

Original Research Article

Decoding Crop Acclimation to Deficit Irrigation under Climate Variability: Hydraulic Signalling, Hormonal Crosstalk, Molecular Reprogramming, and Yield Resilience

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Article Information:

Received: 13 April 2026 | Revised: 14 May 2026 | Accepted: 15 June 2026 | Published: July 12, 2026

Cite this article:

Thokchom A, Singh SR, Birendrajit C, Debnath A, Bordoloi LJ, Pongen M, Haribhushan A, Devi HL and Mohanty AK (2026). Decoding Crop Acclimation to Deficit Irrigation under Climate Variability: Hydraulic Signalling, Hormonal Crosstalk, Molecular Reprogramming, and Yield Resilience. *Public Health Open Journal*. 11(1):716–728. 10.17140/PHOJ-11-716

Abstract

Climate variability is intensifying the mismatch between crop water demand and irrigation supply, making deficit irrigation (DI) an increasingly important strategy for sustaining agricultural production with reduced water availability. Yet, the success of DI depends not simply on the amount of water withheld, but on the capacity of crops to perceive, transmit and integrate water-deficit signals while protecting reproductive development and harvestable yield. This review synthesizes crop acclimation to DI across four interacting levels: hydraulic signalling, hormonal crosstalk, molecular reprogramming and yield resilience. Early declines in soil and root-zone water potential alter root hydraulic conductance, xylem tension, aquaporin activity and root-to-shoot communication, rapidly constraining stomatal conductance and canopy water loss. These hydraulic responses interact strongly with abscisic acid (ABA), auxin, cytokinins, ethylene, jasmonates, salicylic acid and strigolactones to coordinate stomatal behaviour, root-system plasticity, source-sink relations and reproductive survival. At the molecular level, ABA-dependent PYR/PYL–PP2C–SnRK2 signalling, ABA-independent DREB pathways, NAC/MYB/WRKY transcription factors, Ca²⁺ and reactive oxygen species signalling, osmoprotectant metabolism, antioxidant defence, aquaporins and stress-associated proteins collectively reprogram plant growth and metabolism. An additional emerging dimension is the contribution of rhizosphere and endophytic microbiomes to hormonal regulation, root architecture, nutrient acquisition, osmotic adjustment and redox homeostasis under water limitation. Evidence from meta-analyses indicates that DI commonly improves water productivity while imposing context-dependent yield penalties, with responses governed by crop, genotype, soil texture, climate, irrigation method, deficit intensity and phenological timing. Moderate and stage-specific deficits can therefore function as controlled acclimation signals, whereas severe or poorly timed deficits, particularly when combined with heat stress, disrupt carbon assimilation, reproductive processes and grain or fruit filling. Integrating plant signalling biology, microbiome functions, high-throughput sensing and precision irrigation can shift DI from a fixed water-saving practice toward a biologically informed strategy for stabilizing yield and water productivity under climate uncertainty.

Keywords: deficit irrigation; drought acclimation; hydraulic signalling; abscisic acid; hormonal crosstalk.

Highlights

- Deficit irrigation acts both as a water-saving treatment and as a controlled physiological acclimation signal [1,2].
- Root hydraulics, xylem tension, aquaporins and ABA jointly regulate rapid root-to-shoot responses to soil drying [13,14,25,26].
- Hormonal crosstalk determines whether water conservation can be achieved without unacceptable penalties to growth and reproductive development [15–18].
- Beneficial rhizosphere and endophytic microorganisms can reinforce drought acclimation through phytohormone regulation, root modification, osmotic adjustment and antioxidant defence [46,49,50,52,53].
- Heat can intensify drought-induced oxidative damage, reproductive failure and yield loss, making the physiological severity of a given irrigation deficit climate dependent [47].
- Decision-support systems, multispectral sensing and machine learning provide opportunities for adaptive, plant-responsive irrigation under climatic variability [48,51].

1. Introduction

Water scarcity is no longer restricted to chronically arid environments. Increasing atmospheric demand, irregular rainfall, heat waves and shifts in precipitation timing are exposing irrigated and rainfed crops to more frequent episodes of soil drying [6,7,33–35,42]. The simultaneous occurrence of drought and heat is particularly important because their interaction can intensify dehydration, oxidative injury, photosynthetic inhibition, reproductive failure and yield loss beyond the effects produced by either stress individually [47].

Under these conditions, irrigation management must balance two potentially conflicting objectives: conserving limited water resources and maintaining economically acceptable crop yields [1,2]. Deficit irrigation (DI), in which irrigation water is deliberately supplied below full crop evapotranspiration requirements during part or all of the growing season, has emerged as an important strategy for increasing crop water productivity [1,2,40,41].

