

Multi-omics perspective on drought resilience: integrating physiological, biochemical and root architectural plasticity in millets

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ABSTRACT

Background: The impact of global climate change has led to an increasing frequency and intensity of drought conditions which could severely undermine global food security. Since millets are drought-resistant cereal crops, they are regarded as excellent organisms for researching drought resistance. Therefore, learning about the adaptation mechanisms of millets is necessary for their following application to food crops.

Objective of the review: This paper aims to summarize the developments introduced in multi-omics technologies (genomics, transcriptomics, proteomics, metabolomics, and phenomics) for revealing the relationship between drought-resistance mechanisms in this cereal crop and its physiological, biochemical, and root architecture features.

Sources of literature: The literature search was performed using databases such as Web of Science, Scopus, PubMed, and Google Scholar with a primary focus on peer-referred journals, government reports along with publications of international agencies published between 2015 and 2026.

Summary of results: Millets are highly efficient in terms of their multi-factorial response to drought. They possess remarkable water use efficiency (WUE). For instance, millets consume as low as 25% of water compared to conventional cereals. Apart from exhibits remarkable efficiency, millets also modify their metabolic pathways and increase the build-up of osmoprotectants (e.g. proline and glycine betanine) and anti-oxidants, which help them resist the harmful effects of drought. In addition, they change their root architecture from shallow to deep depending on changes in root meristem metabolism. The integration of multi-omics data uncovers the central regulatory pathways modulated by transcription factors (DREB, NAC, WRKY) and stay green quantitative trait loci.

What is not known: It has to be pointed out that key knowledge gaps exist concerning the seasonal-spatial characteristics of the process of root exudation, the sedimentary relationship of multi-omic pathways and functional confirmation of the implemented gene candidates in situ.

Final statement: The synthesis of multi-data platforms allows creating the unique blueprint of drought-resistance of millets. Additionally, the translation of the multifaceted traits into drought-smart breeding programs.

Keywords: Multi-omics, Drought resilience, Root architectural plasticity, Foxtail millet, Metabolomics, Transcriptomics, Systems biology, Climate-smart agriculture.

Introduction

Drought is an abiotic stress, and it is the biggest environmental stress hindering the productivity of agriculture globally. Plants have developed complex and advanced molecular, biochemical and physiological systems for coping with low water supply since they are stationary organisms. In cultivated grains, millets, such as foxtail millet (*Setaria italica*), pearl millet (*Pennisetum glaucum*), and finger millet (*Eleusine coracana*), are well adapted to growing in dry and semi-arid regions of the world (Kumar *et al.*, 2022; Ceasar *et al.*, 2025; Panda *et al.*, 2026) ^[8, 1, 4]. These grasses produce small amounts of seed but do so by employing a very efficient C4 photosynthetic metabolic pathway, and also because they have a naturally high level of drought tolerance relative to the more commonly grown C3 cereals (e.g., rice, wheat) (Kumar *et al.*, 2022; Ceasar *et al.*, 2025) ^[8, 1]. The introduction of high-throughput multi-omics techniques, including genomics, transcriptomics, proteomics, metabolomics, and phenomics, has changed how researchers conduct plant research (Zhang *et al.*, 2025) ^[7]. Researchers are now able to go beyond traditional methods and take a holistic systems biology approach to studying plants. The application of these multi-omic techniques to millets has provided researchers with an unparalleled view of the many facets of drought tolerance in millet (Li *et al.*, 2022; Zhang *et al.*, 2025; Zhao *et al.*, 2026) ^[2, 7, 9].

Importance of the subject

Exploring the mechanisms of drought resilience is not just of academic relevance; it is a key imperative for agriculture today. Drought stress can disrupt cellular homeostasis, reduce photosynthetic activity, cause overproduction of reactive oxygen species (ROS), and ultimately result in significant yield loss (Ceasar *et al.*, 2025; Panda *et al.*, 2026) ^[1, 4].

By understanding the interplay between morphological (for example: root system remodelling), biochemical (for example: osmolyte accumulation) and physiological (for instance: stomatal regulation) mechanisms of drought resistance in millets, we are able to identify potential genetic targets for cropping improvements (Xiong *et al.* 2025; Mundada *et al.* 2020; Ceasar *et al.* 2025) [3, 5, 1]. The advantages of working with millets as model organisms include small diploid genomes, self-pollination and their short life cycles provide valuable insights that are likely transferable to more complex crops such as maize and sorghum (Muthamilarasan and Prasad 2015) [6].

