Review Article

A Comprehensive Analysis of Drought stress responses in Rice (*Oryza sativa* L.): Insights into Developmental stage variations from germination to grain

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ABSTRACT

Rice, a staple food crop, exhibits heightened sensitivity to drought conditions during three pivotal growth stages: the early seedling stage, the vegetative phase and the anthesis or reproductive stage and ripening stage. Enhancing drought resilience in rice is paramount for safeguarding food security and sustaining the livelihoods of countless rice consumers and cultivators across India and globally. Drought stress curtails water accessibility for the plant, precipitating alterations in a spectrum of morphological, physiological, biochemical and molecular characteristics. In response to drought stress across various developmental thresholds, rice plants activate intrinsic drought resistance strategies encompassing escape, avoidance, tolerance and recovery mechanisms. This review delves into the intricate responses of rice under drought stress throughout its life cycle, including seed germination, seedling growth, the vegetative stage, the reproductive stage and the grain ripening stage. The paper endeavors to furnish a thorough synthesis of extant knowledge, coupled with the challenges inherent in comprehending and augmenting the physiological adaptations of rice to drought stress. It also aims to provide a comprehensive overview of the current knowledge and challenges in understanding and enhancing the physiological responses of rice to drought stress.

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Keywords: *sensitivity, anthesis, resilience, drought resistance, vegetative*

1. INTRODUCTION

Rice, a ubiquitous staple food, provides vital nutrients like carbohydrates, thiamin, folate, calcium, iron, pantothenic acid and energy to 3.5 billion people worldwide, nearly 43% of world's population. Given the critical role of rice as an economic staple, its enhancement in both yield and quality is vital for sustaining the expanding human population and fulfilling the vast nutritional demands. In 2050, projections suggest that global warming will reduce irrigated rice production by 7% and rainfed rice yields by 6% (Sarma et al., 2023). Drought, as the most critical abiotic stressor, affects approximately 42 million hectares of rainfed lowland rice and 8 million hectares of upland rice in Asia (Shah et al., 2024). The economic losses due to water stress during critical stages like reproduction and grain filling can range from 48% - 94% and 60% respectively. Globally, drought-related losses in crop and livestock output amount to nearly USD 28 billion, with Asia bearing a substantial burden on rainfed lowland and upland rice areas (Lafitte et al., 2004).

Global Rice Production is estimated to be 516 million tons (milled basis), which is 1.6% less than the record high of 2021-22. Drought can reduce rice yield by up to 90% depending on the intensity, duration and crop growth stage (Kumar et al., 2018). Most recently, in 2022, several states like Uttar Pradesh, Bihar, Jharkhand, West Bengal, Rajasthan, Karnataka, Madhya Pradesh, Maharashtra were significantly affected by water scarcity, the sowing area of rice has declined in India by 12% compared to 2021 and Jharkhand, West Bengal, Bihar and Uttar Pradesh account for most of the reduction (Trent, 2021). Therefore, improving drought tolerance in rice is a key challenge for ensuring food security and livelihoods for millions of rice consumers and farmers in India and other parts of the world.

Rice, unlike other cereals, is a water-loving plant that is susceptible to drought stress (Panda et al., 2021). Drought stress significantly impacts plant morphology, altering leaf anatomy and ultrastructure (Upadhyaya and Panda, 2019). Key morphology responses include reduced leaf growth, decreased leaf area, leaf rolling, wilting, thickened leaves, early senescence, stomatal closure and a cutinized leaf surface. These adaptations help plants conserve water during low-water potential periods (Panda et al., 2021). Rice is particularly sensitive to drought stress at three growth stages: early seedling, vegetative and anthesis (reproductive) (Singh et al., 2012). Water scarcity during the early seedling stage leads to unbalanced and poor stand establishment (Vibhuti et al., 2015). Drought stress interrupts active seed germination, causing osmotic imbalance, membrane impairment, decreased respiration, and ATP production (Kadam et al., 2017). During the vegetative stage, water constraint delays panicle initiation, followed by late maturity, directly correlated with yield decline (Singh et al., 2012). The most significant impact of drought stress on grain yield occurs during the reproductive stage. While plants may recover during the vegetative stage, recovery from drought stress during the flowering phase is more difficult (Hassan et al., 2023). A brief period of drought stress during the reproductive stage severely reduces rice grain yield by diminishing panicle length, poor seed setting, fewer kernels per panicle, and inadequate spikelet development (Wei et al., 2017). Drought stress during flowering negatively affects pollination, resulting in poor seed setting, reduced grain size, and grain number; in severe cases, flower abortion can lead to a total yield decline (Hassan et al., 2023). A brief period of drought stress during the reproductive stage severely reduces rice grain yield by diminishing panicle length, poor seed setting, fewer kernels per panicle and inadequate spikelet development (Wei et al., 2017). Therefore, any level of drought stress, whether mild or severe, during the reproductive phase significantly lowers final grain production due to disrupted translocation of assimilates from leaves to reproductive organs (Panda et al., 2021).

Crop plants exhibit a variety of strategies to mitigate the effects of drought, collectively referred to as drought resistance (Hassan et al., 2023). These strategies include drought avoidance which is the capacity of plants to maintain high water potential and sustain optimal growth despite moisture stress (Kumar et al., 2017), drought escape involves completing the plant’s growth cycle early, thereby evading periods of moisture deficit (Hassan et al., 2023), drought tolerance denotes the plant’s inherent ability to endure water-deficit conditions by maintaining physiological and biochemical functions with minimal damage (Panda et al., 2021), and drought recovery refers to a plant’s ability to reestablish metabolic activity and regain vigor after exposure to severe drought stress and dehydration (Hassan et al., 2023).

