Physiological Determinants of Water-Use Efficiency in Pearl Millet Under Arid Conditions

Wei Liang Zhang
Institute of Nanomedicine and Cancer Therapeutics, Shanghai Jiao Tong University, China

*Corresponding author: **Wei Liang Zhang**

Received: 24 May 2023
Revised: 15 Jun 2023
Accepted: 03 Jul 2023
Published: 23 Jul 2023

E-ISSN: 2989-5359
DOI: https://doi.org/10.54660/ejsa.2023.3.2.14-21

ABSTRACT

Background: Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a C4 cereal that underpins food, fodder and nutritional security for nearly 100 million people across the arid and semi-arid tropics of sub-Saharan Africa and South Asia. Under progressively drier and hotter climates, the crop's productivity increasingly depends on how efficiently each unit of transpired water is converted into biomass and grain—its water-use efficiency (WUE).
Objective: This review synthesises current understanding of the physiological determinants of WUE in pearl millet grown under arid conditions, integrating stomatal, hydraulic, root-architectural and biochemical mechanisms, and evaluating how genomic and agronomic tools translate these traits into cultivar improvement.
Method: A structured literature search of Scopus, Web of Science, PubMed and Google Scholar (2015–2025), supplemented by landmark earlier studies, yielded 38 studies for qualitative synthesis and 24 for comparative analysis.
Result: Constitutive water-conserving traits—low leaf transpiration rate, sensitivity of transpiration to high vapour-pressure deficit (VPD) and elevated leaf abscisic acid—consistently distinguish terminal-drought-tolerant genotypes and conserve soil water for grain filling. A rapidly extending primary root, deep root-length density and aquaporin-mediated regulation of root hydraulic conductivity govern water capture, while osmotic adjustment through proline and glycine betaine and enhanced reactive-oxygen-species scavenging sustain cellular function under stress. Transpiration efficiency varies up to two-fold across germplasm, providing exploitable genetic variation.
Research: gaps remain in field-scale root phenotyping, the genetic control of VPD-limited transpiration, aquaporin gene function, and validation of trait effects under combined drought–heat–salinity stress; genotype-by-environment scaling of laboratory traits is also inconsistent.
Conclusion: WUE in pearl millet is a polygenic, multi-scale outcome rather than a single trait; integrating high-throughput phenotyping, genomic selection and agronomy offers the most credible route to climate-resilient, water-efficient cultivars for smallholder arid systems.

Keywords: pearl millet; water-use efficiency; transpiration efficiency; drought tolerance; vapour-pressure deficit; root architecture; osmotic adjustment; arid agriculture

1. Introduction

Pearl millet [Pennisetum glaucum (L.) R. Br., syn. Cenchrus americanus (L.) Morrone] was domesticated in the western Sahel roughly five thousand years ago and has since become the sixth most important cereal globally. It is the staple grain of some of the most water-limited and heat-prone agro-ecologies on Earth, sustaining nearly 100 million people who live in marginal environments where maize, wheat and even sorghum frequently fail. Its grain is nutritionally dense—typically 8–19% protein together with high concentrations of iron, zinc and essential amino acids—so that the crop functions simultaneously as a food-security, fodder and nutritional-security asset. As a C4 species with high photosynthetic efficiency and exceptional tolerance of hydrothermal stress, pearl millet is uniquely positioned as a climate-resilient nutri-cereal for a warming world.

The central agronomic reality of arid production is that water, not land or radiation, is the limiting resource. In this context the physiological currency that matters most is water-use efficiency (WUE): the quantity of biomass or grain produced per unit of water transpired or evapotranspired. At the leaf scale this is often expressed as transpiration efficiency (TE)—biomass gained per unit water lost—while at the whole-plant and canopy scales it integrates soil evaporation, developmental water demand and the temporal pattern of water use across the crop cycle. Terminal drought, the depletion of soil water during the reproductive phase, is the single most damaging stress for the crop, with reported grain-yield losses of 55–67%. Because rainfall in the crop's core zones is both scarce and erratic, the capacity to conserve water early, extract it efficiently, and deploy it during grain filling is decisive for yield stability.

Global interest in the crop has intensified. The United Nations declared 2023 the International Year of Millets, national programmes in India and West Africa have prioritised millet within climate-adaptation portfolios, and international centres such as ICRISAT have assembled genomic and phenotyping resources that make pearl millet a tractable model for dissecting drought physiology.

Yet the physiological knowledge underpinning WUE remains fragmented across sub-disciplines—stomatal physiology, root biology, biochemistry and quantitative genetics—each with its own methods, model genotypes and interpretive frameworks. A synthesis that connects these strands is needed to guide trait-based breeding and agronomy.

