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Comprehensive Response Mechanisms of Plants to Water Deficit: A Physiological, Biochemical, Molecular, and Ecological Review

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Abstract This study provides a comprehensive insight about complex response mechanisms that plants cope with water deficit conditions in the field, involving physiological, biochemical, molecular, and ecological adaptations changes that finally plants can survive and persistence under drought stress. Key adaptive changes are plants activate a range of natural defense systems to mitigate the adverse effects of drought. These changes in cellular osmotic potential, water potential, and the activation of antioxidant enzymes and osmolytes such as proline, glycine betaine, and soluble sugars. Phytohormones like abscisic acid, jasmonates, and salicylic acid play crucial roles in modulating plant responses to water stress through complex signaling networks. Additionally, plants exhibit morphological changes such as increased root growth and alterations in leaf anatomy to enhance water uptake and reduce water loss. Molecular insight of plants response to drought stress is stress-responsive genes that contribute to cellular protection and metabolic adjustments. In this paper, the multifaceted nature of plant responses to water deficit are described, and the importance of integrated physiological, biochemical, and molecular mechanisms are listed, respectively. Understanding these complex interactions is essential for developing strategies to improve crop resilience and productivity in water-limited environments.
Keywords Water deficit; Drought stress; Plant physiology; Biochemical responses; Molecular mechanisms; Ecological adaptations

1 Introduction

Water deficit, commonly referred to as drought stress, is a condition where water availability is significantly below the optimal level required for plant growth and development. Water deficit condition is one of the most important factors restricting agricultural productions, which seriously affects crop yield (Khan et al., 2013). Moreover, as one of the main restraining factors in the process of plant growth, water deficit can hinder plant respiration, stomatal movement and photosynthesis (Yang et al., 2021), thus reduced plant growth, altered phenology, and impaired photosynthesis and respiration (Farooq et al., 2009; Kaur et al., 2021). The severity and duration of water deficit can vary, influencing the extent of its impact on plant systems (Bray, 1997). Summarize the mechanisms by which plants respond to water deficit is crucial for developing strategies to mitigate its adverse effects (Mullet and Whitsitt, 1996).

Water deficit has profound implications for agriculture and ecosystems. In agriculture, drought stress is a leading factors for crop yield reduction worldwide, and aggravates like heat, salinity and pathogen attack which cause damage of plants (Ahluwalia et al., 2021; Kaur et al., 2021). The impact of water deficit is expected to intensify with climate change, affecting more agricultural lands and leading to prolonged periods of drought (Kaur et al., 2021). This stress not only limits crop productivity but also affects the quality of produce, posing a significant challenge to food security (Yang et al., 2021). In natural ecosystems, water deficit can alter plant community structures, reduce biodiversity, and disrupt plant-pollinator interactions, threaten ecosystem sustainability, thereby affecting ecosystem services (Kuppler and Kotowska, 2021). The anatomical and physiological changes induced by drought stress in plants, such as reduced leaf size and altered root morphology, further highlight the need for comprehensive studies on plant responses to water deficit (Shao et al., 2008; 2009). Studying the response mechanisms of plants to water deficit is essential for several reasons. Firstly, it provides insights into the physiological, biochemical, and molecular adaptations that enable plants to survive and thrive under drought conditions (Mullet and Whitsitt, 1996; Farooq et al., 2009; Yang et al., 2021). These adaptations include stomatal closure, morphological and structural changes, synthesis of hormones, osmotic regulatory substances and expression of drought-resistant genes to alleviate drought stress (Bray, 1997; Kaur et al., 2021). Secondly, understanding these mechanisms can inform the development of drought-resistant crop varieties through breeding and genetic engineering, thereby enhancing agricultural resilience to climate change (Chaves, 2004). Additionally, knowledge of plant responses to water deficit can guide the implementation of sustainable agricultural practices and water management strategies, ensuring efficient use of water resources (Shao et al., 2009). Ultimately, such studies contribute to the broader goal of maintaining ecosystem stability and productivity in the face of increasing water scarcity.

By integrating physiological, biochemical, molecular, and ecological perspectives, this review aims to provide a comprehensive understanding of plant responses to water deficit, highlight the importance of interdisciplinary approaches in addressing this critical environmental challenge.