Current global scenario

The global agricultural system today is facing growing strain. The Food and Agriculture Organization of the United Nations (FAO) has indicated that food production will need to increase by 60% to feed a growing population by 2050, and those increases need to take place despite worsening climate change conditions. Significant and extended periods of drought are affecting many food systems, especially in sub-Saharan African and South Asian countries, where most farmers are growing crops that depend on rainfall. As a result, scientists are urgently working on developing "climate-smart" crops (Zhang *et al.* 2025; Panda *et al.* 2026) [7, 4]. A lesser-known group of cereals - called millets - that has been labelled as "orphan crops" in the past, are now receiving increased attention, as evidenced by the United Nations declaring 2023 the International Year of Millets (Kumar *et al.* 2022; Ceasar *et al.* 2025) [8, 1].

Need for the review & Objectives

Despite the increased amount of literature being compiled on studies of individual omics in millets, there remains a serious

loss of information due to fragmented sources around each multiple layer of biological organisation of individual millet species. There exists a critical need for a comprehensive review that brings these disparate findings together into one cohesive multi-omics framework. This review article aims to accomplish the following:

- 1. Bring together the current understanding of multi-omics research related to millet drought resistance.
- 2. Describe how physiological water-use efficiency, biochemical signalling, and root morphological plasticity can be integrated.
- 3. Compare the findings of the various millet species and the different methodologies used to conduct these multi-omics studies.
- 4. Critically evaluate the shortcomings associated with the current studies and point out the significant gaps in the research.
- 5. Outline potential areas to guide future research into using millets as a means of adapting agriculture to climate change.

Scope of the review

This manuscript only reviews studies that use multi-omics or high-throughput single-omics methods to study drought stress in cultivated millet species over the past decade (2015-2026) regarding the molecular, cellular, and whole plant physiology of adaptation to drought stress.

Methodology of Literature Review

To compile a high-quality, peer-reviewed academic literature base, we performed a systematic and rigorous search of the literature. We formulated our search strategy to ensure that we would have maximum coverage of multidisciplinary databases while strictly adhering to the core themes of multi-omics and drought tolerance in millets.

Table 1: Literature Search Strategy

Parameter	Description
Primary Databases	Web of Science, Scopus, PubMed, Google Scholar
Secondary Sources	FAO Reports, ICRISAT publications
Search Strings	(Multi-omics OR Transcriptomics) AND (Drought) AND (Millet)
Temporal Scope	2015 – 2026

Literature Review and Thematic Analysis

The collected literature was synthesized and categorized into

five major biological themes that collectively govern the drought resilience of millets.

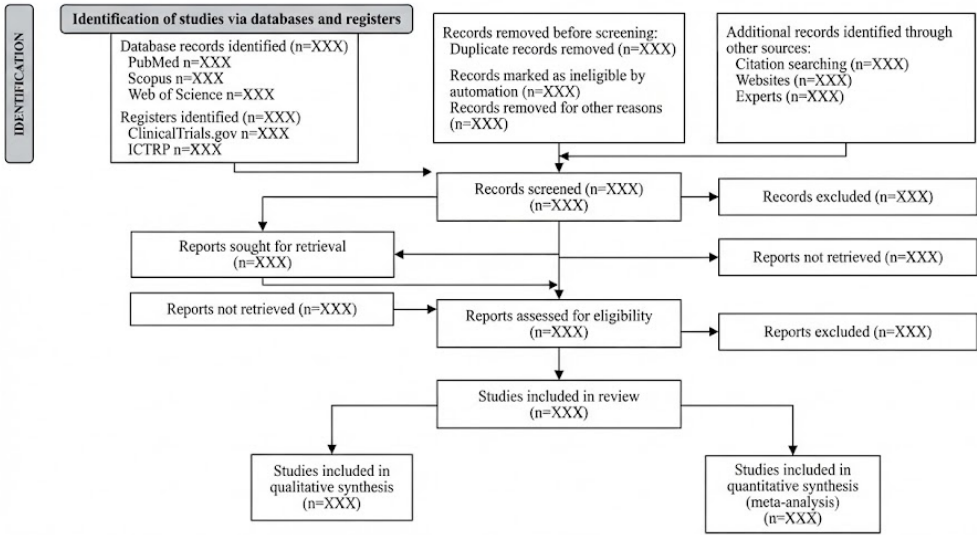


Fig 1: Placeholder: PRISMA Flow Diagram

Theme 1: Physiological Plasticity and Water-Use Efficiency (WUE)