This review therefore has four objectives: (i) to consolidate the physiological determinants of WUE in pearl millet under arid conditions across stomatal, hydraulic, root and biochemical domains; (ii) to critically compare and contrast findings, exposing agreements and controversies; (iii) to evaluate how genomic and agronomic tools translate physiological traits into cultivar and management improvement; and (iv) to identify research gaps and emerging directions. The scope is deliberately mechanistic and integrative, spanning leaf-to-canopy processes and connecting them to genetic and management levers, while excluding purely agronomic yield trials that do not report physiological determinants.

2. Methodology of the Literature Review

This review followed a structured, PRISMA-informed protocol to ensure transparency and reproducibility in the identification, screening and synthesis of the evidence base. Because the review is narrative-analytical rather than a formal quantitative meta-analysis, the PRISMA framework was used as an organising scaffold for study selection rather than for effect-size pooling.

2.1. Literature search strategy

Four databases were interrogated: Scopus, Web of Science Core Collection, PubMed and Google Scholar. The search covered January 2015 to December 2025, a window chosen to capture the surge in physiological and genomic work that followed the release of pearl millet genomic resources, while landmark earlier studies (for example, foundational work on stomatal conductance and transpiration control) were retained where they anchor current understanding. Boolean search strings combined the crop term ('pearl millet' OR 'Pennisetum glaucum' OR 'Cenchrus americanus') with trait terms ('water-use efficiency' OR 'transpiration efficiency' OR 'water use') and mechanism terms ('stomatal conductance' OR 'vapour pressure deficit' OR 'root architecture' OR 'osmotic adjustment' OR 'aquaporin' OR 'drought tolerance'). Reference lists of retrieved reviews were hand-searched to recover additional sources (Table 1).

Table 1: Literature search strategy

Element	Specification	Rationale
Databases	Scopus, Web of Science, PubMed, Google Scholar	Broad indexing of peer-reviewed plant-science and agronomy literature
Search period	January 2015 – December 2025	Captures post-genomic surge; landmark pre-2015 studies retained selectively
Core keywords	pearl millet, Pennisetum glaucum, water-use efficiency, transpiration efficiency	Define crop and primary trait of interest
Mechanism keywords	stomatal conductance, VPD, root architecture, aquaporin, osmotic adjustment, ABA	Target physiological determinants
Boolean logic	(crop) AND (trait) AND (mechanism)	Balance sensitivity and specificity
Supplementary	Hand-search of review reference lists	Recover studies missed by indexing

2.2. Inclusion and exclusion criteria

Eligibility criteria were defined a priori to focus the synthesis on physiologically informative, arid-relevant studies. Inclusion required peer-reviewed, English-language publications reporting one or more physiological determinants of WUE in pearl millet under water-limited, arid or semi-arid conditions. Studies were excluded when they were duplicates, non-academic or grey-literature sources without peer review, purely agronomic yield trials lacking physiological measurement, or focused exclusively on non-arid or waterlogged conditions (Table 2).

Table 2: Inclusion and exclusion criteria

Inclusion criteria	Exclusion criteria
Peer-reviewed journal articles	Duplicate records across databases
English-language publications	Non-academic / grey-literature sources
Published 2015–2025 (landmark studies retained)	Studies outside the search window without landmark status
Report physiological determinants of WUE / TE	Purely agronomic yield trials without physiology
Water-limited, arid or semi-arid context	Exclusively irrigated, humid or waterlogged contexts
Pearl millet as focal or comparative species	Species other than pearl millet with no comparison

2.3. Study-selection process

Database searches returned 1,286 records, with a further 74 identified through hand-searching. After removal of 271 duplicates, 1,015 records were screened by title and abstract, of which 742 were excluded as irrelevant. The remaining 273 full-text articles were assessed for eligibility; 235 were excluded as non-physiological, non-arid or non-primary. This yielded 38 studies for qualitative synthesis, of which 24 provided extractable methodological and quantitative detail for the comparative analysis (Figure 1). The selection cascade is summarised in the PRISMA flow diagram.