The basic principle of DI is to accept a controlled degree of water limitation when the marginal yield response to additional irrigation is relatively small, while protecting developmental stages during which reproductive development and yield formation are highly sensitive [1,2,40]. This approach becomes increasingly complex under climate variability because an irrigation

deficit considered moderate under one combination of temperature, relative humidity and vapour-pressure deficit may become physiologically severe under another [35,42,47].

Evidence accumulated across different crops demonstrates that the response to DI is strongly context dependent [3–5]. Global syntheses generally indicate higher water-use efficiency or water productivity under DI, although these improvements are frequently accompanied by some reduction in yield [3–5]. In wheat, a global meta-analysis based on 381 paired observations reported an average improvement in WUE of approximately 6% together with a yield reduction of approximately 16%, although particular combinations of irrigation intensity and environmental conditions allowed improvements in both yield and WUE [3]. These findings demonstrate why no single DI threshold can be universally recommended.

Plants do not passively deteriorate as soil dries. They actively perceive changes in water availability through alterations in water potential, hydraulic conductance, cell turgor, membrane status and chemical signalling [6,7,9,14]. Roots and shoots communicate through hydraulic signals, hormones, ions, peptides, ROS and calcium-dependent signalling networks [13–24]. In addition, increasing evidence indicates that root-associated microbial communities can modify root architecture, nutrient acquisition, hormone balance and stress-related metabolism, thereby adding a biological rhizosphere component to whole-plant drought acclimation [46,49,50,52,53].

The importance of such plant–microbe interactions is illustrated by field evidence showing that microbial consortia can improve nutrient availability, biological activity and crop productivity under reduced external inputs [46]. Functional profiling of beneficial microorganisms further indicates that PGPR, arbuscular mycorrhizal fungi and endophytes can influence phytohormonal signalling, osmolyte accumulation, antioxidant defence and plant tolerance to drought and other abiotic stresses [49,50,53].

Stomata can adjust transpiration within minutes, whereas root growth, aquaporin activity, osmotic adjustment, microbiome interactions and transcriptional reprogramming develop over longer time scales [14,19–26,49,50]. These responses may conserve water for later developmental stages but simultaneously restrict carbon assimilation [27,28,31,32].

Therefore, the agronomic value of acclimation depends on whether water conserved through stress responses ultimately protects more yield than is lost through reduced photosynthesis and growth. This review inte-

grates hydraulic signalling, hormonal crosstalk, molecular reprogramming, microbiome-assisted acclimation and yield formation under DI, with particular emphasis on climate variability and field-level management.

2. Deficit Irrigation as a Controlled Acclimation Environment

Deficit irrigation encompasses several operational strategies. Sustained DI applies a relatively constant fraction of full crop water requirement during much of the growing season [1,2]. Regulated deficit irrigation imposes stronger deficits during relatively drought-tolerant developmental stages while maintaining adequate irrigation during sensitive stages [1,40]. Partial root-zone drying alternately wets and dries different portions of the root system so that roots exposed to drying soil generate chemical signals while roots in wetter soil continue supplying water [37–39].

These strategies produce distinct spatial and temporal patterns of soil and plant water potential and consequently different signalling environments [37–39]. PRD is especially relevant physiologically because it partially separates root-derived chemical signalling from severe whole-plant dehydration [38,39].

The distinction between stress avoidance, acclimation and injury is essential. Moderate decreases in soil water availability can reduce stomatal conductance before severe leaf dehydration develops and thereby improve intrinsic WUE [13,27]. Root proliferation at depth, osmotic adjustment and changes in aquaporin activity may improve access to residual soil water [10–12,25,26].

Beneficial microorganisms can reinforce some of these responses. PGPR and endophytes can promote lateral root development, modify phytohormone concentrations, stimulate compatible-solute accumulation and enhance antioxidant activity under water deficit [49,53]. Microbial inoculation has also been associated with maintenance of cellular turgor and improved water-use efficiency under abiotic stress [49].

In contrast, prolonged or severe DI decreases leaf water potential, restricts cell expansion and photosynthesis, increases canopy temperature, accelerates senescence and can impair pollen viability, fertilization, seed set and grain or fruit development [31–35,47]. Combined drought and heat are especially damaging during reproductive development because high temperature impairs pollen function while drought limits assimilate delivery to developing sinks [47].

Consequently, the same irrigation treatment may function as beneficial priming, moderate acclima-

tion or damaging stress depending on crop stage, atmospheric demand, genotype and rhizosphere conditions.

3. Hydraulic Signalling: The First Layer of Acclimation

3.1 Soil–Root Hydraulic Continuity and Water-Potential Gradients

Hydraulic signalling begins as water availability declines at the soil–root interface. Water movement through the soil–plant–atmosphere continuum follows gradients in water potential and is constrained by hydraulic resistance in the soil, rhizosphere, roots, xylem and leaves [9,10,25,26].