2 Physiological Adaptation Mechanisms

2.1 Stomatal regulation and transpiration

Stomatal regulation, such as increase stomatal length, stomatal width, stomatal density, and stomatal opening is a critical physiological adaptation mechanism that plants employ to manage water loss and maintain water use efficiency (WUE) under water deficit conditions. Stomata are microscopic pores on the leaf surface that control gas exchange, including the uptake of CO_2 for photosynthesis and the release of water vapor through transpiration. Under drought conditions, plants often close their stomata to reduce water loss, which can also limit CO_2 uptake and affect photosynthesis (Buckley, 2019; Kaur et al., 2021; Lobato et al., 2021).

The plant hormone of abscisic acid (ABA) is a crucial signal molecule in stomatal closure. ABA is synthesized in response to water deficit and signals the guard cells to close the stomata, thereby reducing transpiration rates (Giorio et al., 2018; Kaur et al., 2021; Yari Kamrani et al., 2022). This response is part of a complex signaling network that includes secondary messengers and mitogen-activated protein kinases, which help in the rapid adjustment of stomatal aperture (Kaur et al., 2021; Lawson and Vialet-Chabrand, 2019). Additionally, circadian clocks regulate the diurnal opening and closing of stomata, optimizing WUE day-night (Yari Kamrani et al., 2022).

2.2 Water transport and root structure adjustment

Water transport within the plant and adjustments in root structure are essential for maintaining water uptake during periods of water deficit. The morphological changes of plant roots to enhance water absorption from deeper soil layers. Root system configurations involve root length and root density, root hair, root branches can significantly affect the water deficiency of plants (Gupta et al., 2020; Wu et al., 2022).

Hydraulic conductance within the plant, particularly in the roots and leaves, is also adjusted to optimize water transport. This involves changes in the expression of aquaporins, which are water channel proteins that facilitate water movement across cell membranes (Kaur et al., 2021). The root, stems, leaves system have ability to produce aerenchyma, a tissue with air spaces, helps in maintaining oxygen supply from the stem to the root in plants under waterlogged conditions, which can also be beneficial during drought stress by improving root function and water uptake (Sou et al., 2021; Wu et al., 2022).

2.3 Leaf morphology changes and water conservation strategies

Leaf morphology changes are another crucial adaptation mechanism that helps plants conserve water. Under water deficit conditions, plants may exhibit leaf wilting, crimping, and reduce leaf number and area to minimize water loss through transpiration (Lobato et al., 2021; Wu et al., 2022). These morphological changes are often accompanied by alterations in leaf anatomy, such as a reduction in leaf angle and size, stomatal position, deposition of the cuticle and epidermal thickness, which further contribute to water conservation on the leaf surface (Yavas et al; 2023).

Paraheliotropism, the movement of leaves to minimize direct sunlight exposure, is another strategy employed by some plants to reduce water loss. This mechanism can decrease leaf temperature and reduce transpiration rates, thereby conserving water (Lobato et al., 2020). Additionally, the accumulation of osmolytes, such as proline, helps in maintaining cell turgor and protecting cellular structures during dehydration (Giorio et al., 2018).

In summary, plants employ a range of physiological adaptation mechanisms, including stomatal regulation, root structure adjustments, and leaf morphology changes to cope with water deficit conditions (Wahab et al., 2022) (Figure 1). These strategies are crucial for maintaining water balance, optimizing WUE, and ensuring plant survival under drought stress.

3 Biochemical Regulation Mechanisms

3.1 Accumulation of osmoprotectants (e.g., proline, sugars)

Plants under water deficit conditions often accumulate osmoprotectants such as amino acid compounds (proline), amine compounds (glycine betaine and polyamines), soluble sugars, and trehalose, mannitol, and other compounds, play a major role in maintain cellular osmotic balance and protect cellular structures. For instance, in *Moringa oleifera*, proline content increased significantly with the severity of moisture stress, particularly in the leaves under severe stress conditions (Chitiyo et al., 2021). Similarly, in *Scrophularia striata*, soluble sugars like glucose, mannose, rhamnose, and xylose were found to accumulate under osmotic stress, serving as compatible solutes and aiding in the production of phenolic compounds (Falahi et al., 2018). Additionally, *Quercus robur* and *Q cerris* seedlings showed species-specific accumulation of osmoprotectants, with *Q. robur* primarily accumulating glycine betaine and *Q. cerris* accumulating dimethylsulphoniopropionate (DMSP) under water deficit conditions (Kebert et al., 2022).