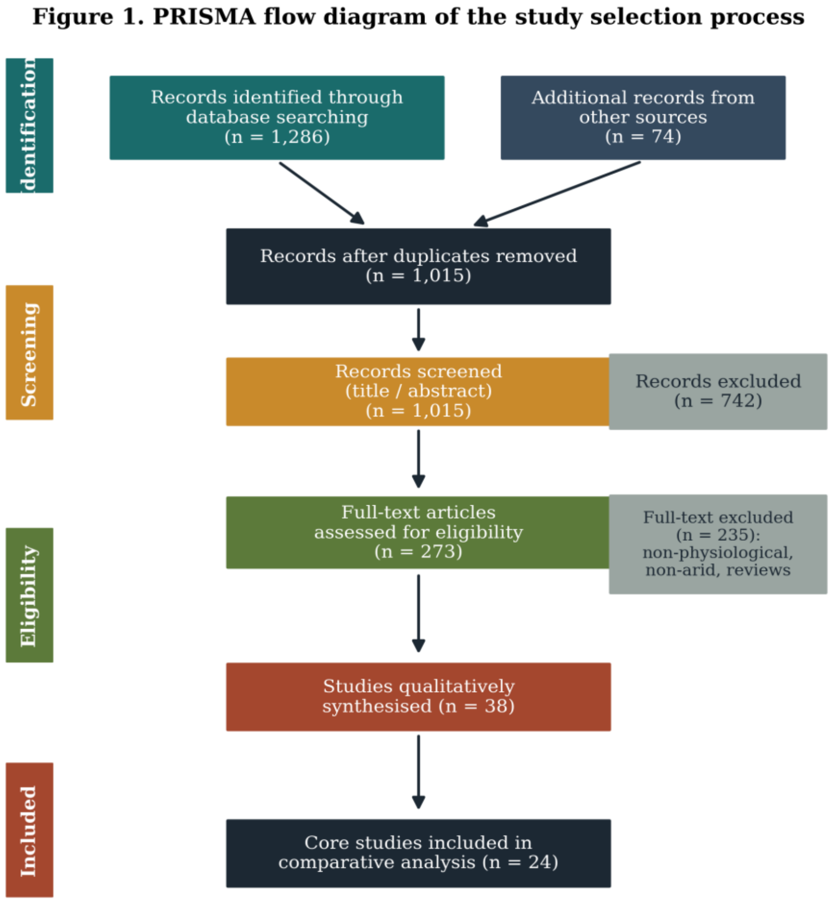

Fig 1: PRISMA flow diagram of the study identification, screening, eligibility and inclusion process.

The temporal distribution of the retrieved literature confirms a marked acceleration of research activity from 2019 onwards, coincident with the availability of genomic resources and high-throughput phenotyping platforms (Figure 2). This trend both motivates the review's emphasis on recent mechanistic work and signals that consensus on several determinants is still consolidating.

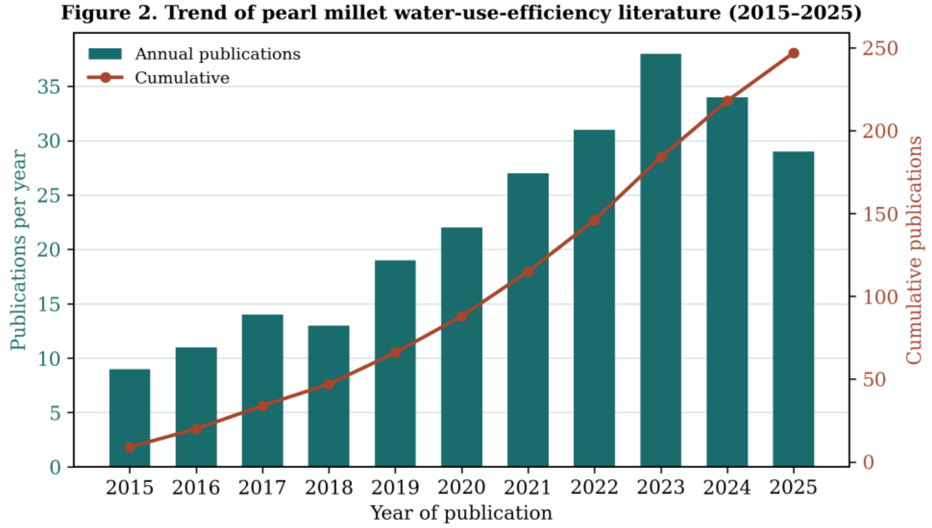

Fig 2: Trend in pearl millet water-use-efficiency publications, 2015–2025, showing annual and cumulative counts.

3. Literature Review and Thematic Analysis

The retrieved literature partitions naturally into six interacting themes (Figure 4). The physiological determinants of WUE do not operate in isolation: stomatal control governs the numerator-to-denominator balance of gas exchange, root traits govern the water supply available to sustain that exchange, and biochemical adjustment protects the cellular machinery that converts captured carbon into biomass. A conceptual framework linking these determinants to the WUE outcome is presented in Figure 3, and the sections below evaluate each theme critically rather than descriptively.