As the rhizosphere dries, hydraulic conductivity can decline sharply, increasing the water-potential gradient required to sustain transpiration [9,10]. These changes can generate rapid alterations in leaf water status and stomatal behaviour before extensive biochemical acclimation occurs.

Root architecture, root hairs and rhizosphere characteristics influence the ability of plants to maintain hydraulic contact with progressively drying soil [10–12]. Rhizosphere microbial restructuring can further influence root architecture, soil aggregation, nutrient cycling and soil ecological functioning, potentially altering the environment through which roots acquire both water and nutrients [50,52].

Regenerative management systems characterized by greater microbial diversity and organic matter have also been associated with improved soil aggregation and water retention compared with biologically simplified systems [52]. Thus, the hydraulic behaviour of crops under DI cannot always be separated from soil biological conditions.

From an agronomic perspective, maximum extraction of available water is not universally desirable. Under seasonal drought, rapid early-season water extraction can leave inadequate reserves for flowering and grain filling [6–8,28]. Hydraulic traits that moderate canopy consumption, maintain access to deeper water or dynamically adjust conductance may therefore increase yield resilience [6,10–12].

3.2 Root Hydraulic Conductance and Aquaporins

Root hydraulic conductance is dynamically regulated through root anatomy, suberization and membrane aquaporins [25,26]. Plasma membrane intrinsic proteins and other aquaporin families facilitate transmembrane water movement and respond rapidly to phosphorylation, cellular pH, Ca^{2+} and ROS [25,26].

Under moderate water deficit, selective regulation of aquaporins can redistribute water flow among tissues and assist root extraction from wetter portions of the soil profile [25,26]. Under severe stress, aquaporin down-regulation may limit cellular water loss, although excessive hydraulic restriction can intensify shoot dehydration.

Recovery after irrigation is equally important. Rewatering requires restoration of root and leaf hydraulic conductance, renewed aquaporin activity and reopening of stomata [14,25,26]. A genotype that conserves water efficiently but recovers photosynthesis slowly may display high instantaneous WUE yet relatively poor seasonal productivity [6,7,27,28].

3.3 Root-to-Shoot Communication and Stomatal Regulation

Root-to-shoot signalling under drying soil involves hydraulic changes together with mobile chemical signals [13,14,38,39]. ABA is the most extensively characterized component, although xylem sap pH, ions, peptides, ROS and calcium-related signals also participate [14,15,23,24].

Under PRD, roots in drying soil can generate signals that restrict stomatal conductance while roots in wetter soil maintain shoot hydration [37–39]. This partial separation of signalling from whole-plant dehydration explains why PRD may increase water productivity without producing the same decline in leaf water potential as uniform drying.

Stomatal closure conserves water but restricts CO₂ diffusion [27,31,32]. Consequently, the objective is not maximum stomatal closure but appropriately timed regulation. Genotypic variation in ABA production and stomatal sensitivity can determine how effectively water is conserved while carbon assimilation is maintained [13].

4. Hormonal Crosstalk under Deficit Irrigation

4.1 ABA as the Central Drought-Response Coordinator

ABA accumulation is one of the central responses to declining water availability [13–17]. ABA is synthesized through carotenoid-cleavage pathways and transported among roots, vascular tissues and leaves [15–17].

ABA perception by PYR/PYL/RCAR receptors inhibits clade-A PP2C phosphatases, enabling SnRK2 protein kinases to activate downstream ion channels and transcription factors [15–17]. In guard cells, this cascade promotes anion efflux, membrane depolarization,

potassium loss and stomatal closure. In other tissues, ABA activates genes associated with dehydration protection, osmotic adjustment and antioxidant defence [16,19–22].

The importance of ABA becomes even greater when water deficit interacts with heat because combined stress produces distinct molecular responses and altered hormonal signalling rather than a simple addition of single-stress effects [47].

ABA responses are strongly dependent on dose, tissue and developmental stage [13,15–17]. Moderate ABA signalling can conserve water and favour root relative to shoot growth, whereas prolonged high ABA concentrations may suppress leaf expansion and carbon assimilation [13,18].

4.2 Auxin, Cytokinins and Root-System Plasticity

Auxin regulates lateral-root initiation, root elongation and vascular development, whereas cytokinins generally promote shoot development and interact with auxin in determining root-to-shoot allocation [18,22].

Water deficit alters auxin transport and local signalling, enabling root architecture to respond to spatial heterogeneity in soil moisture [10,18]. Beneficial rhizosphere microorganisms add another regulatory layer because many PGPR and endophytes produce auxins, cytokinins and gibberellins or modify plant hormone metabolism [49,53].

