example, by utilizing millet genetic material as a reference, we may pinpoint specific sites in the genomes of other cereal crops and make precise alterations to a single or a few base pairs in the regulatory regions of individual genes (Ceasar, 2022). This can result in the activation, inhibition, or modification of the functioning of these genes, increasing their ability to confer environmental stress tolerance in various cereal species (Fig. 3). Table 4 shows CRISPR/Cas applications in rice and tomato

7.1. CRISPR/Cas-based genome editing to improve plant salt tolerance

Salinity stress is a significant threat to agricultural lands, with projections suggesting that over 50% of such lands may become critically salinized by 2050 (Butcher et al., 2016). Plants respond to salt stress by undergoing physiological and morphological changes mediated by altered gene expression and signaling pathways (Zhao et al., 2021). Researchers have utilized CRISPR/Cas-based genome editing to identify and characterize genes associated with salt tolerance. Here are some examples of gene editing studies and their findings in Table 5.

8. Advancement in plant breeding

According to Nair and Devi (2024), third-generation techniques in crop improvement through plant breeding technology, such as speed breeding, genomic selection, genome editing, and high-throughput phenotyping, have altered plant breeding technology. Using these third-generation approaches in crop improvement through plant breeding technology can enable genome-assisted breeding for increasing finger millet's output and quality. This involves genetic data, trait-specific mapping, and improved phenomic capabilities which are considered third-generation approaches in crop improvement by plant breeding technology. Therefore different programs have published the complete whole-genome sequence (WGS) of *Eleusine coracana* commonly known as finger millet since it serves as an important resource towards this end through various genome assisted programs that have released a full WGS for *Eleusine coracana* commonly known as finger millet because it represents a very valuable tool in achieving these goals. Ajeesh et al., (2021), suggest that Genomics-based strategies aimed at improving food security among developing countries should prioritize this neglected orphaned crop called Finger Millet. The nutritional value of this grain was unveiled through genome and transcriptome sequencing. Additionally, crop development has been propelled by advancements in molecular marker technology, gene mapping, and modern breeding techniques (Jacob et al., 2024).

Speed Breeding shortens the time plants spend being grown which can help accelerate research on crops (Joshi et al., 2023). It alters the temperature used, light intensity, and photoperiods so growth and development of plants are faster achieved.

While this technique has found success with other cereals such as wheat or barley, there has been no specific protocol designed for finger millets until now. One may enhance salt tolerance among other traits in finger millets by crossing selected progenies with recurrent parents over several generations (Patel & Vekariya, 2023). Marker-assisted selection can help generate salt-tolerant rice varieties when combined with speed breeding. This breeding approach if used in *Eleusine coracana* will ease global pressure on salt-affected soils which limits food production especially when catering for a growing population worldwide (Rana et al., 2019; Watson et al., 2018).

8.1. Speed breeding

Speed breeding is a technology that makes plants grow and develop faster. It has been used with rice, soybeans, corn, and wheat among other cereals. Nonetheless, there has never been any finger millet variety developed using marker-assisted selection (MAS). This could fasten blast disease control measures through breeding. Finger millet is a tropical short-day plant but it is yet to be bred fast enough. If the feature of low-cost optimization for speed breeding technology in finger millets is realized then its potential will also be realized. This technique can quicken research and enhance stability towards food security challenges by increasing the worldwide output of finger millets (Watson et al., 2018; González et al., 2021). In many crops over the past ten years, new varieties were created and distributed through traditional plant breeding methods involving crossing between parental lines which produce offspring that require selfing or homogeneity preservation in order to advance/stabilize lines for evaluation of productive traits and agronomic performance which limits the number of generation per year (one or two depending on crop) with this strategy alone. The aim behind coming up with the speed breeding technology was to overcome these limitations so as to hasten the breeding program under limited space, money, and labor. Genetic enhancement takes longer periods than conventional techniques which is why breeders use rapid cycle approaches such as controlled environment chambers where they provide necessary conditions like precise light control, temperature regulation, and humidity control (Gudi et al., 2022). The Rapid Generation Advancement(RGA) approach cuts down the time taken for each generation/breeding cycle significantly in this method whereby three generations are possible annually while ordinarily finger millet being a short-day crop would take 4–5 months per field cycle but a few weeks are enough under controlled conditions (Jähne et al., 2020). RGA method for speed breeding has been successfully developed based on light-emitting diodes (LEDs) for various short-day crops such as soybeans, rice, and amaranth (Jähne et al., 2020). Work is also underway to make speed breeding for finger millet a standard practice. Moreover, the Rapid Single Seed Descent(rSSD) method can be used to produce

