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Comparative insights into the molecular networks of stress-responsive pathways governing abiotic stress tolerance in climate-resilient millets

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Abstract

Climate change threatens global food security through increasing temperatures, erratic precipitation, and expanding arid regions, making stress-tolerant crops essential for sustainable agriculture. This review examines the molecular mechanisms underlying stress tolerance in four important millet species: finger millet (*Eleusine coracana*), foxtail millet (*Setaria italica*), little millet (*Panicum sumatrense*), and proso millet (*Panicum miliaceum*). These C4 photosynthetic crops demonstrate exceptional resilience to environmental stresses through sophisticated molecular networks that coordinate cellular responses. Millets employ multiple stress tolerance strategies including efficient osmolyte accumulation, particularly proline and soluble sugars, which maintain cellular homeostasis under adverse conditions. Proline accumulation increases 2-4 fold under drought stress, while soluble sugar content increases up to 2.76 times under salt stress, serving as osmoprotectants and energy sources. Comprehensive antioxidant systems comprising enzymatic components (superoxide dismutase, catalase, ascorbate peroxidase) and non-enzymatic antioxidants (phenolic compounds, carotenoids) effectively manage reactive oxygen species generated during stress. Heat shock proteins play crucial roles in protein homeostasis, with foxtail millet containing 113 HSP genes representing enhanced protein protection mechanisms compared to major cereals. The Salt Overly Sensitive pathway maintains ion homeostasis through coordinated regulation of sodium/potassium transport, while Late Embryogenesis Abundant proteins provide cellular protection under water deficit conditions. Recent omics technologies have identified key genes, pathways, and regulatory networks enabling millets to maintain productivity under adverse conditions. These molecular insights provide valuable resources for developing climate-resilient crop varieties through precision breeding strategies and biotechnological applications, contributing to global food security under changing environmental conditions.

Keywords: Millets, abiotic stress, osmolyte accumulation, heat shock proteins, climate resilience, precision breeding

Introduction

Climate change poses unprecedented challenges to global food security, with increasing temperatures, erratic precipitation patterns, and expanding arid regions threatening agricultural productivity worldwide. In this context, millets emerge as crucial crops for sustainable agriculture due to their exceptional resilience to environmental stresses and superior nutritional profiles. Millets, collectively representing various species within the Poaceae family, have evolved sophisticated molecular mechanisms that enable them to thrive in marginal environments where major cereals fail to produce economically viable yields [1]. The four millet species examined in this review—finger millet (*Eleusine coracana*), foxtail millet (*Setaria italica*), little millet (*Panicum sumatrense*), and proso millet (*Panicum miliaceum*) represent diverse evolutionary lineages that have independently developed remarkable stress tolerance capabilities. These crops are characterized by their C4 photosynthetic pathway, efficient water and nitrogen utilization, and complex molecular networks that coordinate stress responses at multiple levels [2].

Recent advances in omics technologies have revolutionized our understanding of millet stress physiology, revealing intricate molecular mechanisms that underlie their climate resilience [3].

Transcriptomic, genomic, and proteomic studies have identified key genes, pathways, and regulatory networks that enable millets to maintain cellular homeostasis and productivity under adverse conditions. This molecular-level understanding is crucial for developing climate-smart crop varieties and implementing precision breeding strategies.

Osmolyte Accumulation and Cellular Protection

Proline Metabolism and Accumulation

Proline represents one of the most important osmolytes in millet stress responses, serving multiple functions including osmotic adjustment, protein stabilization, and reactive oxygen species (ROS) scavenging [4]. Under stress conditions, millets dramatically increase proline accumulation through enhanced biosynthesis and reduced catabolism [5]. The molecular basis of proline accumulation involves coordinated regulation of biosynthetic and catabolic enzymes [6]. Pyrroline-5-carboxylate synthetase (P5CS) catalyzes the rate-limiting step in proline biosynthesis from glutamate, while proline dehydrogenase (PDH) controls proline catabolism. The SiP5CS2 gene in foxtail millet promotes proline accumulation under stress conditions [7]. In finger millet, proline accumulation under drought stress reaches levels 2-4 fold higher than control conditions, with drought-tolerant genotypes showing greater accumulation capacity (Gupta *et al.*, 2019). The proline content in GBK043137 and GBK043094 varieties showed less reduction under stress, indicating their superior drought tolerance mechanisms [8]. In proso millet, salt stress imposed plants expressed increased levels of proline, with content increasing 2.245 times in 50mM NaCl, 2.573 times in 100mM NaCl, 2.81 times in 150mM NaCl, and 3.66 times in 200mM NaCl compared to control plants [9]. Exogenous zinc application proved beneficial in mitigating salt stress effects, with proline content improving at all concentrations with maximum increase of 66.65% at 2 mg/L Zn [10].