Microbial auxin production can promote lateral roots and root hairs, increasing the effective soil volume explored for water and nutrients, while ACC-deaminase-producing microorganisms can reduce stress-induced ethylene and help maintain root elongation under drought [49,53].

The resulting ABA–auxin–cytokinin–ethylene network therefore reflects both endogenous plant metabolism and microbial activity within the root environment.

4.3 Ethylene and Other Hormonal Signals

Ethylene interacts strongly with ABA in regulating root and shoot growth under water stress [18]. ABA can restrict stress-induced ethylene production in growing tissues, whereas excessive ethylene can accelerate senescence and reproductive abortion.

Beneficial microorganisms possessing ACC deaminase can lower the concentration of the ethylene precursor ACC and alleviate drought-related inhibition of root development [49,53]. Endophytes can also influence jasmonic acid, salicylic acid and other signalling pathways, linking abiotic-stress adaptation with defence priming and redox regulation [53].

These interactions demonstrate that hormonal acclimation to DI should increasingly be interpreted as a network process involving plant tissues, environmental signals and associated microorganisms rather than as an ABA-only response.

4.4 Microbiome-Mediated Hormonal and Physiological Acclimation

The rhizosphere and internal plant microbiome represent an emerging component of drought physiology. Beneficial microbial groups including PGPR, AMF and endophytes can enhance stress tolerance through hormone production, ACC-deaminase activity, improved nutrient acquisition, osmotic adjustment and activation of antioxidant defence [46,49,50,53].

Field evidence in rice has demonstrated that microbial consortia can maintain crop productivity while reducing fertilizer dependence and simultaneously improving soil biological activity, organic carbon and nutrient availability [46]. Although this study was designed primarily around nutrient management rather than DI, its findings demonstrate that microbial functioning can improve the biological and nutritional condition of the root environment in which drought responses occur.

Functional profiling studies further indicate that microbial inoculation can increase compatible solutes such as proline, glycine betaine, trehalose and soluble sugars and may help maintain turgor and WUE during water deficit [49]. Rhizosphere microbiome restructuring has likewise been associated with altered root architecture, phytohormone production, microbial signalling and improved stress resilience [50].

Endophytic microorganisms provide an internal signalling dimension. They can influence auxins, cytokinins, gibberellins, ethylene, ABA, salicylic acid and jasmonates while enhancing root depth, root branching, antioxidant activity and WUE during drought [53].

These observations support an expanded model of DI acclimation in which hydraulic and hormonal responses of the plant are influenced by the biological state of both the rhizosphere and internal tissues.

5. Molecular Reprogramming during Water Deficit and Recovery

5.1 ABA-Dependent and ABA-Independent Transcription

Water deficit rapidly modifies gene expression in roots and shoots [19–22]. In ABA-dependent pathways, SnRK2 kinases activate AREB/ABF transcription factors,

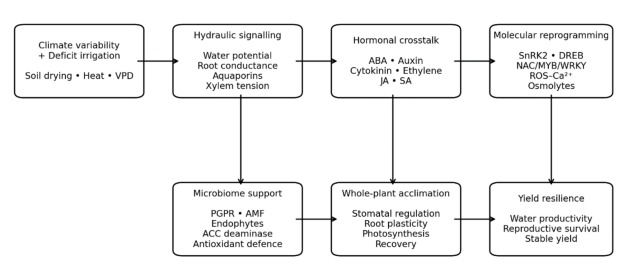


Figure 1. Integrated pathways of crop acclimation to deficit irrigation under climate variability. The figure integrates climate variability and deficit irrigation with hydraulic signalling, hormonal crosstalk, molecular reprogramming, microbiome-assisted responses, whole-plant acclimation and final yield resilience.

which bind ABA-responsive elements and induce protective genes [15,16,19,21].

ABA-independent pathways involve dehydration-responsive element binding proteins such as DREB2 [16,19,21]. NAC, MYB and WRKY transcription-factor families further integrate drought signalling with growth regulation, antioxidant metabolism and senescence [19–22].

Downstream products include late-embryogenesis-abundant proteins, dehydrins, heat-shock proteins, osmolyte-biosynthesis enzymes and antioxidant systems [19–24,33,34].

Under simultaneous heat and drought, transcriptional responses can differ from those activated by either stress independently, emphasizing the need to investigate combined-stress molecular networks rather than extrapolating from isolated drought responses [47].

5.2 Calcium and ROS Signalling

Calcium and ROS are not simply products of injury; at controlled concentrations both function as second messengers [14,23,24]. Water-deficit perception generates tissue-specific Ca^{2+} signatures and ROS signals that interact with ABA signalling and protein phosphorylation.

Guard-cell ROS contributes to ABA-induced stomatal closure, whereas systemic ROS- Ca^{2+} communication helps transmit stress information between tissues [14,23,24]. Productive acclimation requires a balance between signalling ROS and antioxidant detoxification.