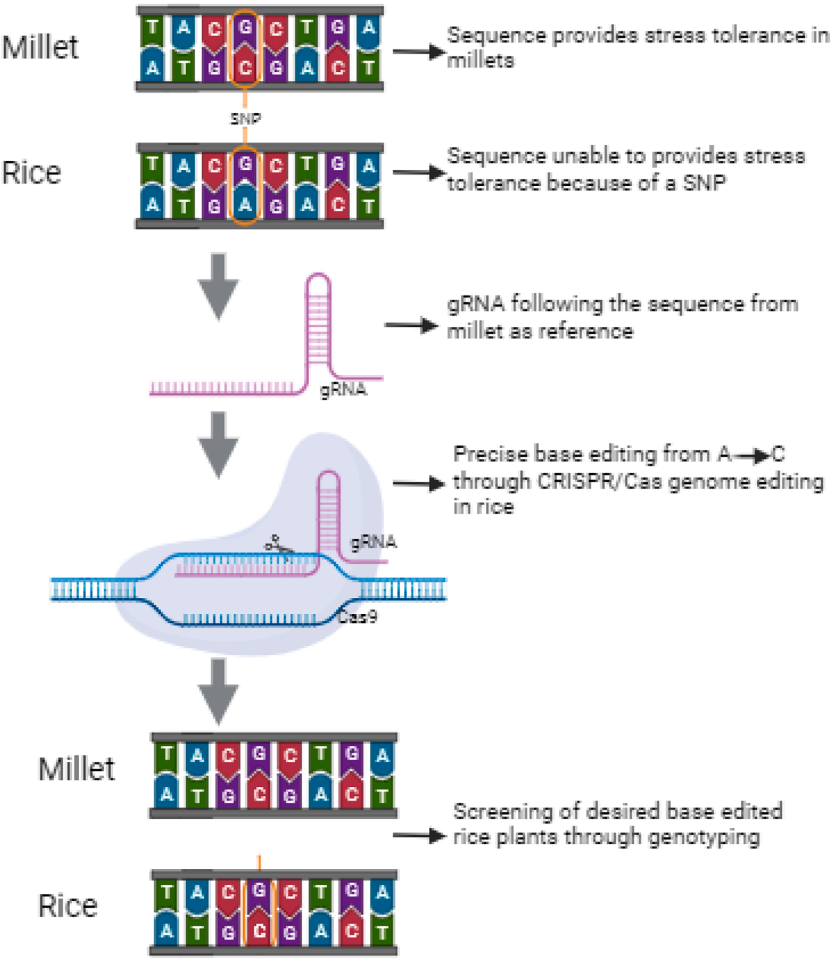

Fig. 3. Applications of the CRISPR/Cas system (Singh, R. K. et al., 2021).

Table 4
Applications of the CRISPR/Cas system.

Application in rice	CRISPR/Cas has been used to improve salinity tolerance in rice by targeting the OsRR22 gene, resulting in higher tolerance in mutants (Zhang et al., 2019)
Application in tomato	CRISPR/Cas has been employed to study tomato salinity tolerance by mutating the SlARF4 gene, producing similar responses to wild-type (Li et al., 2022).
Challenges in applying CRISPR/Cas to finger millet	Lack of a complete assembled genome, limited gRNA design options, and inefficient regeneration and transformation protocols.

near-homozygous lines within a year or two depending on crop species and duration where five generations per year can be achieved with soybean using the technique proposed Jähne et al.(2020). This method is both commercially and scientifically important because it offers a quicker alternative than conventional breeding methods and shuttle breeding procedures.

8.2. Integrating breeding and omics technologies

To elaborate on the methods used in developing crops such as finger millet, it is necessary to combine classical breeding methods with state-of-the-art omics technology. In this case, the traditional way involves crossing different types of finger millets with desirable characteristics through several steps that may be time-consuming because there is limited genetic diversity among them (Choi, 2019). Different high-throughput omics technologies like genomics, transcriptomics, and metabolomics should be integrated to provide detailed molecular knowledge needed to understand how finger millet develops at its most fundamental level. Once these genes that are responsible for good qualities have been identified using data integration from various kinds of omics; then it is possible to make directed attempts at breeding them into new varieties (Jähne et al., 2020; Choi, 2019). We know integrated omics databases can help with global food security. They give us a way to use molecules as signals for which crops should be bred next and then grown most often – especially finger millet, which needs to survive more stressful environments while still producing more food (Chao et al., 2024). Also, no other crop has had so many “omics” done on its genes: genomic, transcriptomic, proteomic, and metabolomic (Kayastha et al., 2023). The Genomic Characteristics and Parameters in Finger Millet and Pearl Millet are shown in (Table 6)