3.2 Activation of antioxidant systems and free radical scavenging

Water deficit conditions lead to the overproduction of reactive oxygen species (ROS), causing oxidative stress in plants. To mitigate this, plants activate antioxidant systems, including both enzymatic and non-enzymatic antioxidants. For example, in *Isatis indigotica*, activities of antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) increased significantly under moderate and severe water deficits (Zhou et al., 2023). Similarly, the tea plants (*Camellia sinensis*), tolerant genotypes exhibited higher activities and expression levels of antioxidative enzymes, including superoxide dismutase (SOD), ascorbate peroxidase (APX), peroxidase (POX) and catalase (CAT), which helped in reducing oxidative damage compared to susceptible cultivars (Nalina et al., 2021). Furthermore, in *Moringa oleifera*, antioxidant activity increased with drought progression, indicating a robust defense mechanism against oxidative stress (Chitiyo et al., 2021).

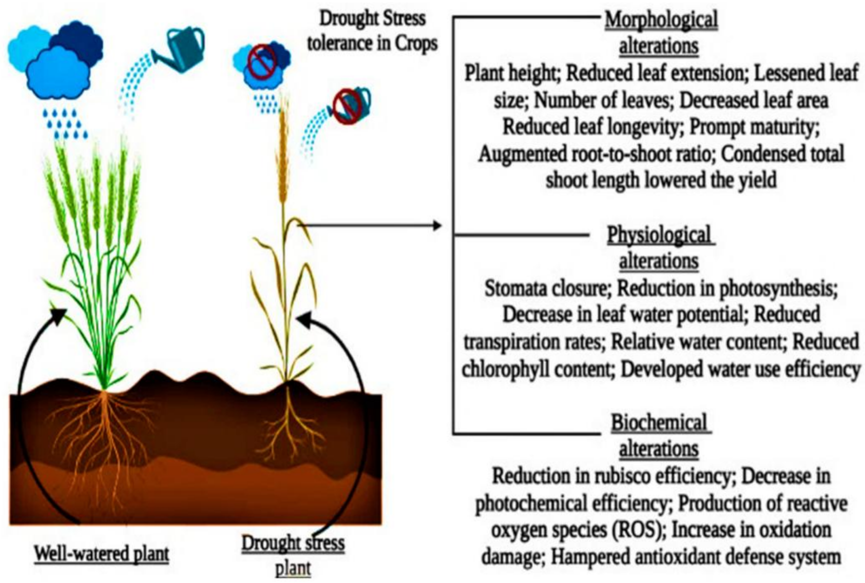

Figure 1 Drought stress impacts plants' morphological, physiological, and biochemical processes (Adopted from Wahab et al., 2022)

3.3 Hormonal regulation (e.g., ABA) in water stress

Hormonal regulation plays a crucial role in plant responses to drought stress, with ABA being a key hormone involved in this process. ABA can regulate various physiological processes by its negative and positive crosstalk with phytohormones in response to drought conditions. In pennyroyal (*Mentha pulegium* L.), ABA content is highest in the plants, inoculated with plant growth-promoting rhizobacteria (PGPR) under severe drought stress (Asghari et al., 2020). Additionally, ABA, interacts with other hormones like jasmonates (JA), salicylic acid (SA), and ethylene (ET), modulates developmental processes and signaling networks that contribute to plant defense against water stress (Wahab et al., 2022). In *Quercus* species, hormonal changes were observed under water deficit conditions, with *Q. cerris* showing a higher antioxidant capacity and hormonal modulation compared to *Q. robur* (Kebert et al., 2022; Sobrino-Plataen et al., 2024).

By understanding these biochemical regulation mechanisms, researchers can formulate the strategies to improve plant resilience and in water deficit stress response, ensure sustainable agricultural productivity under changing climatic conditions.