The yield and the stability of rice depend on multiple factors that affect its growth and development, such as the number of panicles producing tillers which is indicative of the plant’s reproductive potential, the number of filled grains within each panicle, the weight of 1000 grains, which serves as a measure of grain quality at a specific moisture content (Yadav et al., 2017). Additionally, the height of the plant from the ground to the panicle tip can affect light interception and photosynthetic capacity, while the length of the panicle and the size and weight of individual grains

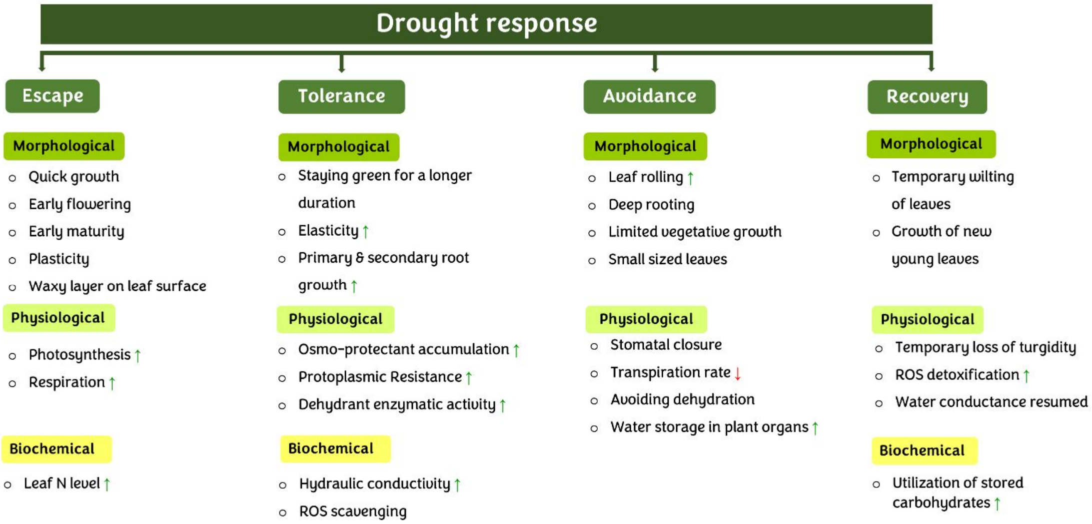

Figure 1: Spectrum of Adaptive Strategies in Rice to Water Deficit Stress; Source: Hassan et al (2023)

are critical determinants of overall yield (Shobbar et al., 2012). These agronomic traits are not only vital for

assessing rice productivity but also serve as key indicators in breeding programs aimed at enhancing drought tolerance.

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The insights gained from studying drought stress responses across different growth stages will be instrumental in guiding breeding programs and agricultural practices aimed at securing rice production for further generations. This review paper aims to synthesize current knowledge and highlight key areas where further research is needed. By unraveling the complex web of physiological, molecular, biochemical and morphological changes that occur in rice under drought conditions, we can pave the way for innovative solutions that will ensure food security and sustainability in an increasingly unpredictable world.

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1. Impact of drought stress on seed germination and seedling growth of rice (*Oryza sativa* L.)

Water scarcity during the early seedling stage exacerbates drought stress, resulting in unbalanced and poor stand establishment. Drought stress disrupts active seed germination by causing osmotic imbalance, membrane impairment, and reduced respiration and ATP production (Kadam et al., 2017).

1.1 Seed germination Stage

Rice seed germination comprises three distinct stages: water uptake, metabolism reactivation, and radicle protrusion and seedling emergence. Each stage is crucial and can be significantly influenced by water availability (Zampieri et al., 2023).

1.1.1 Water uptake

Water uptake is the initial and most critical phase in seed germination, wherein dry seeds absorb water, leading to seed coat rupture and activation of metabolic processes. During this stage, water activates various metabolic pathways including respiration, enzyme synthesis, and mobilization of stored starch and proteins, which are essential for embryo growth and development (Zampieri et al., 2023).

Drought stress severely limits water availability, reducing the water uptake by seeds. This reduced water uptake delays or inhibits the germination process, causing osmotic stress and oxidative stress, leading to hormonal imbalances and metabolic impairments.

1.1.2 Metabolism Reactivation and Reserve Mobilization

Following water uptake, the second stage involves the reactivation of metabolism, marked by the synthesis of RNA, proteins, and hormones essential for cell structure repair, cell wall loosening, and coleoptile elongation (Vibhuti et al., 2015). Water scarcity impedes the transport of hydrolyzed starch from the endosperm to the embryo, reducing the energy and nutrients essential for growth. Drought stress inhibits alpha-amylase activity, crucial for starch degradation in the endosperm, thereby limiting energy for seedling growth (Hasanuzzaman et al., 2013). Additionally, oxidative damage from increased reactive oxygen species (ROS) production under drought stress affects cell structure repair and cell wall loosening, further hindering coleoptile elongation (Luo et al., 2019).

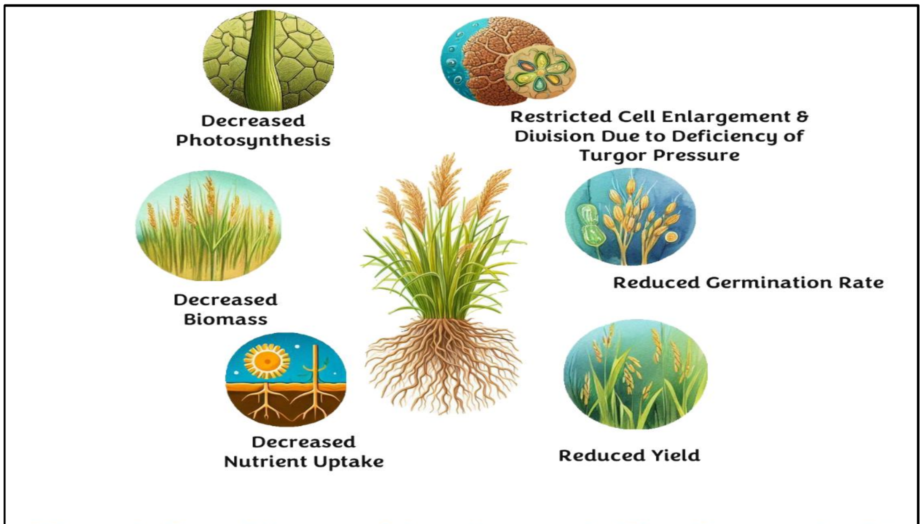

Figure 2: Overall impact of drought stress in Rice (Oryza sativa L.)