9. Enhancing stress tolerance through plant omics technologies

Plant omics act as a vast toolset for improving stress resistance in finger millet breeding. The adaptability of this crop to survive under different abiotic conditions including droughts, high temperatures and saline soils among others makes it an excellent candidate for genetic modification (Kayastha et al., 2023). Scientists can use transcriptomes, proteomes, and metabolomes, to study how this cereal reacts to stress at the molecular level which could help them create new breeds capable of thriving in extreme environments (S. Singh et al., 2021). Analysis of the transcriptome has revolutionized our comprehension of how genes are

Table 5
Gene editing studies and findings on salt stress response in various plant species.

Gene	Function	Plant Species	References
AtWRKY3 and AtWRKY4	Up-regulation of genes under salt and methyl jasmonate stresses	A. thaliana	(Li et al., 2021)
Acquired Osmotolerance (AtACQOS)	Salt stress tolerance	Arabidopsis	(Koramutla et al., 2024)
ABA-induced transcription repressors (AITRs)	Salt stress tolerance	Soybean (*Glycine* max)	(Wang et al., 2021)
GmDrb2a and GmDrb2b	Enhanced salinity stress tolerance	Soybean (*Glycine* max)	(Curtin et al., 2018)
OsRAV2	Salt stress tolerance	Rice	(Duan et al., 2016)
OsDST	Salt stress tolerance	Rice	(Santosh et al., 2020)
OsNAC$_4$5	Salt stress tolerance	Rice	(Zhang et al., 2019)
AGO2	Salt stress tolerance	Rice	(Yin et al., 2020)
OsRR22	Salt stress tolerance	Rice	(Zhang et al., 2019)
OsBBS1	Salt stress tolerance	Rice	(Zeng et al., 2018)
TaHAG1	Enhanced salt tolerance	Wheat	(Zheng et al., 2021)
OsbHLH024	Role in salt stress response	Rice	(Alam et al., 2022)
OsNAC041	Salt stress sensitivity	Rice	(Bo et al., 2019)
OsDOF15	Regulation of primary root elongation	Rice	(Qin et al., 2019)
OsPQT3	Enhanced oxidative and salt stress resistance	Rice	(Alfatih et al., 2020)
SLENDER RICE1 (SLR1)	Promotion of growth under salt stress	Rice	(Mo et al., 2020)

Table 6
Genomic characteristics and parameters in finger millet (*Eleusine coracana*) and pearl millet (*Pennisetum glaucum*).

Parameter	Finger Millet (*Eleusine coracana*) (Hittalmani et al., 2017)	Pearl Millet (*Pennisetum glaucum*) (Varshney et al., 2017)
Genome size	Approximately 1.2 Gb	Approximately 1.7 Gb
Estimated number of genes	85,243	38,579
Repetitive DNA content	Approximately 49.92%	Approximately 77.2%
Average GC content	44.76%	47.9%
tRNA genes	-	909
rRNA genes	-	235
snRNA genes	-	752
microRNA (miRNA) genes	333	183
Number of chromosomes	36	14

expressed during different growth stages in finger millet. This method involves converting RNA into cDNA and then sequencing it using platforms such as Illumina HiSeq X Ten or Pacific Biosciences RSII sequencers. It tells us how many copies there are for each gene and whether they are turned on or off at different times of an organism's life cycle. In addition, it also uncovers alternative splicing events where exons from the same gene could be joined together differently thus creating various proteins with diverse functions (Mirza et al., 2014). A few recent investigations have indicated that some nutrient management related genes might only express themselves during grain filling while others may abound under conditions that enhance distribution throughout the whole plant including the roots system (Mirza et al., 2014). Significantly, calcium signaling alone identified eighty-two calcium sensor genes on a large scale among other known or putative ones that respond to stresses thereby giving a basis for more functional characterization as well as breeding efforts (Kokane et al., 2018).

Proteomics allows us to see all the proteins being made by a cell at any one time or under particular conditions and complements transcriptomics thus giving insight into global protein composition structure function within cells/tissues Proteomic Analysis. Therefore we can determine what kinds of proteins are produced and where their demand is highest depending on the surrounding environment, For example during drought heat shock plants alter amounts of many different types of proteins some of which may help them withstand such adverse conditions (Li et al., 2021). However determining nutritional value still remains one biggest challenge in science so far but joint transcriptome proteome approaches may yield new discoveries where some proteins were found not only highly expressed under normal growth conditions but also substantially induced during drought stress methyl jasmonate treatment thus implying towards possible roles played by these molecules towards adaptation (Singh et al., 2024; Devos et al., 2023).