Sugar Metabolism and Soluble Sugar Accumulation

Soluble sugars serve as crucial osmolytes and energy sources during stress conditions in millets [11]. These compounds include simple sugars like glucose and fructose, as well as complex sugars such as trehalose and raffinose family oligosaccharides (RFOs) [12]. The molecular regulation of sugar metabolism involves multiple enzymes and regulatory proteins [13]. Sucrose phosphate synthase (SPS), sucrose synthase (SuSy), and invertases play key roles in controlling sugar partitioning and accumulation. Transcriptomic studies have shown differential expression of these genes under stress conditions across millet species [14]. In proso millet leaves under salt stress, total soluble sugar (TSS) content increased 1.48 times in 50mM NaCl, 2.066 times in 100mM NaCl, 2.199 times in 150mM NaCl, and 2.76 times in 200mM NaCl compared to control plants, demonstrating their role as osmoprotectants in maintaining turgor pressure and stabilizing cellular membranes [9]. Trehalose and trehalose-6-phosphate (T6P) represent particularly important sugars in millet stress responses. These compounds not only serve as osmolytes but also function as signaling molecules that regulate stress-responsive gene expression and metabolic processes [15].

Antioxidant Systems and ROS Management

Enzymatic Antioxidant Systems

Millets possess sophisticated enzymatic antioxidant systems that enable them to manage reactive oxygen species (ROS) generated under stress conditions. The primary enzymatic components

include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione peroxidase (GPX) [16]. Superoxide dismutase (SOD) represents the first line of defense against ROS, catalyzing the dismutation of superoxide radicals to hydrogen peroxide and oxygen [17]. Millets contain multiple SOD isoforms including Cu/Zn-SOD, Mn-SOD, and Fe-SOD that are localized in different cellular compartments [18]. In foxtail millet, comprehensive analysis has identified multiple SOD genes (SiFSD1, SiFSD2, SiMSD) that show differential expression patterns under drought stress. The expression of all SiSOD genes initially decreases after 1 hour of drought stress, followed by significant upregulation, indicating dynamic regulation of antioxidant responses [19]. Application of molybdenum fertilizer significantly improved antioxidant enzyme activities in millet, with superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities reaching maximum levels under optimal treatment conditions. Under drought stress in finger millet, significant increases in SOD, POD, CAT, and glutathione reductase (GR) activities were observed after 19 days of stress treatment [20].

Non-enzymatic Antioxidants

In addition to enzymatic systems, millets accumulate various non-enzymatic antioxidants including ascorbic acid, tocopherols, carotenoids, and phenolic compounds [21]. Pearl millet cultivars showed significant antioxidant activity through DPPH radical scavenging, with heat treatments enhancing antioxidant activity mainly due to flavonoid content. Phenolic compounds, including flavonoids and phenylpropanoids, represent particularly important antioxidants in millets [22]. The phenylpropanoid biosynthesis pathway is significantly enriched under stress conditions, leading to accumulation of protective secondary metabolites [23]. Research has shown that DPPH radical scavenging activity and reducing power assay in pearl millet was largely due to the presence of flavonoid content.

Heat Shock Proteins

Heat shock proteins (HSPs) play crucial roles in maintaining protein homeostasis under stress conditions in millets [24]. HSPs function through various mechanisms including protein folding assistance, prevention of protein aggregation, and facilitation of protein refolding after stress relief. These proteins are essential for maintaining cellular function under proteotoxic stress conditions. These molecular chaperones are classified into several families based on their molecular weights: HSP100, HSP90, HSP70, HSP60, and small heat shock proteins (sHSPs) [25]. Comprehensive genome-wide analysis in foxtail millet has identified 113 HSP genes, including 20 HSP100, 9 HSP90, 27 HSP70, 20 HSP60, and 37 sHSP genes [26]. This represents a higher number of HSP genes compared to rice, indicating enhanced protein protection mechanisms in millets [27]. Under heat stress conditions, millet HSP genes show dramatic upregulation, with different family members exhibiting distinct temporal and spatial expression patterns [28]. In foxtail millet, the sHSP-27 gene shows substantially higher expression in response to heat stress in tolerant cultivars compared to sensitive ones [26]. The regulation of HSP gene expression involves heat shock transcription factors (HSFs) that bind to heat shock elements (HSEs) in gene promoters (Schöffl *et al.*, 1998). Multiple HSF genes have been identified in millets, with differential expression patterns observed under various stress conditions [28]. Comparative synteny analysis demonstrated greater collinearity between foxtail millet and pearl millet HSP genes compared to proso millet, rice, and sorghum [3].