This balance becomes particularly important under combined heat and drought because simultaneous stress can strongly increase ROS accumulation and overwhelm antioxidant defence, resulting in damage to lipids, proteins and nucleic acids [47].

Beneficial microorganisms can modify this balance by stimulating antioxidant enzymes and redox-regulatory

Table 1. Major physiological and biological pathways controlling crop acclimation to deficit irrigation

Acclimation component	Major signals/processes	Principal crop response	Relevance to yield resilience	Key references
Hydraulic regulation	Soil–root water potential, xylem tension, root hydraulic conductance, aquaporins	Rapid adjustment of plant water transport and stomatal behaviour	Prevents excessive dehydration while regulating seasonal water use	[9,10,25,26]
ABA-mediated signalling	PYR/PYL–PP2C–SnRK2 pathway, guard-cell ion regulation	Stomatal closure, water conservation and activation of drought-responsive genes	Conserves water but excessive activation may restrict carbon assimilation	[13–17]
Hormonal crosstalk	Auxin, cytokinin, ethylene, jasmonates, salicylic acid	Root-system plasticity, senescence regulation and stress adaptation	Balances root development, shoot growth and reproductive survival	[18,22,53]
ROS–Ca ²⁺ signalling	Reactive oxygen species, calcium signatures, antioxidant defence	Signal transmission, stomatal control and cellular protection	Distinguishes productive acclimation from oxidative damage	[14,23,24,47]
Molecular reprogramming	AREB/ABF, DREB, NAC, MYB, WRKY, osmolytes and stress proteins	Transcriptional, metabolic and cellular adjustment	Improves tolerance, recovery and maintenance of physiological function	[19–24]
Rhizosphere microbiome	PGPR, AMF, microbial hormones, nutrient mobilization	Improved root architecture, nutrient availability and osmotic adjustment	Supports crop function under water and nutrient limitation	[46,49,50,52]
Endophytic microbiome	ACC deaminase, auxin production, redox regulation, defence priming	Improved rooting, photosynthesis, antioxidant activity and WUE	Strengthens acclimation under drought and interacting stresses	[53]

processes [49,53]. Thus, the oxidative status of a DI-treated crop reflects interactions among stress intensity, temperature, endogenous antioxidant capacity and microbiome-assisted protection.

5.3 Omics and Epigenetic Regulation

Transcriptomics, proteomics and metabolomics have expanded drought biology from individual genes to regulatory networks [14,19–24]. Drought-responsive networks commonly involve photosynthesis, carbohydrate metabolism, amino-acid metabolism, lipid remodelling, cell-wall processes and defence pathways.

Small RNAs, alternative splicing, DNA methylation and histone modifications provide additional levels of control. However, translation from severe laboratory dehydration to moderate and fluctuating field DI remains a major challenge.

Multi-omics approaches are also transforming understanding of plant–microbe interactions. Functional profiling and microbiome restructuring studies have emphasized the value of metagenomics, transcriptomics and metabolomics for identifying microbial functions associated with plant stress tolerance [49,50].

Metagenomic analysis using 16S rRNA and shotgun sequencing can characterize microbial diversity and functional potential, while regenerative management has been associated with higher microbial diversity, nutrient-cycling capacity and ecological resilience [52]. Integrating host transcriptomics with rhizosphere

metagenomics and metabolomics could therefore reveal how DI simultaneously reprograms the plant and its associated microbiome.

5.4 Stress Memory, Microbiome Memory and Recovery

Repeated mild water deficits may alter the speed and magnitude of subsequent responses through physiological and molecular stress memory. Such memory can involve transcriptional priming, chromatin modifications, persistent metabolites, antioxidant status and altered hydraulic behaviour [19–24].

An additional possibility is that repeated irrigation cycles alter rhizosphere community structure, root exudation and endophytic colonization. Because microbial communities respond to soil moisture, crop genotype and management intensity [50,52], part of the apparent acclimation of repeatedly stressed plants may involve persistent changes in plant–microbiome interactions.

This hypothesis remains insufficiently tested under field DI and represents an important research frontier.

6. From Acclimation to Yield Resilience

Yield resilience is the capacity to maintain economically useful production despite temporal variation in water supply [6–8]. It emerges from integration of water capture, transpiration regulation, carbon assimilation,

nutrient status, phenology, reproductive stability and post-stress recovery [6–8,27,28].

A trait that improves plant survival does not necessarily improve crop yield [27,28]. Strong stomatal closure may increase intrinsic WUE while reducing biomass production if maintained excessively [27,28,31]. Similarly, extensive root systems are useful only when water remains available at depth [10–12].