Metabolomics and ionomics are used to study finger millet under stress conditions. They can find this information by using many advanced metabolic profiling methods such as HPLC, ESI-MS, and NMR that show what happens when a plant is stressed out. It also shows the nutritional value of different phytochemicals like benzoic acid derivatives of cinnamic acid or quercetin which makes it better for you. Ionomics studies how physiological parameters relate to genetic makeup through mineral/ion transport in finger millet so that they can select better kinds of crops that will have more nutrients (Singh et al., 2022; Muthamilarasan et al., 2016).

Pan-GWAS studies have the potential to change everything we know about abiotic stress responses. However, some things need to happen before this can be realized in full. For instance, with complex genome structures such as finger millet crop varieties; hence, it would still take some time before we reach there. Therefore, all these types ought to be combined so that we gain the best understanding of them possible. Thus scientists should combine several "omic" levels which will help give a complete view of what causes tolerance towards adverse conditions at different points including below-ground and above-ground levels (Weckwerth et al., 2020; Subramanian et al., 2020; Derbyshire et al., 2022).

Plant omics technologies can be used to make finger millet resistant to stress in breeding programs. This technique allows us to see what happens in different plants when they are exposed to different conditions to come up with better crops next time by revealing the molecular foundation of trait inheritance like metabolic pathways and genetic diversity among others; additionally, multi-omics data integration offers a glimpse into events happening at present therefore helping researchers breed types that can survive adverse surroundings (Parray et al., 2019).

10. Utilizing a multi-dimensional database for crop improvement in finger millet

It is necessary to amend agricultural practices while inspecting various finger millet databases. These kinds of genomic databases are unique in the sense that they help to understand plant genetics more precisely by pointing out useful genes linked with desirable traits (Mahesh et al., 2022). In addition, epigenomic databases provide a deeper understanding of gene regulation which in turn makes interventions for crop betterment targeted or specific (Banshidhar et al., 2023; Meena et al., 2024).When each gene is translated into messenger RNA (mRNA), it indicates what it does and how different parts should operate together thus this informs us about the selection of preferable varieties where some traits have been optimized at the transcript level (Kadri et al., 2022). Proteins do different jobs within cells; therefore, proteomic databases show all those functions played by different proteins during the growth processes of plants such as photosynthesis and respiration among others (Ravichandran et al., 2023). Metabolism involves one compound being converted into another hence metabolomic databases indicate which compounds participate where along metabolic pathways; thus they help in improving nutritional value as well as raising overall quality standards for crops like finger millet (Banshidhar et al., 2023; Wang et al., 2023). Additionally although seeming separate initially integrating them together constitutes a comprehensive approach to fastening cycles of breeding for finger millets. Apart from the above mentioned, there exist also many other millets as depicted in Fig. 4 that provide valid evidences as they all are from same genus or family (Sun et al., 2022; Panda et al., 2022; Shekhar et al., 2023). Furthermore, large amounts of data collected from such platforms allow the creation of models predicting how crops will perform under different environmental conditions thus aiding the selection of superior varieties adapted to specific regions; this is only made possible through leveraging on insights provided by genomic, epigenomic, transcriptomic, proteomic and metabolomic databases unique to finger millet (Thulasinathan et al., 2022; Sun et al., 2023).

11. Conclusion and future perspectives

Finger millet emerges as a resilient and nutritionally rich crop, displaying extraordinary resilience to environmental challenges and