Ion Transport and Salinity Tolerance Salt Overly Sensitive (SOS) Pathway

The SOS (Salt Overly Sensitive) pathway represents a crucial mechanism for maintaining ion homeostasis under salinity stress in millets [29]. This pathway involves three key components: SOS1 (Na⁺/H⁺ antiporter), SOS2 (protein kinase), and SOS3 (calcium-binding protein) [30]. Under salt stress conditions, increased cytosolic calcium activates the SOS3-SOS2 protein kinase complex, which subsequently phosphorylates and activates SOS1. The activated SOS1 transporter then extrudes excess sodium ions from cells, maintaining cellular ion balance. In foxtail millet, the SOS pathway components (SiSOS1, SiSOS2/SiCIPK24, SiSOS3/SiCBL4) have been identified and characterized [31]. Additional CBL (Calcineurin B-like) proteins such as SiCBL5 also contribute to salt stress signaling through interaction with SOS₂.

Sodium and Potassium Transport

Maintenance of appropriate Na⁺/K⁺ ratios is crucial for cellular function under salinity stress [32]. Millets employ various transporters including NHX (Na⁺/H⁺ exchangers), HKT (High-affinity K⁺ Transporters), and HAK (High-Affinity K⁺ uptake) proteins to regulate ion homeostasis. The NHX antiporters, particularly those localized to vacuolar membranes, play important roles in sodium sequestration [33]. In foxtail millet, multiple NHX genes (SiNHX1-4) have been identified and shown to be responsive to salt stress. Proso millet exhibits distinctive growth mechanisms and sodium ion (Na⁺) toxicity resistance strategies from germination to seedling stage, demonstrating comprehensive tolerance mechanisms from root to leaf and from outside to inside cellular compartments [34].

Calcium Signaling

Calcium signaling plays a central role in salt stress perception and response in millets [35]. Calcium-dependent protein kinases (CDPKs) and calcineurin B-like interacting protein kinases (CIPKs) serve as key calcium sensors and signal transducers. Comprehensive analysis has identified large families of CDPK and CIPK genes in millets, with many members showing differential expression under salt stress conditions [36]. The SiCDPK24 gene in foxtail millet activates drought stress response gene expression and promotes drought stress recovery. These proteins regulate various downstream targets including ion transporters, transcription factors, and metabolic enzymes [37].

Late Embryogenesis Abundant (LEA) Proteins

LEA Protein Classification and Structure

Late Embryogenesis Abundant (LEA) proteins represent a diverse group of hydrophilic proteins that accumulate under water deficit conditions [38]. These proteins are classified into several groups based on sequence similarity and structural features [39]. In millets, multiple LEA protein families have been identified, including Group 1 (LEA1), Group 2 (Dehydrins), Group 3 (LEA3), and Group 4 (LEA4) proteins [40]. Each group has distinct structural characteristics and functional properties [41]. Dehydrins, which belong to Group 2 LEA proteins, are characterized by conserved sequence motifs including Y-segments, S-segments, and K-segments. The K-segment, in particular, is important for protein-protein interactions and cellular protection functions [42].

Functional Mechanisms

LEA proteins function through various mechanisms including

protein stabilization, membrane protection, and maintenance of cellular hydration. These intrinsically disordered proteins can undergo conformational changes in response to dehydration, enabling them to protect cellular components [43]. The SiLEA14 gene from foxtail millet has been functionally characterized and shown to confer salt and osmotic tolerance when overexpressed in transgenic plants. This atypical LEA protein contains unique structural features that may contribute to its protective functions [44].

Stress-Responsive Expression

LEA genes show dramatic upregulation under dehydration, salinity, and low temperature stresses in millets. The expression patterns vary among LEA families and environmental conditions, indicating functional specialization within this gene family [45]. Transcriptomic studies have revealed that LEA genes are among the most highly upregulated genes under drought stress in multiple millet species, highlighting their crucial roles in dehydration tolerance [46].

Conclusion

The molecular foundations of millet stress tolerance involve complex networks of transcription factors, signaling proteins, metabolic enzymes, and protective molecules that coordinate cellular responses to environmental challenges. Key components include sophisticated antioxidant systems that manage oxidative stress, efficient osmolyte accumulation mechanisms that maintain cellular hydration, and specialized transport proteins that regulate water and ion homeostasis. The C4 photosynthetic pathway emerges as a fundamental adaptation that underpins millet climate resilience, providing enhanced water and nitrogen use efficiency that enables productivity under resource-limited conditions. This metabolic foundation is complemented by comprehensive stress tolerance mechanisms that protect cellular components and maintain physiological function under adverse conditions. The identification of functionally validated candidate genes and regulatory mechanisms provides valuable resources for crop improvement programs and biotechnological applications. The translation of these molecular insights into practical breeding tools will be crucial for developing climate-resilient crop varieties that can ensure food security under changing environmental conditions. Future research should focus on integrating multi-omics approaches to develop systems-level understanding of millet stress responses, implementing precision breeding strategies that leverage molecular insights, and exploring synthetic biology applications for engineering enhanced climate resilience. The continued study of millet stress physiology will undoubtedly yield additional insights that can contribute to sustainable agriculture and global food security.

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