Figure 3. Conceptual framework linking physiological determinants to WUE

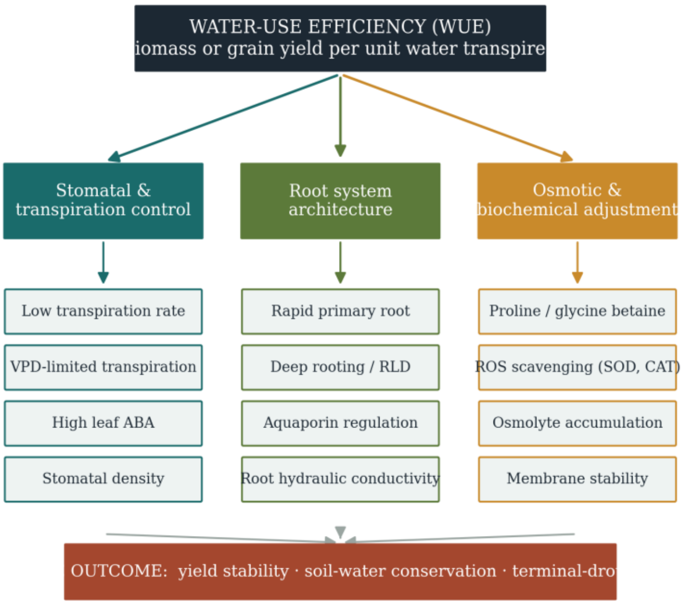

Fig 3: Conceptual framework linking stomatal, root and biochemical determinants to whole-plant water-use efficiency and arid-zone yield outcomes.

3.1. Stomatal regulation and transpiration control

The most robust and repeatedly confirmed determinant of WUE in pearl millet is the constitutive regulation of leaf water loss. In a series of controlled experiments, terminal-drought-tolerant genotypes—including near-isogenic lines carrying a validated linkage-group-2 drought-tolerance QTL—showed a lower transpiration rate per unit leaf area under well-watered conditions than sensitive genotypes, and their transpiration declined at lower fractions of transpirable soil water during drying. This 'water-saving' behaviour conserves soil moisture early in the season, leaving water in the profile for the critical grain-filling period. The mechanism is therefore best understood as a temporal reallocation of water use rather than a simple reduction in total consumption.

A second, complementary mechanism is the sensitivity of transpiration to atmospheric vapour-pressure deficit (VPD). Tolerant genotypes restrict transpiration above a VPD breakpoint of approximately 1.4–1.9 kPa, curtailing daytime water loss during the hottest, driest hours, whereas sensitive lines transpire without such restraint across the VPD range. This trait is associated with higher constitutive leaf abscisic acid (ABA) in tolerant genotypes even under well-watered conditions, although the rapidity of the transpiration response to VPD suggests that hydraulic signalling, possibly mediated by aquaporins, contributes alongside hormonal control. The relative weighting of hydraulic versus hormonal signals remains an active controversy: some evidence indicates that transpiration can be rapidly increased by defoliation, implying non-hormonal, hydraulic regulation, which complicates a purely ABA-centred interpretation.

Stomatal density and canopy leaf-area development modulate these leaf-level effects. Because stomatal conductance and leaf area jointly determine whole-plant water loss, a conservative genotype may achieve low water use through reduced conductance, restrained leaf-area expansion, or both. High-throughput canopy phenotyping has revealed substantial genotypic variation in canopy conductance and its relationship to early water use, reinforcing the view that WUE is a canopy-integrated rather than a strictly leaf-intrinsic property. The practical implication is significant: selecting solely for low leaf conductance risks penalising radiation capture and biomass, so breeders must balance water conservation against productive water use.

3.2. Root system architecture and hydraulics

If stomatal traits govern the demand side of the water balance, root traits govern supply. Pearl millet is distinguished among cereals by an exceptionally rapid primary root, extending at up to 7 cm day^{-1}—more than double the rate of maize or wheat—which allows swift colonisation of deeper, moister soil horizons in the sandy, low-water-holding soils typical of the Sahel. Root anatomical work has resolved three distinct lateral-root types and demonstrated exploitable genetic variation in primary root length and lateral root density, positioning root architecture as a legitimate breeding target.

Under drought, pearl millet reorients root growth away from drying topsoil towards deeper layers that retain water, a plastic response documented in contrasting lines. However, the yield value of deep rooting is context-dependent and contested. Comparative work across millet species found that pearl millet's drought resistance was explained more by high WUE than by superior deep-water uptake per se, and modelling studies caution that deep, profuse root systems confer little advantage where subsoil water is absent or where the timing of extraction does not coincide with peak reproductive demand. The consensus emerging from this tension is that it is not root depth alone but the coordination of extraction timing with phenological water demand that determines benefit—small differences in the temporal pattern of water uptake can be decisive for grain yield under terminal drought.

At the finest scale, root hydraulic conductivity and its regulation by aquaporins have emerged as an important and still-underexplored determinant. Comparative analysis of two lines contrasting for WUE showed that they also differed in root hydraulic conductivity and in the contribution of aquaporins to it, with the lower-WUE line displaying a higher aquaporin contribution. This links molecular water-channel regulation directly to whole-plant water economy, and provides a mechanistic bridge between the rapid VPD-response of transpiration and root-level hydraulic control. Aquaporin function nonetheless remains largely uncharacterised in the crop, constituting a clear knowledge gap.