Phenological timing is one of the strongest determinants of DI response [1,2,40]. Vegetative-stage deficits can reduce leaf area and tillering but may conserve water for reproductive growth. Water deficits around flowering are especially damaging because pollen development, fertilization and early seed set are sensitive to dehydration and temperature [33–35,47].

Combined heat and drought can intensify reproductive injury. Heat impairs pollen viability and fertilization, while drought restricts assimilate supply; during grain filling, heat accelerates development and drought restricts assimilate translocation, resulting in reductions in grain number and grain weight [47].

Meta-analyses reinforce this conditional response. DI generally improves WUE while reducing yield relative to full irrigation [3–5]. Therefore, irrigation recommendations should be treated as environmentally dependent management ranges rather than fixed prescriptions.

7. Crop-Specific Patterns and Genotype × Environment × Management Interactions

Cereals demonstrate the importance of seasonal water allocation. In wheat, conserving soil water for anthesis and grain filling can maintain productivity during terminal drought [3,6,13]. In maize, reproductive stages surrounding tasselling, silking and early kernel establishment are especially sensitive to drought and heat [34,35,44,47].

Rice differs because conventional flooded production has a high irrigation requirement. Controlled soil drying and water-saving irrigation can reduce water demand, but water stress during panicle initiation and flowering requires careful management [1,2].

Legumes combine drought responses with sensitivity of nodulation and biological nitrogen fixation [36]. Water deficit can restrict nodule activity before severe shoot symptoms become apparent.

Horticultural crops provide opportunities for regulated DI because moderate water limitation can modify quality as well as yield [1,37]. However, responses are highly dependent on crop developmental stage, genotype and concurrent environmental conditions.

Field evidence from tomato demonstrates the broader importance of genotype × environment × management interactions. Different combinations of transplanting window and genotype produced marked differences in disease incidence and yield under changing temperature, rainfall and humidity conditions [56]. The highest-yielding combinations occurred within favourable planting windows, whereas very early or late establishment increased exposure to disease-conducive environments. Although this experiment addressed disease rather than DI, it illustrates an important principle relevant to irrigation acclimation: genotype performance is conditional on the environmental window in which management is imposed.

Therefore, breeding for DI resilience should evaluate genotypes across contrasting irrigation timing, atmospheric demand and phenological stages rather than under a single standardized drought treatment.

8. Climate Variability Changes the Meaning of a Moderate Deficit

Climate variability modifies crop water stress through simultaneous effects on soil-water supply and atmospheric demand [6,7,34,35,42,47].

VPD can rise rapidly during hot and dry atmospheric conditions, strengthening the hydraulic gradient from leaves to the atmosphere. Consequently, a soil-moisture threshold that is safe under moderate VPD may become damaging during a heat wave [6–8].

High temperature increases respiratory losses, accelerates phenological development, destabilizes reproductive processes and interacts with drought to intensify oxidative stress and premature senescence [35,47]. Combined stress can shorten canopy duration and grain-filling periods, producing yield losses greater than those associated with either stress in isolation [47].

Rainfall variability creates the opposite management problem. Unexpected rainfall can remove an intended acclimation signal, whereas a missed rainfall event can convert moderate DI into severe stress.

The tomato sowing-window study further demonstrates how changing environmental exposure can strongly alter biological outcomes even within the same crop and geographical region [56]. This reinforces the need for DI recommendations to be dynamically linked to weather rather than based solely on fixed seasonal schedules.

9. Integrating Physiology with Precision Irrigation and Decision-Support Systems

A biologically informed irrigation system should increasingly treat the plant as a sensor rather than relying exclusively on soil-water content [29,30]. The most useful decision variable is likely to combine soil-water status, atmospheric demand and crop physiological response.

Decision-support systems provide a practical framework for this integration. Climate-responsive DSS can combine weather data, soil properties, crop models and management information to generate site-specific recommendations for irrigation, sowing, nutrient management and risk reduction [48]. Modern DSS increasingly incorporate artificial intelligence, remote sensing, IoT sensors and predictive analytics, allowing recommendations to respond dynamically to changing field conditions [48].

Soil-moisture sensors can provide continuous information on root-zone water availability, while automated systems can use these data to trigger irrigation when crop-specific thresholds are reached [48]. When combined with canopy temperature, leaf water potential, thermal imaging or crop models, such systems could distinguish a useful acclimation-level deficit from damaging stress.

9.1 Multispectral Imaging, Machine Learning and Plant-Stress Phenotyping

Multispectral and hyperspectral sensing combined with machine-learning algorithms provide additional opportunities for high-throughput crop monitoring. Although these technologies have been extensively developed for disease detection, the physiological variables detected by spectral imaging include changes in chlorophyll, photosynthesis, tissue water status, pigments and cellular integrity [51].