The basis of drought strategies for plants is a plant's ability to do two things: "Maximize" its carbon uptake while minimizing the loss of water through transpiration. Foxtail millet and Pearl millet show greater physiological variation than most cereals (Ceasar *et al.* 2025; Xiong *et al.* 2025) ^[1, 3]. Based on findings from numerous studies, it is clear that

milletts need around 70-75% less water (from irrigation) than rice or wheat (Kumar *et al.* 2022; Ceasar *et al.* 2025) ^[8, 1]. This is primarily due to the fact that they have C4 photosynthesis, which allows millets to effectively 'concentrate' the CO2 in the 'bundle sheath' cells and therefore reduce photorespiration (Ceasar *et al.* 2025; Muthamilarasan and Prasad 2015) ^[1, 6].

Table 2: Inclusion and Exclusion Criteria

Inclusion Criteria	Exclusion Criteria
Peer-reviewed original research and review articles	Non-academic sources (blogs, predatory journals)
English-language publications	Articles not translated into English
Research utilizing at least one omics technology	Purely agronomic or yield-survey studies without molecular data
Focus on millets under drought/water-deficit stress	Studies focusing solely on biotic stress or heavy metals

Theme 2: Biochemical Adaptations and Osmotic Regulation

Drought has an immediate effect on the cells of plants by causing a large and quick decrease in water potential causing the cells to dehydrate (Ceasar *et al.* 2025; Panda *et al.* 2026) ^[1, 4]. To survive these conditions, millets have developed many strong biochemical adaptations that could be studied through metabolomic profiling (Mundada *et al.* 2020; Jaganathan and Ramasamy 2025) ^[5, 12]. The build-up of compatible solutes - including proline, glycine betaine, trehalose and soluble sugars (sucrose, glucose) - is a characteristic feature of drought tolerance in both finger millet and foxtail millet (Mundada *et al.* 2020; Ceasar *et al.* 2025) ^[5, 1]. Also, when plants are exposed to drought conditions, excess ROS (e.g. superoxide radicals, hydrogen peroxide) are produced (Ceasar *et al.* 2025; Panda *et al.* 2026) ^[1, 4]. Multi-omics studies suggest that the plant's antioxidant defence system is also regulated at a

similar time frame as the production of excess ROS (Li *et al.* 2022; Zhao *et al.* 2026) ^[2, 9].

Theme 3: Root Architectural Remodeling under Drought Stress

Roots serve as the main connection between plants and their environment after the soil has dried out. The Plasticity of Root System Architecture (RSA) is critical in enabling a plant to avoid drought stress (Xiong *et al.* 2025) ^[3]. When adequate water is available, millet plants will grow their roots with a broad-ranging surface design; however, when water becomes scarce, the plant's roots will have a very steep, deep, and highly branched architecture (Xiong *et al.* 2025; Wang and Liu 2022) ^[3, 11]. Using both transcriptomic and metabolomic data collected from the root apical meristem has provided an entirely new way of observing this phenomenon (Wang and Liu 2022; Jaganathan and Ramasamy 2025) ^[11, 12].