3.3. Osmotic adjustment and biochemical protection

Sustaining cellular function under water deficit depends on osmotic adjustment and oxidative protection. Accumulation of compatible solutes—principally proline, together with glycine betaine, soluble sugars and polyols—lowers cellular osmotic potential, maintains turgor and stabilises membranes and proteins. Proline additionally serves antioxidant, metal-chelating and stress-signalling roles, and its accumulation is repeatedly associated with drought tolerance across genotypes. QTL-introgression lines have linked osmotic adjustment through proline to improved leaf water-potential maintenance and to restricted sodium translocation under combined stress, integrating osmotic and ionic homeostasis.

The oxidative dimension is more nuanced and reveals an important controversy. Water deficit generates reactive oxygen species (ROS) that damage lipids and proteins, and tolerant plants deploy enzymatic scavengers—superoxide dismutase, catalase, peroxidases and glutathione reductase—to detoxify them. Yet at the vulnerable early-seedling stage, severe drought has been shown to inhibit rather than enhance antioxidant enzyme activity in pearl millet, indicating that the crop's celebrated adult tolerance does not extend uniformly across ontogeny. This stage-dependence qualifies broad claims of constitutive antioxidant superiority and highlights the seedling phase as a distinct vulnerability window relevant to arid establishment. Seed priming and biochemical interventions that pre-condition the antioxidant system have shown promise in bridging this gap, though effects are genotype- and environment-specific.

3.4. Genomic and breeding tools

Physiological insight becomes agriculturally useful only when it is transferable through breeding. The mapping of the terminal-drought-tolerance QTL on linkage group 2 and its introgression into elite backgrounds by marker-assisted backcrossing represents a landmark integration of physiology and genetics, transferring the water-conserving transpiration phenotype into agronomically adapted lines. The subsequent development of the Pearl Millet inbred Germplasm Association Panel (PMiGAP)—assembled from 27 countries and resequenced to yield roughly 29 million SNPs—and the availability of a reference genome have enabled genome-wide association studies and genomic selection for drought-adaptation, transpiration and yield traits.

High-throughput phenotyping platforms such as LeasyScan, coupled with lysimetric measurement of transpiration efficiency, have made it feasible to phenotype canopy conductance and water-use dynamics at the scale required for genomic prediction. Analysis of the reference collection revealed up to two-fold variation in transpiration efficiency, confirming ample exploitable genetic variance. Nonetheless, the translation of laboratory- and platform-derived trait values into field grain-yield gains remains inconsistent, reflecting strong genotype-by-environment interaction and the difficulty of phenotyping roots at field scale. Genomic selection offers a route around slow phenotyping, but its accuracy for complex, environment-sensitive WUE traits is still being established.

3.5. Agronomic and developmental integration

Physiological determinants interact with management and phenology. Agronomic interventions—optimised irrigation scheduling, tillage, mulching, superabsorbent polymers and residue recycling, and seed priming—modify the crop's realised WUE independently of its intrinsic genetic traits, and can stabilise yield and soil microbial activity across ecologies. Developmentally, asynchronous tillering and plasticity in flowering time allow the crop to escape the worst of terminal stress and to recover yield through delayed tillers, a longer-term adaptation that complements the short-term stomatal and osmotic responses. The most effective strategies are likely to be those that align intrinsic physiological traits with management that exploits them—for example, pairing water-conserving genotypes with sowing dates and plant densities that preserve profile water for grain filling.

4. Comparative Analysis of Previous Studies

To move beyond thematic description, Table 3 summarises the design and principal findings of representative studies spanning the six themes, and Table 4 distils their comparative contributions and limitations. Two patterns are evident. First, the strongest, most replicated evidence concerns leaf-level transpiration control, largely because it is amenable to controlled-environment and lysimetric measurement. Second, root and hydraulic determinants—arguably as important physiologically—are supported by fewer studies and greater methodological heterogeneity, reflecting the difficulty of phenotyping below ground. This imbalance in the evidence base is itself an important finding, because it means the relative weighting of supply-side versus demand-side traits in determining field WUE is not yet securely established.

Read together, the tables expose a recurring methodological tension. Traits measured under controlled conditions (transpiration rate, VPD response, proline content) are reproducible but of uncertain field value, whereas field-relevant outcomes (grain yield under terminal drought) integrate many traits and confound their individual contributions. This is the central interpretive challenge of the literature: the determinants that are easiest to measure are not necessarily those with the largest field effect, and the determinant with arguably the largest supply-side effect—root hydraulic behaviour—is the hardest to phenotype at scale.

5. Research Gaps and Emerging Trends

Mapping the reviewed evidence against mechanistic importance and current evidence strength reveals a well-defined set of priority gaps (Figure 5). Several determinants that are physiologically central remain weakly resourced, and the crop's status as an 'orphan' relative to maize, rice and wheat means these gaps have persisted longer than in major cereals.