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1.1.3 Radicle Protrusion and Seedling Emergence

The final stage of germination involves radicle protrusion and seedling emergence, where the seedling establishes itself by breaking through the seed coat and contacting the soil. Drought stress reduces the water potential gradient between the seed and the soil, diminishing turgor pressure and the expansion force necessary for radicle protrusion. This results in a lower success rate of seedling emergence as the radicle cells struggle to penetrate the seed coat and establish contact with the soil (Atta et al., 2020).

1.1.4 Germination percentage and rate

Under optimal conditions, rice seeds exhibit high germination percentages, essential for a healthy crop start. Drought stress disrupts this process by limiting water availability necessary for seed imbibition. Reduced water potential under drought stress hinders water absorption, significantly lowering germination percentages. For example, germination can drop from 68.8% under normal conditions to 4.4% at severe drought stress levels (-15 bar) (Yang et al., 2001). Atta et al. (2020) found that severe drought conditions could decrease germination percentages by up to 80%, with some genotypes showing as low as 10%. Nawaz & Farooq (2017) reported that drought reduced the germination rate by 40-60% compared to non-stressed conditions, severely affecting the timely establishment of rice seedlings.

1.2 Seedling Growth Parameters

The early growth and development of rice seedlings are critical stages that determine the future health and productivity of the plant. Once seeds have successfully germinated, the seedlings enter a phase of rapid growth, during which they establish their root and shoot systems. This establishment phase is highly sensitive to environmental conditions, particularly water availability.

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1.2.1 Root and Shoot Length

Roots are essential for water and nutrient uptake in rice plants. Under drought conditions, water scarcity directly affects root elongation, inhibiting cell elongation and division in the root meristem due to decreased turgor pressure (Kim et al., 2020). While rice plants may develop thicker and deeper roots to access water from deeper soil layers, severe drought can still decrease root growth. The response of root growth to drought is highly genotype-dependent and varies with stress intensity and duration (Hassan et al., 2023).

The shoot system, including stems and leaves, relies on cell turgidity for growth. Water deficit decreases cell turgidity, leading to reduced cell elongation in the shoot apex, resulting in stunted growth, shorter plant height, and fewer tillers. This limits photosynthetic capacity and biomass accumulation, ultimately affecting crop yield. Drought-stressed rice seedlings showed a 25% increase in root length but a 20% reduction in shoot biomass, indicating a trade-off between root and shoot growth under water-limited conditions (Wei et al., 2022).

1.2.2 Seedling Vigor and Establishment

Seedling vigor, which encompasses the early growth and development stages, is critical for the successful establishment of rice plants in the field. Water stress increases mean germination time which indicates the average time required for seeds to germinate and decreases the germination index, which quantifies the speed of germination. This is critical because rapid and uniform germination is essential for early seedling establishment and vigor (Zhu et al., 2020).

1.2.3 Leaf Development

Leaves are the primary sites for photosynthesis, the process by which plants convert light energy into chemical energy. Water stress often leads to smaller leaves and a reduced number of leaves. This not only decreases the photosynthetic capacity of the plant but also affects transpiration and the overall energy balance, crucial for growth and development (Shao et al., 2008).

1.2.4 Root-to-Shoot Ratio

Under drought stress, rice plants may alter their root-to-shoot ratio to enhance water uptake efficiency (Kim et al., 2020). An increase in the root-to-shoot ratio means that more assimilates are allocated to root growth rather than shoot growth, which can help the plant survive under water-limited conditions. However, extreme drought conditions can still limit overall root development due to increased soil resistance and low water availability (Kim et al., 2020). Although, this adaptation can come at the cost of shoot growth, potentially limiting the plant's ability to capture light and perform photosynthesis effectively (Lafitte et al., 2006).

1.2.5 Biomass accumulation

Biomass accumulation is a critical measure of growth and overall vigor in rice, significantly influencing their ability to establish and develop into mature plants. Drought stress typically results in a substantial reduction in biomass accumulation in rice seedlings. This reduction is primarily due to limitations on cell division and expansion caused by insufficient water availability. Studies have shown that drought stress can lead to a reduction in total dry biomass by 30-50% during the seedling stage (Shankar et al., 2023). This study indicates that under drought conditions, root biomass in rice seedlings can decrease by approximately 25-35% compared to well-watered controls. Consequently, shoot biomass in drought-stressed rice seedlings can be reduced by 35-45% (Wei et al., 2017).

1.3 Disrupted water balance

Water stress disrupts the balance of water movement within a rice plant a decrease in turgor pressure within cells which creates a force pulling water out of the plant cells, resulting in plasmolysis or shrinking of cells which subsequently lead to wilting of plantand stunted growth (Radha et al., 2023).Limited water uptake leads to a significant reduction in plant water status, as evidenced by lower relative water content (RWC). A study by Panda et al. (2016) found that RWC in drought-stressed rice seedlings decreased by 20%, indicating severe water deficit conditions. Praba et al. (2009) found that stomatal conductance in rice seedlings under drought stress decreased by up to 50%, significantly reducing photosynthetic rates and biomass accumulation.