4 Molecular Response Mechanisms

4.1 Gene expression and regulatory networks related to water deficit

Plants respond to water deficit through complex gene expression and regulatory networks. Key transcription factors (TFs) and genes are activated in drought stress response. For instance, overexpression of 9-cis-epoxycarotenoid dioxygenase (NCED) and acetaldehyde dehydrogenase (ALDH) enhances drought resistance by increasing ABA biosynthesis, which are crucial TFs for stress response. Additionally, genes such as *EgrNCED3*, *EgrPYR1*, and *EgrDREB2.5* are upregulated in drought-tolerant clones of Eucalyptus, indicating their role in ABA-dependent and independent pathways (Martins et al., 2018). The regulatory networks also involve TFs such as DREBs and AREBs, which mediate stress-responsive gene expression to enhance drought resistance (Takahashi et al., 2020).

4.2 Activation of signaling pathways (e.g., ABA signaling)

ABA signaling is a central pathway in plant response to water deficit. ABA is synthesized mainly in leaves upon receiving drought signals from roots and regulates various physiological and molecular responses, including stomatal closure to reduce water loss (Takahashi et al., 2018; 2020). The ABA signaling pathway involves several protein kinases such as SnRK2s and MAPKs, which detect ABA influx in guard cells and mediate stomatal closure (Takahashi et al., 2018). Furthermore, the SAPK9-OsMADS23-OsAOC pathway in rice modulates ABA and JA biosynthesis, influence drought tolerance (Lv et al., 2022). The circadian clock system also plays important role in regulating ABA production and signaling, thereby influences stomatal responses and water-use efficiency (Yari Kamrani et al., 2022).

4.3 Roles of proteomics and metabolomics in water deficit response

Proteomics and metabolomics provide advanced insights into the biochemical changes in plants under water deficit. Xiong et al. (2019) identification and analysis differential metabolites and differentially expressed proteins functions of rice spikes indicate that the drought mainly promoted carbohydrate metabolic process, carbon fixation in photosynthetic organism pathway, the energy metabolism pathway, and ROS metabolic process functions. The dynamic regulatory networks in wheat roots, characterized through transcriptomics and proteomics, highlight the involvement of various biosynthetic pathways and protein-protein interactions in drought tolerance (Rahimi et al., 2021). These studies underscore the importance of integrating proteomic and metabolomic data to understand the comprehensive response mechanisms of plants to water deficit.

5 Ecological Adaptation and Evolution

5.1 Changes in plant community structure and species diversity

Water deficit significantly impacts plant community structure and species diversity. Studies have shown that drought conditions lead to a shift in species composition, favoring drought-tolerant species over those less adapted to water scarcity. For instance, a meta-analysis revealed that water stress inhibits plant growth and photosynthesis but increases ROS and antioxidant activities, which are crucial for plant survival under drought conditions (Sun et al., 2020). Variations in leaf water content (LWC) among different plant communities indicate that species in arid environments have evolved higher LWC to cope with water scarcity, thereby altering community structure (Wang et al., 2021). These adaptations result in more homogeneous community structure dominated by drought-resistant species, reducing overall species diversity.

5.2 Impact on ecosystem functions and services

Drought-induced changes in plant communities have profound effects on ecosystem functions and services. The reduction in plant growth and photosynthesis under water stress conditions can lead to decreased primary productivity, evapotranspiration (ETP), and WUE, affect the structure, composition and function of ecosystem (Sun et al., 2020). Moreover, alterations in floral traits due to water deficit can impact plant-pollinator interactions, potentially reducing pollination services and affecting plant reproduction and biodiversity (Kuppler and Kotowska, 2021). The modulation of CO_2 fertilization effects on plant gas exchange and water use efficiency under drought conditions further complicates the carbon-water cycle in terrestrial ecosystems, potentially altering ecosystem services such as carbon sequestration and water regulation (Li et al., 2021). Water deficit reduced plant growth over a season or permanently, local species reduction or extinction, freshwater ecosystems may change flow regimes (Sadiqi et al., 2022). These changes underscore the need for a comprehensive understanding that drought how to impacts ecosystem functions to develop effective conservation and management strategies.