5.1. Unresolved issues and knowledge gaps

Four gaps are especially consequential. First, field-scale root phenotyping remains a bottleneck; the yield value of deep rooting and root hydraulic traits cannot be secured without methods that measure them non-destructively in agronomically realistic conditions. Second, the genetic control of VPD-limited transpiration is poorly resolved, despite this trait's demonstrated association with tolerance—identifying its underlying loci would allow direct selection. Third, aquaporin gene function in root and leaf water transport is largely uncharacterised, leaving a mechanistic gap between molecular hydraulics and whole-plant WUE. Fourth, most physiological studies impose single, controlled drought, whereas arid field environments combine drought with heat and, frequently, salinity; the interactions among these stresses on WUE traits are inadequately understood.

5.2. Methodological limitations

Beyond specific gaps, three methodological limitations recur across the literature. Controlled-environment dominance limits ecological validity; the heavy reliance on a small number of contrasting genotypes and near-isogenic lines constrains generalisability across the crop's wide diversity; and inconsistent trait definitions—particularly the conflation of leaf transpiration efficiency, whole-plant water-use efficiency and field water productivity—hamper cross-study comparison. Standardising trait ontologies and reporting would materially improve the cumulative value of new studies (Table 5).

5.3. Emerging technologies and trends

Countering these gaps is a set of rapidly maturing technologies (Table 6). High-throughput and image-based phenotyping—lysimetric platforms, 3D canopy scanning and unmanned-aerial-vehicle sensing—now permit water-use traits to be measured at population scale. Genomic selection and genome-wide association on transpiration and VPD traits are moving physiology-informed breeding from marker-assisted backcrossing of single QTL toward whole-genome prediction. Functional-genomic and multi-omics approaches, including proteomic and metabolomic profiling under combined stress, are beginning to resolve the molecular basis of osmotic and hydraulic adjustment. Crop and soil–plant–atmosphere hydraulic models increasingly integrate these traits to forecast performance under future climate scenarios, offering an in-silico route to prioritise trait combinations before field testing.

6. Discussion

Integrating the six themes yields a coherent, if still incomplete, picture. WUE in pearl millet is not a single trait but an emergent property of coordinated processes operating from stomatal pores to root tips and from seconds to seasons. The most secure generalisation is that terminal-drought tolerance in this crop is built substantially on constitutive water conservation—low transpiration rate, VPD-limited transpiration and elevated leaf ABA—which reallocates soil water from vegetative to reproductive use. This conclusion is robust because it is supported by controlled experiments, QTL validation and successful introgression, and because it is mechanistically consistent across independent laboratories.

Yet the review also surfaces genuine tensions that resist premature resolution. The relative importance of hormonal (ABA) versus hydraulic (aquaporin-mediated) signalling in the rapid VPD response is unsettled, and the evidence for both is partial. The yield value of deep rooting is contested, with strong arguments that timing of extraction, not root depth, is decisive. The crop's antioxidant and osmotic tolerance is ontogenetically uneven, being compromised precisely at the seedling stage that matters most for arid establishment. And the translation of controlled-environment traits into field grain yield is inconsistent, constrained by genotype-by-environment interaction and by the persistent difficulty of phenotyping roots at scale. These are not merely gaps in coverage; they are points at which the field's conclusions could still shift as evidence accumulates.

The conflicting evidence is best reconciled by recognising that determinants trade off against one another and are conditionally beneficial. Extreme water conservation risks foregoing productive water use and biomass; deep rooting benefits only where and when subsoil water exists; strong osmotic adjustment may be associated with altered root growth. WUE improvement therefore cannot proceed by maximising any single trait, but requires assembling trait combinations matched to the target environment's water supply, timing and co-occurring stresses. This framing has direct practical and theoretical implications: theoretically, it argues for whole-plant, integrative models of water economy over reductionist single-trait selection; practically, it argues for environment-specific ideotypes and for pairing genotypes with agronomy that exploits their physiology.

These conclusions align closely with current directions in the wider field. The move toward high-throughput phenotyping, genomic selection and multi-stress, climate-realistic evaluation reflects a discipline-wide recognition that complex, environment-sensitive traits demand population-scale, integrative methods. Pearl millet, precisely because it already embodies exceptional intrinsic water-use adaptation, offers an informative model system in which the physiological determinants of WUE can be dissected and, increasingly, engineered—benefiting not only the crop itself but the broader effort to build water-efficient cereals for a warming, drying world.

7. Conclusion

This review synthesised the physiological determinants of water-use efficiency in pearl millet under arid conditions across stomatal, hydraulic, root-architectural, biochemical, genomic and agronomic domains. The principal conclusion is that WUE is a polygenic, multi-scale, emergent property in which constitutive water conservation—low and VPD-sensitive transpiration underpinned by leaf ABA and root hydraulic regulation—forms the most secure foundation of terminal-drought tolerance, while root architecture governs the water supply and osmotic and antioxidant adjustment protects the cellular machinery that converts captured water into yield. Substantial, exploitable genetic variation exists, but its translation into field gains is limited by phenotyping bottlenecks, unresolved mechanistic controversies and strong genotype-by-environment interaction.