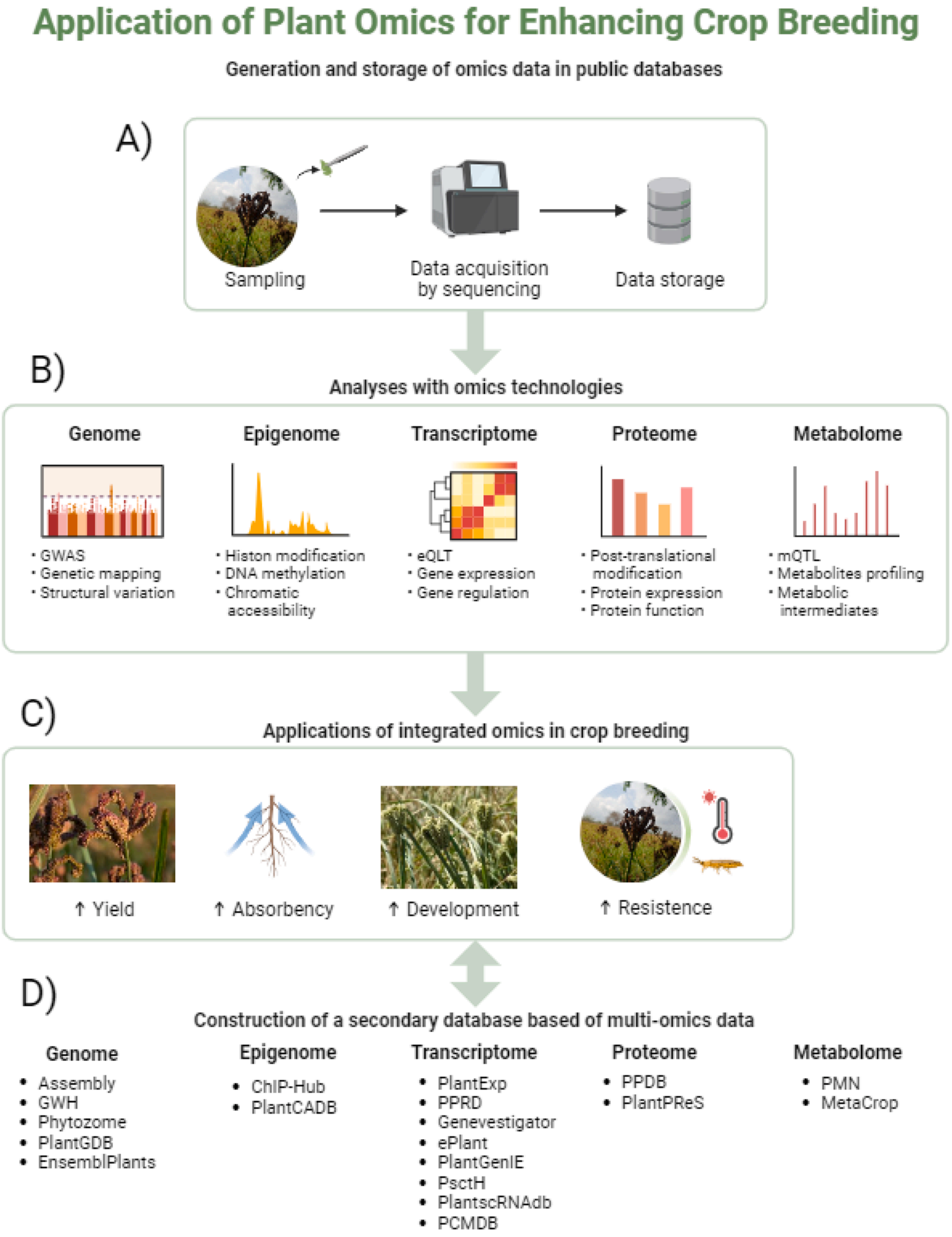

Fig. 4. Various databases for crop improvement.

establishing itself as a key asset for global food security. Ongoing genomic and biotechnological developments, notably in investigating the C_4 pathway and applying CRISPR/Cas genome editing, provide unique insights into increasing stress tolerance and overall crop output. The integration of multiple techniques, including speed breeding and omics technology, holds the potential for generating stress-tolerant finger millet variants with enhanced yields. The specific properties of finger millet make it a vital role in sustainable agriculture, particularly in locations prone to abiotic stresses. Future views involve diving further into the genetic subtleties, perfecting breeding tactics, and fully harnessing omics technology to speed the production of climate-resilient finger millet cultivars. Looking forward, joint efforts should concentrate on enhancing breeding tactics, incorporating cutting-edge biotechnological tools, and harnessing the richness of genomic knowledge to adapt finger millet cultivars for specific environmental problems. Addressing these issues and leveraging emerging technologies, finger millet shows tremendous promise as a cornerstone of sustainable agriculture, providing a robust and nourishing future amid altering environmental dynamics.

CRediT authorship contribution statement

Yuvaraj Dinakarkumar: Writing – review & editing, Validation. **J. Bevin Nishanth:** Writing – original draft. **A. Premkumar:** Visualization, Validation. **S. Suji:** Writing – original draft, Conceptualization. **S. Balachandran:** Writing – original draft. **R. Gnanasekaran:** Supervision, Resources, Conceptualization. **Baburao Gaddala:** Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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