1.4 Increased Production of Reactive Oxygen Species (ROS)

Drought stress induces oxidative stress, leading to the accumulation of ROS such as hydrogen peroxide (H_2O_2) and superoxide anion ($O_2^{\bullet -}$). These reactive molecules are byproducts of disrupted electron transport chains in chloroplasts and mitochondria. Excess ROS can damage cellular components, causing lipid peroxidation, protein oxidation, and DNA damage. However, rice plants activate antioxidant defences to mitigate this damage. Shobbar et al. (2012) observed 2-3 times increase in H_2O_2 levels in drought-stressed rice seedlings, indicating significant oxidative stress.

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1.5 Altered Enzyme Activities

Enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) play crucial roles in detoxifying ROS. Drought stress enhances the expression and activity of these antioxidant enzymes. Enhanced enzyme activities are crucial for protecting plant cells from oxidative damage. Wang et al (2021) found that SOD activity increased by 50%, CAT by 30%, and POD by 40% in rice seedlings under drought stress, significantly improving the plant's ability to scavenge ROS and maintain cellular integrity.

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1.6 Changes in Photosynthetic Pigments

Drought stress often leads to the degradation of chlorophylls and carotenoids, essential pigments for photosynthesis. This degradation is partly due to oxidative stress and the downregulation of genes involved in pigment biosynthesis (Panda et al., 2021). Reduced levels of photosynthetic pigments decrease the photosynthetic capacity of rice seedlings, limiting growth and productivity. Shobbar et al. (2012) reported a 25-30% reduction in chlorophyll content in drought-stressed rice seedlings, correlating with a similar decline in photosynthetic rate.

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1.7 Accumulation of Osmo-protectants

Under drought stress, rice seedlings synthesize and accumulate osmo-protectants like proline, soluble sugars, and glycine betaine. These compounds help maintain cell turgor by balancing the osmotic pressure inside cells (Mishra and Panda, 2017). Osmo-protectants protect cellular structures by stabilizing proteins and membranes. Proline content, for example, can increase several folds in response to drought stress. Yadav et al. (2017) reported a 4-fold increase in proline concentration in drought-stressed rice seedlings, which helped sustain cell turgor and metabolic functions under water deficit conditions.

2. Impact of drought stress on vegetative phase (tillering stage) of rice (*Oryza sativa* L.)

In rice cultivation, drought stress during the vegetative stage can significantly impede growth by restricting cell elongation and root development. This stress leads to a reduction in leaf water potential, net photosynthesis, and nutrient uptake. Additionally, it diminishes stomatal conductance and stem elongation, further affecting cell division and expansion. The culmination of these effects results in smaller leaves, underdeveloped roots, and ultimately, reduced grain yield (Khotasena et al., 2022).

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2.1 Leaf area and Leaf Rolling

Leaf rolling in rice, a response to drought stress, may aid in water conservation, though its role in drought tolerance is not fully established. Agustin et al., (2023) studied this phenomenon in four rice genotypes under varying drought conditions using cryo-microscopy. They observed a marked decrease in stomatal conductance and leaf rolling before completing stomatal closure, which significantly reduced water loss compared to unrolled leaves. The threshold leaf water potential for initial rolling varied between -1.95 and -1.04 MPa among genotypes. Notably, leaf rolling coincides with over an 80% reduction in photosynthesis and stomatal conductance when leaf edges touched. Genotypic differences were evident in the leaf water potential threshold for declines in leaf hydraulic conductance, gas exchange, and chlorophyll fluorescence, except for leaf hydraulic conductance. Xiao et al., (2023) suggests that leaf rolling correlates with drought avoidance and tolerance, potentially valuable for rice breeding in drought-prone environments.

2.1.1 Mechanism of leaf rolling:

Under drought stress, rice plants experience significant turgor pressure loss, triggering leaf rolling to minimize surface area and reduce transpiration. Zhang et al., (2018) found that reduced turgor pressure in rice leaves increased leaf rolling as a natural drought avoidance strategy. Bulliform cells on the adaxial leaf surface play a crucial role in this process; their collapse under water deficit conditions causes the leaf to roll under drought stress (Zhang et al., 2018). Pandey and Shukla (2015) observed that rice varieties with higher leaf rolling during the tillering stage conserved more water and maintained higher relative water content under drought. Okami et al., (2015) reported that rice plants rapid;y recovered leaf morphology and function after rewatering, showing the reversible nature of drought-induced leaf rolling. Lower soil moisture during tillering reduced the leaf are index (LAI), diminishing photosynthetic capacity and growth (Xu et al., 2020).

2.1.2 Tillering dynamics

The initiation and development of tillers are highly sensitive to water availability. Drought stress can reduce the number of tillers by up to 40%, as reported in various studies (Sandhu et al., 2019). This reduction is attributed to decreased cell division and elongation in the tiller buds due to limited water supply. Drought conditions delay the onset of tillering by affecting the hormonal balance, particularly by reducing the levels of cytokinin, which are crucial for tiller initiation (Abbasian&Aminpanah, 2021).

2.2 Plant Height

2.2.1 Reduced plant height

Drought stress leads to decreased turgor pressure, hindering cell expansion and reducing plant height in rice. Okami et al., (2015) noted a 20-30 % decrease in height during the tillering stage under severe drought. A range of physiological changes occurs, including diminished photosynthesis, transpiration, and stomatal conductance, as well as lower water use efficiency, relative water content, chlorophyll content, and photosystem II activity, alongside increased abscisic acid content (Panda et al., 2021). Laila and Waluyo (2016) reported a 25-40% reduction in plant height during the vegetative phase under extended drought. Biochemical adaptation involves the accumulation of osmo-protectants like proline, sugars, and antioxidants to maintain osmotic balance and reduce oxidative stress, but these adjustments can limit growth, as observed by Ray et al., (2015).