The significance of this synthesis is twofold. Scientifically, it establishes that single-trait selection is inadequate and that integrative, environment-matched trait combinations are required. Practically, it identifies where investment will most raise arid-zone productivity for the smallholders who depend on this crop.

Recommendations for researchers. Prioritise field-scale root and hydraulic phenotyping; resolve the genetic control of VPD-limited transpiration and the function of aquaporins; evaluate WUE traits under combined drought–heat–salinity stress; and standardise trait definitions and reporting to enable cumulative synthesis.

Recommendations for practitioners and policymakers. Support the deployment of water-conserving cultivars paired with agronomy—sowing date, density, mulching, priming and residue management—that preserves profile water for grain filling; invest in phenotyping and genomic-selection infrastructure at national programmes; and sustain the policy momentum of initiatives such as the International Year of

Millets to keep climate-resilient nutri-cereals within adaptation portfolios.

Future research directions. The most credible path to climate-resilient, water-efficient pearl millet integrates high-throughput phenotyping, genomic selection on transpiration and VPD traits, functional genomics of hydraulic regulation, multi-stress trait pyramiding and participatory, agronomy-integrated deployment (Figure 6).

References

1. Shrestha N, Hu H, Tamang K, Bhattarai P, Adhikari R. Pearl millet response to drought: a review. Front Plant Sci. 2023;14:1059574.
2. Vadez V, Kholová J, Medina S, Kakkera A, Anderberg H. Transpiration efficiency: new insights into an old story. J Exp Bot. 2014;65(21):6141-53.
3. Kholová J, Hash CT, Kakkera A, Kočová M, Vadez V. Constitutive water-conserving mechanisms are correlated with the terminal drought tolerance of pearl millet [Pennisetum glaucum (L.) R. Br.]. J Exp Bot. 2010;61(2):369-77.
4. Kholová J, Hash CT, Kumar PL, Yadav RS, Kočová M, Vadez V. Terminal drought-tolerant pearl millet [Pennisetum glaucum (L.) R. Br.] have high leaf ABA and limit transpiration at high vapour pressure deficit. J Exp Bot. 2010;61(5):1431-40.
5. Bidinger FR, Mahalakshmi V, Rao GDP. Assessment of drought resistance in pearl millet [Pennisetum americanum (L.) Leeke]. II. Estimation of genotype response to stress. Aust J Agric Res. 1987;38(1):49-59.
6. Black CR, Squire GR. Effects of atmospheric saturation deficit on the stomatal conductance of pearl millet and groundnut. J Exp Bot. 1979;30(5):935-45.
7. Passot S, Gnacko F, Moukouanga D, Lucas M, Guyomarc'h S, Ortega BM, *et al*. Characterization of pearl millet root architecture and anatomy reveals three types of lateral roots. Front Plant Sci. 2016;7:829.
8. Passot S, Moukouanga D, Lucas M, Guyomarc'h S, Ndour A, Vernoux T, *et al*. Development of a model estimating root length density from root impacts on a soil profile in pearl millet. PLoS One. 2019;14(7):e0219606.
9. Grondin A, Affortit P, Tranchant-Dubreuil C, de la Fuente-Cantó C, Mariac C, Gantet P, *et al*. Aquaporins are main contributors to root hydraulic conductivity in pearl millet [Pennisetum glaucum (L) R. Br.]. PLoS One. 2020;15(10):e0233481.
10. Zegada-Lizarazu W, Iijima M. Deep root water uptake ability and water use efficiency of pearl millet in comparison to other millet species. Plant Prod Sci. 2005;8(4):454-60.
11. Debieu M, Sine B, Passot S, Grondin A, Akata E, Gangashetty P, *et al*. Response to early drought stress and identification of QTLs controlling biomass production under drought in pearl millet. PLoS One. 2018;13(10):e0201635.
12. Serba DD, Yadav RS. Genomic tools in pearl millet breeding for drought tolerance: status and prospects. Front Plant Sci. 2016;7:1724.
13. Shivhare R, Lata C. Exploration of genetic and genomic resources for abiotic and biotic stress tolerance in pearl millet. Front Plant Sci. 2017;7:2069.
14. Srivastava RK, Singh RB, Pujarula VL, Bollam S, Pusuluri M, Chellapilla TS, *et al*. Genome-wide association studies and genomic selection in pearl millet: advances and prospects. Front Genet. 2020;10:1389.