5.3 Niche distribution and succession of drought-adapted plants

Drought conditions drive the niche distribution and succession of drought-adapted plants. Species with inherent drought tolerance mechanisms, such as increased root biomass allocation and enhanced antioxidant enzyme activities, are more likely to thrive and dominate in water-scarce environments (Nosalewicz et al., 2018; Luo et al., 2022). For example, other important morphophysiological strategies such as increased root growth, increased vascular bundles and density of *Lippia grata* improved the plant's ability to adapt to and survive in drought-prone areas under water deficit conditions (Palhares Neto et al., 2020). In addition, the different transcriptomic profiling of *Pinus pinaster* revealed that drought-tolerant genotypes exhibit pre-adapted stress-related gene expression, allowing individuals to better cope with water deficit (De María et al., 2020). These adaptive traits facilitate the establishment and succession of drought-tolerant species, leading to a shift in niche distribution and community dynamics over time.

6 Applications of Multi-omics in Water Deficit Research

6.1 Advances in genomics and transcriptomics

Genomics and transcriptomics have significantly advanced our understanding of plant responses to water deficit. For instance, a study on durum wheat utilized next-generation sequencing to provide a comprehensive description of the small RNAome, mRNA transcriptome, and degradome under water-deficit conditions. This study identified differentially expressed miRNAs and genes linked to processes such as hormone homeostasis, photosynthesis, and signaling, revealing key miRNA-mRNA regulatory pairs that play significant roles in stress adaptation (Liu et al., 2020) (Figure 2). Similarly, research on maize seedlings under water deficit stress highlighted the incongruence between protein and transcript levels, suggesting complex gene expression mechanisms in response to drought (Xin et al., 2018). These advance findings underscore the importance of integrating genomic and transcriptomic data to unravel the intricate regulatory networks involved in drought tolerance.

6.2 Latest discoveries in metabolomics and proteomics

Metabolomics and proteomics profiles were integrated to provide a systematic insight about the biochemical and physiological changes in plants under water deficit conditions. A study on proteomic analysis maize seedlings revealed that 104 proteins were differentially accumulated under water stress, with significant roles in photosynthesis, carbohydrate metabolism, stress defense, energy production, and protein metabolism (Xin et al., 2018). Another study on eastern cottonwood identified over 108 000 peptide sequences, providing a comprehensive view of the proteome changes in response to cyclic and prolonged water deficit, and highlighting the RD26 TF as a key drought marker (Abraham et al., 2018). Metabolomic studies have also shown that plants reconfigure their metabolic pathways to cope with water deficit, with specific metabolites substance, ferulic and cinnamic acids playing crucial roles in drought tolerance (Kravic et al., 2021). A study integrates metabolomic, transcriptomic, and gene co-expression network analysis confirmed that the key to adaptation to drought by millet was to enhance lignin metabolism, promote the metabolism of fatty acids to be transformed into cutin and wax, and improve ascorbic acid circulation (Cui et al., 2023). These present studies emphasize the potential of metabolomics and proteomics in identifying biochemical markers and understanding the metabolic adjustments in plants under drought stress.