2.2.2 Genetic determinants and plant height

The genetic predisposition of a plant determined its potential height, but environmental factors such as drought can significantly influence the expression of these traits. The interaction between genotype and environment (G × E) plays a critical role in phenotypic outcomes (Ma et al., 2016). Under drought stress, plants may adjust their growth patterns, exhibiting phenotypic plasticity; however, severe or prolonged drought can cause irreversible changes in plant architecture (Manikanta et al., 2022).

2.3 Root Development

Drought stress induces changes in root architecture, after resulting in deeper and more extensive root systems to access residual soil moisture. While this can be beneficial, it often comes at the expense of above-ground biomass (Uga et al., 2013). Despite the tendency for deeper roots, overall root biomass may decrease under severe drought stress due to limited carbon allocation and reduced photosynthesis (Henry et al., 2011).

2.4 Yield and Grain Quality

Drought stress during the tillering stage significantly impacts yield components such as panicle number, grain number per panicle, grain weight. These reductions are often attributed to impaired water uptake, reduced photosynthesis, and compromised plant growth (Guo, 2015). Yield reduction of 29.3% and decrease in 1000-grain weight by 3.34% were observed under drought conditions (Panda et al., 2021). Drought stress during the vegetative phase can also affect the subsequent grain filling phase, as the plant may not fully recover from early stress, leading to poor grain development and reduced weight (Jeong et al., 2013).

2.5 Photosynthesis and Carbon Assimilation

2.5.1 Photosynthetic rate

Drought stress significantly impacts the photosynthetic rate of rice plants by causing stomatal closure, which reduces CO2 availability and the carboxylation efficiency of Rubisco, which leads to a sharp decline in photosynthesis. Under severe drought, photosynthetic rates in rice can decrease by up to 50% (Lawlor and Tezara, 2009). This decline is due to both stomatal limitations and non-stomatal limitations and non- stomatal factors, such as damage to the thylakoid membrane and inhibition of key Calvin cycle enzymes (Chaves et al., 2009).

Additionally, water scarcity induces the production of reactive oxygen species (ROS) in chloroplasts, causing oxidative damage to photosynthetic components and further reducing efficiency. The activity of photosystem II (PS – II) declines under drought due to damage to D1 protein, a core PS-II component, decreasing photochemical efficiency (Zhou et al., 2016; Farooq et al., 2009).

2.5.2 Chlorophyll content

Under drought conditions, accelerated chlorophyll degradation occurs due to increased chlorophyllase activity and oxidative stress, leading to chlorophyll peroxidation and chloroplast dismantling. This results in reduced leaf greenness and a decrease in chlorophyll a and b contents by up to 40% under moderate to severe drought stress (Anupama et al., 2018). The decline in chlorophyll content is linked to reduced maximum quantum yield of PS-II, indicating lower photosynthetic efficiency. This reduction in chlorophyll and photosynthetic capacity contributes to decreased biomass accumulation and stunted growth during the vegetative phase, including the critical tillering stage.

2.6 Antioxidant defense mechanism

2.6.1 Reactive Oxygen Species (ROS) and Antioxidant Enzymes

A study by Sharma & Dubey (2005), shows that after 24 hours of drought stress at pressures of –0.5 and -0.2 MPa, Superoxide anion concentrations rose, lipid peroxidation occurred, and total soluble protein and thiols decreased in rice plants. Ascorbic acid and H_2O_2 Concentrations decreased, while glutathione concentrations only decreased in response to extreme stress. While ascorbate regeneration-related enzymes were more abundant in drought -stressed plants, total superoxide dismutase and ascorbate peroxide activity increased with drought stress. The *activities of enzymes* like *superoxidedismutase (SOD)*, *catalase, Peroxidases (POD)* which includes ascorbate peroxidase (APX), which are crucial for mitigatingoxidative damage, are enhanced under such stress (Basu et al., 2009; Nahar et al., 2018; Singh et al., 2020). Additionally, *non-enzymatic antioxidants* like ascorbate and glutathione play a vital role in scavenging reactive oxygen species and regenerating other antioxidants (Basu et al., 2009). The expression of genes related to antioxidant enzymes is also upregulated, improving the plant's antioxidant defense and resilience to drought stress (Nahar et al., 2018; Singh et al., 2020).

2.7 Overall impact on vegetative growth phase

Drought can affect upland rice plants at any point in their growth, and how different growth processes react to water stress may vary depending on when the drought occurs in relation to different phases of crop growth. Due to their low water demand, young plants - 33 days old at the start of stress – maintained their high leaf water potential, as demonstrated by two tests. The young plants in the drought treatment had a radiation -use efficiency comparable to the watered control, but a 68% decrease in radiation interception resulted in a 71% decrease in shoot dry matter production. In comparison to older plants, the younger plants had a slower rate of water extraction and a lower water use efficiency (Boonjung and Fukai, 1996).

3. Impact of drought stress on reproductive phase (anthesis stage) of rice (*Oryza sativa* L.)

The reproductive stage of rice is crucial for determining grain yield and is highly sensitive to water deficit. Drought during this phase can significantly reduce yield, impacting food security and agricultural sustainability. Water shortage disrupts physiological and metabolic processes, leading to reduced seed set, impaired grain filling, and decreased yield quantity and quality (Gupta et al., 2023). This section will explore the effects of drought stress on rice during the reproductive stage, focusing on physiological changes and their implications for yield.