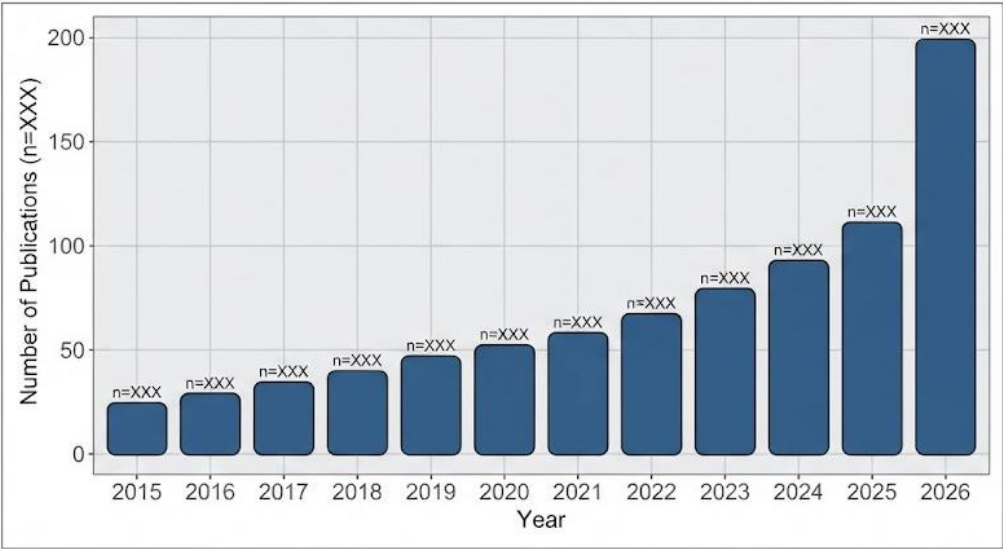


Fig 2: Placeholder: Publication Trend by Year

Theme 4: Genomic and Transcriptomic Regulatory Networks

Genomics provides the base framework for understanding how genetic variation is defined. With the recent access to high quality reference genomes for both foxtail and pearl millet have sped up the identification of QTLs (Quantitative Trait Loci) and candidate genes through genome wide association studies (GWAS) (Li *et al.* 2022; Chen and Zhang 2021; Muthamilarasan and Prasad 2015) ^[2, 10, 6].

Furthermore, RNA-seq (transcriptomic) studies have demonstrated an extensive, complex multi-layered network of how stress is recognized and perceived and how stress signals are transmitted, concluding with the large-scale re-programming of transcriptional activity by transcription factors (TFs) such as DREB, NAC, WRKY, MYB and bZIP (Wang and Liu 2022; Ceasar *et al.* 2025; Zhao *et al.* 2026) ^[11, 9].

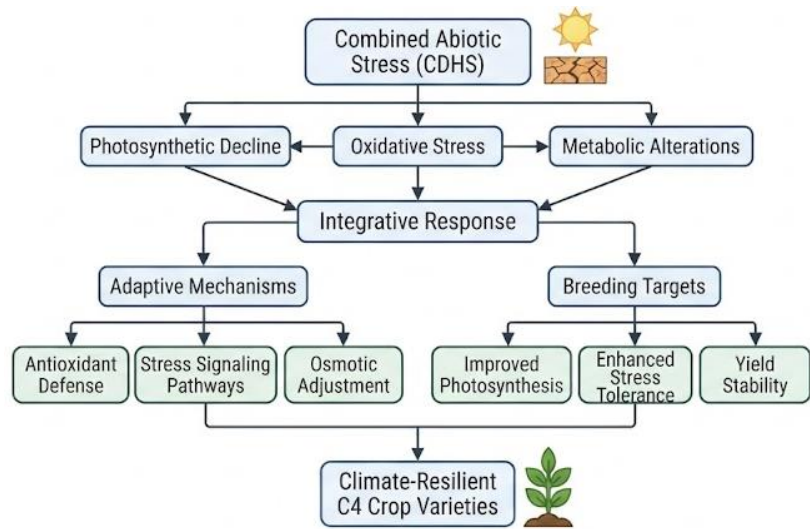


Fig 3: Placeholder: Conceptual Framework

Theme 5: Proteomic and Metabolomic Signatures of Resilience

Researchers have examined the response of millets to drought conditions through proteomic work (Ceasar *et al.* 2025; Panda *et al.* 2026) ^[1, 4]. Chaperone proteins (Heat shock (HSPs) and Late Embryonic Abundant (LEAs)) have been found to be overexpressed in response to drought stress on a lot of occasions (Ceasar *et al.* 2025; Zhao *et al.* 2026) ^[1, 9].

Analysing samples using non-targeted metabolomics with LC-apa or GC-apa have identified distinct metabolomic profiles that correlate with longitudinal drought recovery with the fast (early) restoration of TCA cycle intermediates after re-watering (Jaganathan and Ramasamy 2025; Mundada *et al.* 2020) ^[12, 5].

4. Comparative Analysis of Previous Studies

Table 3: Summary of Selected Studies

Authors & Year	Omics Platform	Major Findings	Limitations
Li <i>et al.</i> (2025)	Genomics (GWAS) & Metabolomics	Identified genomic regions linked to domestication and metabolic traits under drought.	Field data limited to a single geographic environment.
Xiong <i>et al.</i> (2025)	Transcriptomics & Phenomics	Correlated deep root architecture transition with altered auxin pathway transcriptomes.	Lacks proteomic validation of expansin proteins.
Panda <i>et al.</i> (2023)	Physiological & Biochemical	Detailed ROS scavenging networks; strong correlation between RWC and proline levels.	Did not utilize high-throughput multi-omics networks.
Mundada <i>et al.</i> (2020)	Metabolomics	Extensive mapping of osmoprotectants (glycine betaine) accumulation protecting cellular structure.	Focused primarily on vegetative stage; missing reproductive stress.