Multispectral imaging offers rapid, non-destructive field assessment, while UAV-based platforms can extend measurements over large areas [51]. Machine-learning approaches such as support-vector machines, random forests, convolutional neural networks and vision transformers can identify complex spectral patterns and classify plant stress conditions [51].

For DI research, these approaches could be adapted to distinguish water-deficit signatures from heat, nutrient or disease stresses by integrating multispectral, thermal, weather and soil-sensor information. The objective should not merely be stress detection but identification of the transition from reversible acclimation to yield-threatening dehydration.

9.2 Toward Integrated Smart Irrigation

The integration of remote sensing, AI, IoT, big data and crop models within DSS can provide real-time monitoring and predictive irrigation recommendations [48]. Machine-learning systems may help identify nonlinear relationships among VPD, soil moisture, canopy temperature and crop response, whereas physiological models can constrain predictions within biologically meaningful limits.

Such hybrid systems are particularly attractive under climate variability because they can update irrigation decisions when heat waves, rainfall or unexpected crop responses alter the severity of an intended deficit.

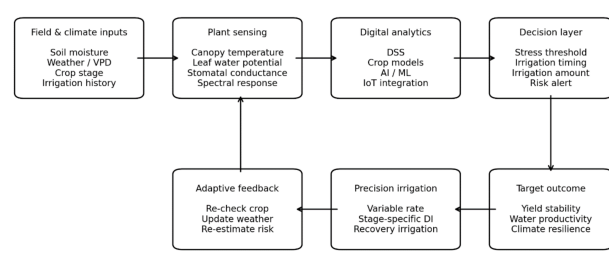


Figure 2. Climate-responsive precision irrigation decision framework. The figure links field and climatic observations with plant sensing, DSS, crop models, AI/ML, adaptive feedback and precision irrigation decisions directed toward yield stability and improved water productivity.

10. Translating Deficit-Irrigation Research to Farmers' Fields

Physiological optimization alone does not guarantee successful field adoption. Technologies that perform well experimentally may produce yield gaps under farmers' conditions because of incomplete adoption, input constraints, knowledge gaps and climatic heterogeneity.

Field studies in banana in northern Tripura provide a useful example. Integrated nutrient management combining organic inputs, biofertilizers and reduced mineral fertilizer substantially improved yield relative to farmers' practice and demonstrated measurable technology and extension gaps [54]. The study also showed substantial farmer adoption following front-line demonstrations, illustrating how visible field performance and technical support can accelerate uptake of resource-efficient practices [54].

Although nutrient management and DI are different technologies, the implementation lesson is directly relevant: water-saving irrigation will require farmer-accessible thresholds, demonstrations, advisory support and evidence of yield and profitability under local conditions.

Table 2. Plant, soil, climatic and digital indicators for climate-responsive deficit irrigation

Monitoring domain	Representative indicator	Information provided	Potential irrigation decision	Key references
Soil	Soil moisture, matric potential, root-zone water storage	Available water and depletion rate	Determine onset and intensity of DI	[29,30,41,48]
Atmosphere	Temperature, rainfall, relative humidity, VPD	Atmospheric evaporative demand and climatic risk	Modify DI during heat waves or rainfall events	[35,42,47]
Plant hydraulics	Leaf/stem water potential, sap flow	Actual physiological water status	Detect transition from acclimation to damaging dehydration	[9,29,30]
Canopy response	Canopy temperature, stomatal conductance	Transpiration restriction and plant stress	Trigger recovery irrigation	[13,29,30]
Spectral sensing	Multispectral/hyperspectral reflectance	Chlorophyll, tissue water and physiological changes	Spatial identification of stressed zones	[51]
Remote sensing/UAV	Thermal and multispectral field imagery	Field-scale stress variability	Variable-rate irrigation and targeted monitoring	[48,51]
DSS and crop models	Soil-weather-crop integration	Forecast crop water requirements and risk	Stage-specific and climate-responsive scheduling	[48]
AI/ML	Pattern recognition and nonlinear prediction	Integrates complex sensor and environmental data	Adaptive prediction of irrigation need	[48,51]

Similar evidence from commercial marigold cultivation showed that recommended technology was agronomically feasible, but significant extension gaps persisted because farmers adopted some practices more readily than others [55]. Extension contact, training, market access and input availability influenced the realized performance of the technology [55].

These findings suggest that DI research should move beyond physiological water productivity and explicitly quantify adoption feasibility, irrigation infrastructure requirements, labour demand, risk perception, economic return and extension gaps. A technically optimal DI schedule that farmers cannot reliably implement will contribute little to climate resilience.

11. Research Gaps and Future Priorities

First, DI experiments require greater physiological standardization. Reporting only the percentage of full irrigation is insufficient [1–5]. Studies should document soil texture, rooting depth, soil and plant water potential, VPD, crop stage, irrigation frequency, stress duration and recovery.