3.1 Days to flowering and maturity

The phenological development of rice, particularly the transition from vegetative to reproductive stages marked by flowering and maturity, is highly sensitive to environmental cues. The delay in flowering and maturity under drought conditions is a manifestation of the plant's intrinsic survival strategy. By conserving water and slowing down growth, the plant aims to extend its life span until more favorable conditions arise (Sarma et al., 2023). The synchronization of flowering with optimal environmental conditions is crucial for successful pollination and seed set of rice plant. A delay can result in a mismatch with these conditions, leading to reduced fertilization rates and poor grain filling (Hassan et al., 2023). Moreover, the extended duration under stress conditions can lead to prolonged period of recourse allocation to survival rather than reproduction, further diminishing yield potential (Sarma et al., 2023).

3.2 Effects on flowering

Drought stress, particularly during the flowering stage, which is inherently sensitive to water deficits, imposes significant constraints on reproductive success of rice. The occurrence of drought during this period can lead to various physiological disruptions resulting into compromised fertility and reduced yield potential.

3.2.1 Pollen Viability

Under drought stress, rice pollen grains may desiccate, reducing their germinability and viability due to decreased moisture content (Salgotra& Chauhan, 2023). This premature drying impairs the pollen's fertilization ability. Additionally, drought alters the pollen's biochemical composition, further diminishing its functionality (Gokulraj et al., 2018).

3.2.2 Stigma receptivity

Drought stress can affect the morphology and physiology of the stigma which reduces pollen adhesion and hydration while decreased stigmatic fluid secretion hampers pollen tube growth (Qi & Wu, 2022). The combined effects of reduced pollen viability and stigma receptivity under drought conditions are manifested by anther dehiscence, which can result in insufficient pollen available for pollination (Da Costa et al., 2021). Also pollen germination and subsequent pollen growth can be hindered due to the lack of adequate moisture and nutritional support (Da Costa et al., 2021). Thus, the reduction in seed set due to these measures can lead to substantial decrease in rice grain yield.

3.3 Panicle Exertion and spikelet fertility

3.3.1 Panicle exertion

Panicle exertion, crucial for rice pollination and grain setting, involves the elongation of the peduncle. Under drought stress, peduncle elongation is significantly reduced, leading to up to 70-75% spikelet sterility due to decreased turgor pressure in peduncle cells, inhibiting their expansion (Da Costa et al., 2021). This stress also disrupts hormonal balance, lowering gibberellic acid (GA) level and increasing abscisic acid (ABA) levels, further hindering panicle exertion (Eragam et al., 2023).

3.3.2 Spikelet fertility

The failure of panicle exertion leads to spikelet sterility. Sterile spikelets fail to produce viable rice grains which directly impact the yield. The sterility arises from the inability of the spikelets to be adequately exposed for pollination and the potential thermal stress experiences by the enclosed floral organs (Eragam et al., 2023).

3.4 Grain formation and quality

3.4.1 Grain formation

The reproduction stage is pivotal for grain formation as it involves developments of spikelets, the flowering units rice panicle. Drought stress during reproductive phase can inhibit panicle exertion and can trap spikelet within the leaf sheath, preventing proper pollination and leading or increased spikelet sterility (Hassan et al., 2023). Consequently, the number of grains formed per panicle is significantly decreased, directly affecting the yield.

3.4.2 Grain quality

During the grain filling stage, drought stress can induce changes in grain quality attributes. An increase in head rice ratio, the proportion of whole grain obtained after milling, is observed due to the production of harder grains less prone to breakage during processing (Hussain et al., 2022). However, this improvement in milling quality is offset by adverse effects on cooking quality and grain appearance (Hussain et al., 2022). Drought stress can increase grain protein content through the mobilization of stored carbon reserves and accelerated plant senesces, negatively affecting the taste and texture of cooked rice (Meena et al., 2024). Additionally, amylose content, which influences cooking and eating qualities, can decrease under drought conditions, altering the rice's cooking properties (Meena et al., 2024).

3.5 Yield and Yield Attributes

Incidence of drought at reproductive stage has a profound effect on yield and yield attributes. Various studies report under multi-stage drought (MSD) conditions average grain yield reductions can be ranging from 68.2% to 97.7% compared to optimal water conditions (Kharel et al., 2018).

3.5.1 Spikelet fertility

Spikelet fertility, a crucial indicator of reproductive success, has been reported to decrease by as much as 53.7% under drought conditions (Kharel et al., 2018). This reduction is primarily due to the impaired anther dehiscence and pollen viability, which are critical for successful fertilization.

3.5.2 Effective grains per panicle

The number of effective grains per panicle is another crucial yield attribute that is significantly affected by drought stress. The decrease in grain number is attributed to the failure of spikelet to develop into grains, as well as the abortion of developing grains due to insufficient photosynthate supply or hormonal imbalance caused by the water stress (Singh et al., 2012).

3.5.3 Seed test weight

The test weight is adversely affected by drought stress. The reduction in the test weight under drought conditions is indicative of poor grain filling and reduced grain size, which are consequences of disrupted carbohydrate metabolism and assimilate translocation (Shao et al., 2015).

3.6 Physiological Parameters

The reproductive stage of rice is a period of heightened sensitivity to environmental stressors, particularly drought. During this stage, the physiological processes that are fundamental to plant growth and development, such as photosynthesis, stomatal conductance, and transpiration, are significantly compromised under conditions of water scarcity.

3.6.1 Photosynthetic rate

According to studies photosynthetic rate of rice plant reduces up to 49.4% at the reproductive stage compared to non-stress condition (Zhang et al., 2018). This decline is primarily due to the closure stomata, which limits the diffusion of CO_2 into the leaf mesophyll, thereby reducing the substrate availability for the Calvin cycle (Sandeep & Godi, 2023).