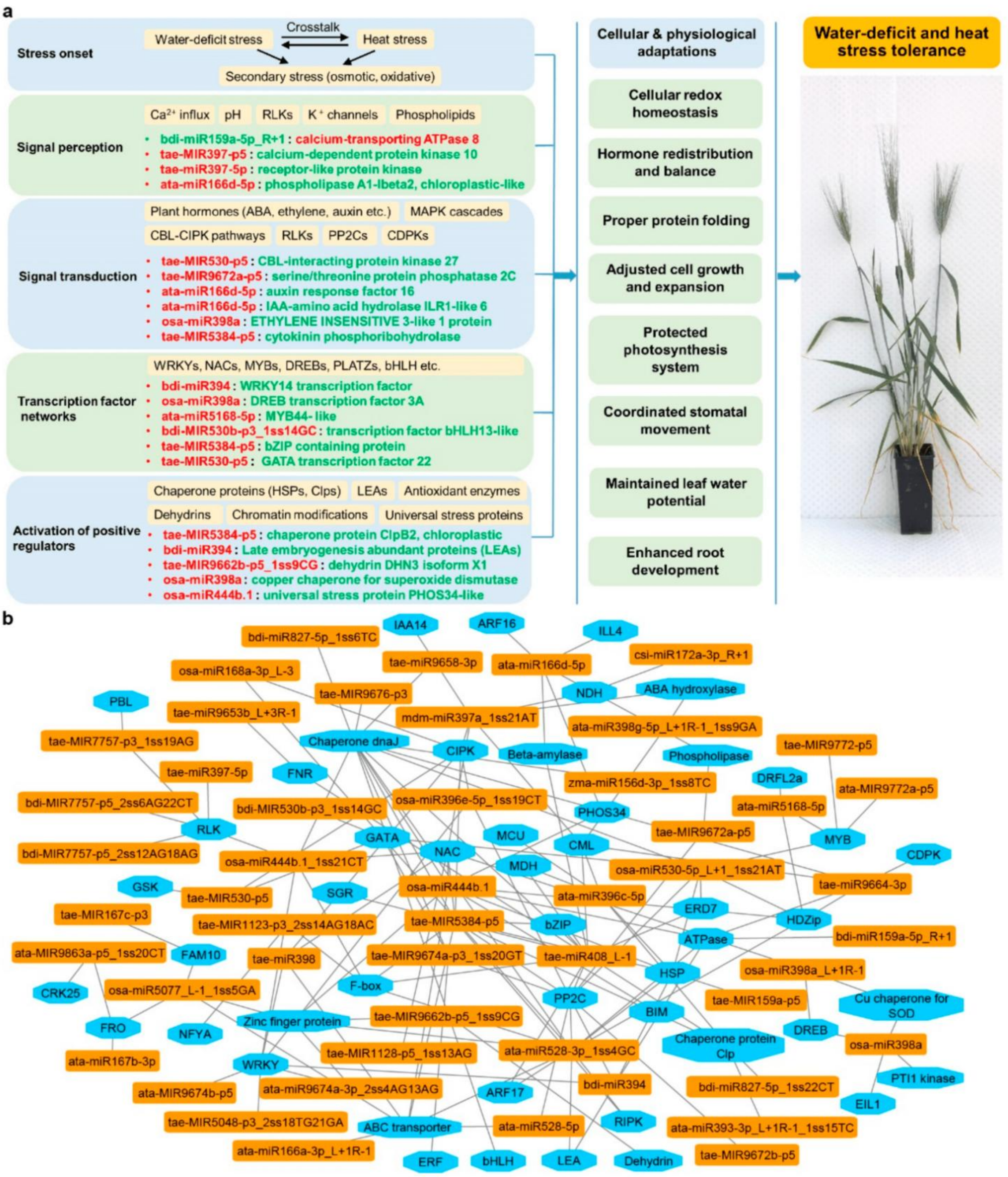

Figure 2 Water-deficit and heat stress response network mediated by key miRNA-RNA modules in durum wheat (Adopted from Liu et al., 2020)

Image caption: (a) Examples of key miRNA-mRNA modules involved in the stress response networks. miRNA or gene names highlighted in green represent up-regulation under water-deficit plus heat stress; miRNA or gene names highlighted in red represents up-regulation under water-deficit plus heat stress; (b) multiple-to-multiple regulatory connections between miRNAs (orange) and their targets (blue) (Adopted from Liu et al., 2020)

6.3 Data integration and systems biology analysis

The integration multi-omics data and systems biology approaches has opened new avenues for understanding the complex responses of plants to water deficit. A multi-omics integration (MOI) study on oil palm under drought stress combined transcriptomics, proteomics, and metabolomics data to reveal several pathways affected by water deficit, with cysteine and methionine metabolism being the most impacted (Leão et al., 2022). This comprehensive approach can identify candidate genes for engineering drought-resistant crops. Additionally, bioinformatics tools and computational models have been developed to manage and analyze multi-omics data, as demonstrated in a case study on maize nodal root growth under water deficit, which highlighted the power of integrated datasets in uncovering the landscape of drought responses (Wang et al., 2022). These integrative analyses are crucial for developing a holistic understanding of plant responses to water deficit and for identifying potential targets for genetic and agronomic interventions.

In summary, it is necessary to combine genomic, transcriptomic, proteomic, and metabolomic to clarify the water deficit reponse mechanism. The integration of these datasets through systems biology approaches is essential for unraveling the complex regulatory networks and metabolic pathways involved in drought tolerance, ultimately aiding in the development of drought-resistant crop varieties.