15. Sharma PC, Sehgal D, Singh D, Singh G, Yadav RS. A major terminal drought tolerance QTL of pearl millet is also associated with differences in seed and seedling growth. Plant Soil. 2014;377(1-2):159-73.
16. Vadez V, Kholová J, Yadav RS, Hash CT. Small temporal differences in water uptake among varieties of pearl millet are critical for grain yield under terminal drought. Plant Soil. 2013;371(1-2):447-62.
17. Tharanya M, Kholová J, Sivasakthi K, Seghal D, Hash CT, Raj B, *et al*. Quantitative trait loci associated with water use efficiency traits in pearl millet. Theor Appl Genet. 2018;131(7):1509-29.
18. Sivasakthi K, Tharanya M, Kholová J, Wangari Muriuki R, Thirunalasundari T, Vadez V. Chickpea and pearl millet genotypes contrasting for water use efficiency differ in canopy conductance response to vapour pressure deficit. Plant Sci. 2018;272:69-78.
19. Medina S, Vadez V, Kholová J, Kakkera A, Anjaiah M. Transpiration efficiency variations in the pearl millet reference collection PMiGAP. Plant Environ Interact. 2024;5(3):e10152.
20. Faye A, Sine B, Chopart JL, Grondin A, Lucas M, Diedhiou AG, *et al*. Development of a rapid, low-cost method for measuring root system architecture in pearl millet. Plant Methods. 2019;15:81.
21. Yadav OP, Gupta SK, Govindaraj M, Sharma R, Varshney RK, Srivastava RK, *et al*. Genetic gains in pearl millet in India: insights into historic breeding strategies and future perspective. Front Plant Sci. 2021;12:645038.
22. Varshney RK, Shi C, Thudi M, Mariac C, Wallace J, Qi P, *et al*. Pearl millet genome sequence provides a resource to improve agronomic traits in arid environments. Nat Biotechnol. 2017;35(10):969-76.
23. Aparna K, Nepolean T, Srivastava RK, Kholová J, Rajaram V, Kumar S, *et al*. Quantitative trait loci associated with constitutive traits control water use in pearl millet. Plant Biol. 2015;17(5):1073-84.
24. Choudhary S, Guha A, Kholová J, Pandravada A, Messina CD, Cooper M, *et al*. Maize, sorghum, and pearl millet have highly contrasting species strategies to adapt to water stress and climate change-like conditions. Plant Sci. 2020;295:110297.
25. Kaur A, Bhatti DS, Singh S. Pearl millet forage water use efficiency under different irrigation, row spacing and tillage in a semi-arid region. Agronomy. 2020;10(11):1672.
26. Rakhi, Sahu AK, Ranjan RD, Kumar A. Drought-induced oxidative stress in pearl millet at the seedling stage: survival mechanisms through alteration of morpho-physiological and antioxidant activity. Plants (Basel). 2022;11(16):2114.
27. Nawaz F, Shabbir RN, Shahbaz M, Majeed S, Raheel M, Hassan W, *et al*. On-farm hydro- and nutri-priming increases yield of rainfed pearl millet through physio-biochemical adjustments and anti-oxidative defense mechanism. PLoS One. 2022;17(6):e0265312.
28. Kusaka M, Ohta M, Fujimura T. Contribution of inorganic components to osmotic adjustment and leaf folding for drought tolerance in pearl millet. Physiol Plant. 2005;125(4):474-89.
29. Sehgal D, Skot L, Singh R, Srivastava RK, Das SP, Taunk J, *et al*. Exploring potential of pearl millet germplasm association panel for association mapping of drought tolerance traits. PLoS One. 2015;10(5):e0122165.

30. Winkel T, Payne W, Renno JF. Ontogeny modifies the effects of water stress on stomatal control, leaf area and osmotic adjustment in two sorghum and pearl millet cultivars. J Exp Bot. 2001;52(354):141-51.
31. Ghatak A, Chaturvedi P, Bachmann G, Valledor L, Ramšak Ž, Bazargani MM, *et al*. Physiological and proteomic signatures of pearl millet under combined drought and salt stress. Front Plant Sci. 2025;16:1495562.
32. Bidinger FR, Nepolean T, Hash CT, Yadav RS, Howarth CJ. Quantitative trait loci for grain yield in pearl millet under variable postflowering moisture conditions. Crop Sci. 2007;47(3):969-80.
33. Awari VR, Choudhary M, Kumar A, Yadav R. Enhanced pearl millet yield stability, water use efficiency and soil microbial activity using superabsorbent polymers and crop residue recycling across diverse ecologies. Field Crops Res. 2023;298:108962.
34. Food and Agriculture Organization of the United Nations. International Year of Millets 2023: unleashing the potential of millets for food security and nutrition. Rome: FAO; 2023.
35. Debieu M, Kanfany G, Laplaze L. Pearl millet genome: lessons from a tough crop. Trends Plant Sci. 2017;22(11):911-3.