3.6.2 Stomatal conductance and transpiration rate

Another critical parameter, Stomatal conductance markedly reduced up to 58.9% during the reproductive stage of rice plant under drought conditions (Zhang et al., 2018). Stomata are the primary gateways for both CO_2 influx and water vapor efflux; thus, their closure is a direct response to conserving water. This necessary survival mechanism comes at the cost of reduced CO_2 uptake, which is essential for photosynthesis (Sandeep & Godi, 2023).

Transpiration rate is closely linked to stomatal conductance, also sees a maximum decreases of 65.4% during the reproductive stage under multi-stage drought (MSD) condition limits the plant's ability to cool itself, potentially leading to thermal stress (Vijayalakshmi et al., 2023).

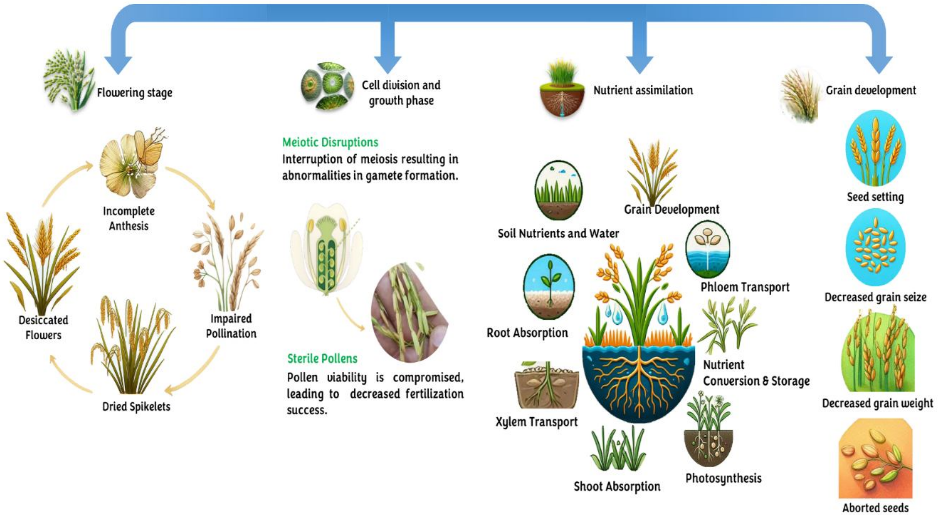
3.6.3 Chlorophyll content

Drought stress can lead to substantial reduction in the ratio of chlorophyll a to b and the overall chlorophyll concentration, leading to a decline in the photosynthetic rate as decrease in chlorophyll content limits the light-harvesting efficiency of the plant, resulting in a lower photosynthetic rate and, consequently, affect biomass production (Wang et al., 2023).

3.6.4 Relative water content (RWC)

RWC is crucial for maintaining turgor pressure and a direct indicator of the cell's hydration status, can affect flowering and seed development during reproductive stage. Under prolonged drought stress RWC can decline by an average 30% (Ahmadizadeh, 2013). Decrease in RWC can

Figure 3: Drought Stress during Reproductive Stage Rice (Oryza sativa L.)



lead to reduced cell expansion and retarded growth, directly impacting the development of reproductive organs and, consequently, grain yield (Ahmadizadeh, 2013).

3.6.5 Membrane Stability Index (MSI)

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Membrane stability Index (MSI) reflects the integrity of cellular homeostasis. MSI can be significantly lower on rice plants under drought stress ranging between 34-37% (Awaji et al., 2022). This damage is particularly detrimental during reproductive stage as it can lead to the disruption of metabolic processes essential for grain filling and development, and because of loss of membrane integrity, leakage of electrolytes and other solutes take place, further exacerbating the stress on the plant (Sandeep &Godi, 2023).

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3.6.6 Proline accumulation

Proline acts as an osmolyte, aiding in plant stress tolerance by balancing intracellular and extracellular osmotic pressure, which is crucial for cell turgor and growth, especially during the reproductive phase in rice (Hassan et al., 2023). It stabilizes proteins and membranes, protecting them from dehydration (Dien et al., 2019). Higher proline levels during this stage mitigate drought effects, preserving reproductive tissue and ensuring development continuity, resulting in less yield reduction and better grain-filling potential (Hassan et al., 2023; Dien et al., 2019).

3.6.7 Oxidative stress and Antioxidant defense systems

During the reproductive stage of rice (*Oryza sativa* L.) the plant is particularly susceptible to oxidative stress caused by drought. Reactive oxygen species (ROS) such as superoxide radicals (O2-), hydrogen peroxide (H2O2), hydroxyl radicals (OH), and singlet oxygen are generated excessively due to disrupted cellular metabolism under water-deficit conditions (Sarma et al., 2023). These ROS can cause severe oxidative damage, including lipid peroxidation, chlorophyll bleaching, protein oxidation, and nucleic acid damage, comprising cellular integrity and function critical for reproduction (Sarma et al., 2023).

To counteract oxidative stress, rice plants employ a sophisticated antioxidant defense system, especially active during reproduction. This system includes enzymatic and non-enzymatic mechanisms that scavenge ROS and protect cellular components (Wang et al., 2022).

3.6.7.1 Enzymatic Antioxidant Defense

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Superoxide Dismutase (SOD) catalyzes the conversion of superoxide radicals to H2O2, reducing the levels of highly reactive superoxide radicals (Wang et al., 2023). Catalase (CAT) then detoxifies H2O2 by converting it into water and oxygen, preventing toxic accumulation of H2O2 (Wang et al., 2021).

3.6.7.2 Non enzymatic Antioxidant Defense

Ascorbate and Glutathione are major non-enzymatic antioxidants that directly scavenge ROS and regenerate oxidized enzymatic antioxidants, maintain cellular redox homeostasis (Dien et al., 2019). Carotenoids and Tocopherols are lipid-soluble antioxidants that protect membrane lipids from peroxidation, preserving cellular membrane integrity essential for reproductive tissue function (Dien et al., 2019).