Second, future experiments should incorporate combined heat-drought scenarios. Crop responses to simultaneous stresses cannot always be predicted from individual-stress experiments because combined stress produces distinct physiological, hormonal and molecular responses [47].

Third, the field relevance of molecular markers needs improvement. Candidate genes identified under

severe laboratory dehydration should be tested under moderate, fluctuating and repeated field deficits [6,7,14,19–24].

Fourth, research should progress from single-hormone models toward integrated plant-microbiome hormonal networks. ABA remains central, but auxin, cytokinins, ethylene and other hormones interact with microbial hormone production and ACC-deaminase activity [49,50,53].

Fifth, rhizosphere and endophytic microbiomes should be incorporated explicitly into DI studies. Microbiome-assisted production, functional microbial profiling, rhizosphere restructuring and endophytic inoculation collectively suggest possible contributions to nutrient acquisition, root architecture, osmotic regulation, antioxidant capacity and WUE [46,49,50,53]. Metagenomics provides a route for determining how repeated drying and rewetting restructure these communities [52].

Sixth, crop multi-omics should be integrated with microbiome multi-omics. Combining plant transcriptomics, metabolomics and hormone profiling with metagenomic or metatranscriptomic characterization of roots and rhizosphere could reveal the biological networks that distinguish useful acclimation from irreversible damage [49,50,52,53].

Seventh, high-throughput phenotyping and digital monitoring should be integrated with DI. DSS platforms can combine soil, weather, crop and management data [48], while multispectral and machine-learning approaches can provide non-destructive spatial

information about crop physiological condition [51].

Eighth, breeding programmes should emphasize dynamic rather than constitutive traits. Responsive stomata, effective root hydraulics, appropriate rooting depth, reproductive stability, osmotic adjustment and rapid recovery are more promising than permanently conservative growth [6–13,25,26].

Ninth, genotype $\times$ environment $\times$ management interactions require more explicit evaluation. Evidence from tomato shows that genotype performance and yield can change strongly with sowing window and environmental exposure [56]. Comparable factorial designs should be used for genotype $\times$ irrigation timing $\times$ climatic environment.

Finally, adoption and economic analysis should be integrated into irrigation research. Field technology studies in banana and marigold demonstrate that demonstration, extension contact, local adaptability and partial adoption strongly influence the gap between experimental and farmer-level productivity [54,55]. Future DI research should therefore evaluate not only physiological efficiency but also practical feasibility and farmer adoption.

12. Conclusion

Deficit irrigation is most effective when understood as a managed acclimation process rather than simply a reduction in irrigation volume [1–5]. The earliest response to soil drying is hydraulic: altered soil–root conductance, xylem tension and aquaporin regulation change water transport and initiate root-to-shoot communication [9,10,25,26].

Hormonal networks, particularly ABA and its interactions with auxin, cytokinins and ethylene, translate these signals into stomatal, growth and developmental responses [13–18]. Beneficial rhizosphere and endophytic microorganisms can further modify these networks through hormone production, ACC-deaminase activity, altered root architecture, osmotic adjustment, nutrient acquisition and antioxidant defence [46,49,50,53].

Molecular reprogramming reinforces acclimation through ABA-dependent and independent transcription, ROS–Ca²⁺ signalling, osmotic regulation, protein protection and metabolic redistribution [19–24]. Metagenomics and other multi-omics approaches provide opportunities to extend this framework from the plant genome to the plant–microbiome system [49,50,52].

The yield consequences remain conditional. Moderate and well-timed deficits can reduce non-essential wa-

ter use, improve water productivity and conserve soil moisture for critical reproductive stages [1–5]. Severe, prolonged or poorly timed deficits restrict carbon assimilation and reproductive development, and these effects can become substantially more damaging when drought coincides with heat [47].

Climate variability therefore makes fixed irrigation thresholds increasingly unreliable. DSS, real-time sensors, remote sensing and machine-learning approaches can help integrate atmospheric, soil and crop information into adaptive irrigation decisions [48,51].

At the same time, farmer-level evidence demonstrates that technological effectiveness alone does not ensure adoption. Demonstration, extension support, local adaptability and economic feasibility determine whether improved management is translated into stable productivity [54,55].

The next generation of DI should consequently integrate plant hydraulics, hormonal biology, molecular reprogramming, microbiome ecology, climate monitoring, artificial intelligence and farmer-centred management. Such integration can identify when a crop is productively acclimating, when stress is approaching irreversible yield loss, and when irrigation will provide the greatest physiological and economic benefit. This transition from fixed volume-based irrigation toward dynamic response-based management offers a promising pathway for stabilizing crop yield and water productivity under increasingly variable climates.

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