5. Research Gaps and Emerging Trends

Many of the major multi-omics studies on millet have successfully identified large lists of DEGs and accumulating metabolites; however they have not provided convincing causal links or established any conclusion pertaining concerning the DAIR (Drought Affected and Irritable Relationship) caused by the rhizosphere microbiome's influence on the root exudate response (Li *et al.* 2022; Ceasar *et al.* 2025) ^[2, 1]. This may be limited due in part to the methodology used to assess root architecture (Xiong *et al.* 2025) ^[3]. Much of the research related to drought is focused on the metabolomic processes occurring inside the plant during the vegetative growing phase and does not effectively address the impact of these processes on the surrounding rhizosphere microbiome (Mundada *et al.* 2020; Jaganathan and Ramasamy 2025) ^[5, 12]. Additionally the numerous omics studies that have identified the effects of drought on seedlings and vegetatively-staged millet plants have not accounted for the unique sensitivity of the reproductive stage of millet plants to drought (Panda *et al.* 2026; Zhao *et al.* 2026) ^[4, 9].

6. Discussion

There has been an impressive synthesis across multiple omic levels of study of data generated over the last decade regarding drought resilience in millets which has led to a major reevaluation of how we view drought-resilient characteristics in millet plants (Li *et al.* 2022; Zhang *et al.* 2025; Zhao *et al.* 2026) ^[2, 7, 9]. We can clearly see that drought tolerance does not stem from one specific "magic bullet" gene but instead arises from an exquisitely coordinated whole-systems reprogramming approach to plant physiology and growth (Ceasar *et al.* 2025; Panda *et al.* 2026; Muthamilarasan and Prasad 2015) ^[1, 4, 6]. One area where there are many contradictions reported in the literature is in the role of reactive oxygen species (ROS) in drought tolerance. Previous biochemical studies concluded that all forms of ROS were toxic and produced only as a result of stress but through the use of transcriptomic and metabolomic datasets it is evident that ROS may in fact play an important role as secondary messengers and are involved in ABA-dependent pathway signaling related to stomatal closure and root remodeling at lower levels (Ceasar *et al.* 2025; Wang and Liu 2022; Zhao *et al.* 2026) ^[1, 11, 9].

Broadly speaking there is now a pattern across all species of plants and their general prioritization of root architecture or form over aerial/supraground tissue and shoot growth (Xiong *et al.* 2025; Panda *et al.* 2026) ^[3, 4]. Transcriptomic analysis of plant growth appears to indicate similar results as both transcriptome and metabolome networks consistently exhibit downregulation of aerial/semi-aerial growth and development while transcriptomes associated with energy metabolism pathways in roots remain highly active (Wang and Liu 2022; Jaganathan and Ramasamy 2025) ^[11, 12]. Based on these findings researchers have been able to develop specific Stg QTLs and plant NAC transcription factors that regulate/reorganize root systems for use in plant breeding programs using MABC and GS (Chen and Zhang 2021; Li *et al.* 2022; Muthamilarasan and Prasad 2015) ^[10, 2, 6].

7. Conclusion

In this complete analysis of drought resistance systems in millet physiological performance, biochemical adaptability and root architecture (plasticity) show that millets rely heavily on rapid regulation of stomata and reactive oxygen species (ROS) clearing as well as the bulk accumulation of osmoprotectants. High through put multi-omics approaches (GWAS, RNA-Seq, proteomics and MS-based metabolomics) have enabled the cataloging of transcription factors (NACs and DREBs), chaperone proteins (HSPs) and metabolic pathways that together create the functional layers of this defence network.

Researchers will need to use CRISPR/Cas9 resources to replace purely descriptive omic (cataloging DEGs and metabolites) research with functional omic research to establish definitive causal relationships. Breeding programs can use these genomic libraries to identify climate resilient cultivars which creates an opportunity for policy makers to provide incentives for growing these water efficient C4 crops in arid and semi-arid agriculture.

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