7 Applications and Future Research Directions

7.1 Molecular breeding strategies for drought-resistant crops

Molecular breeding strategies have emerged as a pivotal approach to developing drought-resistant crops. These strategies include marker-assisted selection (MAS), genomic selection (GS), and targeted gene editing, which have shown promise in enhancing drought tolerance in various crops (Ranjith and Srinivasa Rao, 2021; Ghadirnezhad Shiade et al., 2023a). The integration of multi-omics technologies has furthered our understanding of the complex genetic and molecular networks involved in drought response (Seleiman et al., 2021; Raza et al., 2023). For instance, the identification and manipulation of drought-responsive genes and TFs can breeding the crops with improved WUE and stress resilience (Kaur et al., 2021; Yang et al., 2021c). Additionally, use of the speed breeding platforms can accelerate the development of drought-smart cultivars, contributing to global food security (Raza et al., 2023).

7.2 Sustainable agriculture and water resource management

Sustainable agriculture practices and efficient water resource management are crucial for mitigating the adverse effects of drought on crop productivity. Agronomic strategies such as conservation tillage, crop rotation, and optimized plant density can increase soil moisture retention and reduce water loss (Ghadirnezhad Shiade et al., 2023b). The application of plant growth regulators and beneficial rhizobacteria has also been shown to improve crop drought tolerance by modulating physiological and biochemical process (Zhang et al., 2022). Moreover, the use of exogenous treatments like foliar sprays, seed priming, and the application of osmoprotectants can help plants cope with water deficit conditions (Seleiman et al., 2021). Integrating these practices with advanced irrigation techniques and precision agriculture can offer important practical guidance for sustainable and resilient agricultural systems (Wang et al., 2022).

7.3 Future research hotspots in water deficit response mechanisms

Future research should focus on unraveling the intricate mechanisms underlying plant responses to water deficit at the dynamic regulatory networks, epigenetic regulation, environmental interactions, and translational research (Marques and Hu, 2024).. Key areas include the temporal and spatial dynamics of regulatory networks and DNA methylation, histone modifications, and small RNA-mediated gene silencing, play pivotal roles in modulating plant responses (Yang et al., 2021a; 2021b; Kaya et al., 2024). Additionally, exploring the potential of advanced technologies such as CRISPR/Cas9 and bisulfite sequencing for precise genome editing and the drought memory in the plant (Kou et al., 2022; Raza et al., 2023). Understanding the cross-talk between different signaling pathways and the integration of multi-omics data and epigenetic markers will provide a comprehensive insight into plant responses to water deficit conditions, pave the way for innovative solutions to develop drought-tolerant crops in the face of climate change (Ranjith and Srinivasa Rao, 2021; Seleiman et al., 2021).

8 Concluding Remarks

As mentioned above, the comprehensive response mechanisms of plants to water deficit encompass a wide array of physiological, biochemical, molecular, and ecological adaptations. Physiologically, plants alter root architecture, close stomata, and adjust WUE to mitigate the effects of drought. Biochemically, the plant increases the production of ROS and activate antioxidant enzymes to combat oxidative stress. Molecularly, plants regulate the expression of drought-responsive genes and phytohormones such as ABA, which play crucial roles in signaling pathways that mediate stress responses. Ecologically, water deficit can lead to community rearrangement, resulting in changes to the dominant species, alterations in important ecosystem functions.

The importance of integrated multidisciplinary approaches in research cannot be overstated. Combining physiological, biochemical, molecular, and ecological perspectives provides a holistic understanding of plant responses to water deficit. This integrated approach allows for the identification of key regulatory mechanisms and the development of strategies to enhance drought tolerance in crops. For instance, understanding the role of phytohormones in drought response can lead to the engineering of hormone signaling pathways to improve plant resilience.

Looking forward, future research should focus on the application of advanced genetic and biotechnological tools to develop drought-resistant plant varieties. Additionally, there is a need for more field-based studies to validate laboratory findings and understand the plant performance under water deficit and ecosystem services. The integration the omics technologies, such as genomics, proteomics, and metabolomics, will further elucidate the complex networks involved in drought response and facilitate the development of comprehensive models to predict plant behavior under varying environmental conditions.

In conclusion, addressing the challenges posed by water deficit requires a concerted effort from multiple scientific disciplines. By leveraging the strengths of each field, we can develop innovative solutions to ensure sustainable agricultural practices and maintain healthy ecosystems to face with increasing water scarcity.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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