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4. Impact of drought stress on ripening phase (grain filling stage) of rice (*Oryza sativa* L.)

The ripening phase of cereals are crucial for determining their final yield and grain quality. Drought stress during this phase can have severe consequences on the rice plant's agro-morphological, physiological and phenological traits. This part of review delves into the detailed impacts of drought stress on rice plants during the ripening stage, explaining the underlying mechanics and effects.

4.1 Grain filling and weight

During the ripening phase, grain filling is a critical process of rice plant, where photo-assimilates are transported from the leaves to the developing grains. Drought stress reduces the plant's photosynthetic capacity by causing stomatal closure to conserve water. This limits CO2 uptake, thereby decreasing the synthesis of photo-assimilates. Additionally, drought stress impairs the vascular system's efficiency, reducing the translocation of these photo-assimilates to the grain (Upadhyaya & panda, 2019). As a result, grain receives fewer carbohydrates, leading to incomplete grain filling and reduced grain weight. Upadhyaya and Panda (2019) also reported that drought stress during rice filling could decrease grain weight by up to 30%. This reduction in grain weight directly translates to lower yield, impacting food security and economic returns for farmers.

4.2 Starch Accumulation

Starch synthesis in rice grains is highly sensitive to drought stress. The enzymes involved in starch biosynthesis, such as ADP-glucose pyro-phosphorylase and starch synthase, are downregulated under water-deficit conditions. This is partly due to the reduced availability of substrates i.e., glucose and fructose and ATP, essential for starch biosynthesis (Yang et al., 2001). The reduction in starch accumulation leads to poorer grain quality and lower energy content. Incomplete starch synthesis results in grains that are less plump and have inferior cooking and eating qualities. Studies by kumar et al. (2020) indicates that drought stress could reduce starch content in rice grains by 15-20%.

4.3 hormonal imbalance

Drought stress induces significant hormonal changes, which accelerates senescence and reduce grain filling duration in rice plants. Abscisic acid (ABA) levels typically increase under drought conditions, promoting stomatal closure, premature ripening and senescence. While reduced cytokinin levels limits cell division and grain growth. Gibberellins and auxins, which are vital fir growth and development, are also negatively affected (Yang et al., 2001).

4.4 Molecular Responses

4.4.1 Gene Expression

Drought stress in rice during ripening phase triggers the expression of various drought-responsive genes. These include genes encoding for dehydrates, late embryogenesis abundant (LAE) proteins and other stress-related proteins. Transcription factors such as DREB (Dehydration Responsive Element Binding) proteins play a crucial role in regulating these gene expressions (Hassan et al., 2023). The expressions of these genes help the plants to cope with water deficit by stabilizing cellular structure, promoting proteins and maintaining membrane integrity. However, the energy and resources diverted to stress response genes can limit resources available for rice grain filling and development (Sandeep & Godi, 2023).

4.4.2 Protein Synthesis

Drought stress affects protein synthesis in rice plants by altering the levels of both structural and enzymatic proteins. Stress conditions lead to the synthesis of heat shock proteins (HSPs) and other protective proteins that help mitigate damage. While these protective proteins are essential for survival, the synthesis of growth-related proteins negatively impacts grain development. This shift in protein synthesis priorities can lead to poor grain filling and lower nutritional quality of the rice grains (Guan et al., 2010).

Conclusion

Rice production can undergo severe effects of drought stress that can affect all growth phases from seed germination to grain filling. There are holistic approaches to combat this challenges, such as developing drought-resistant varieties using breeding and genetic engineering techniques and adapting better agronomic practices. Efficient water management, soil and water conservation, climate smart agriculture viral components of this strategy. Finally, it is crucial to come up with supportive policies and interdisciplinary research to promote innovation thereby facilitating the dissemination and adoption of resilient practices. All these measures are intended to protect rice production which contributes significantly to food security worldwide against the rise in climate variability. The review shows comprehensive impact of drought in rice growth stages; simultaneously calls for urgent action and continued research to develop sustainable solutions for stabilizing rice yield while at the same time protecting the livelihoods of small farmers who rely on this stable crop.

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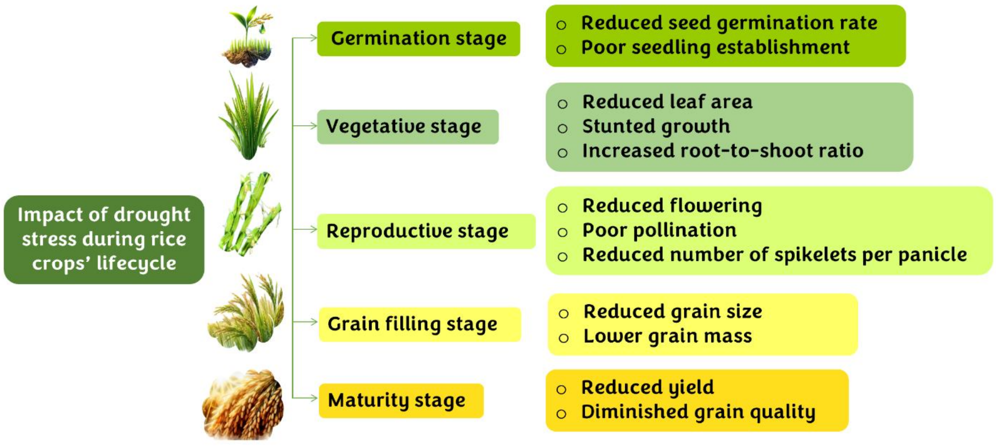

Figure 4: Impact of drought stress during rice (Oryza sativa L.) crop's lifecycle

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