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Review

Drought Stress Tolerance in Rice: Physiological and Biochemical Insights

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Abstract: Rice (*Oryza sativa* L.), an important food crop, necessitates more water to complete its life cycle than other crops. Therefore, there is a serious risk to rice output due to water-related stress. Drought stress results in morphological changes, including the inhibition of seed germination, reduced seeding growth, leaf area index, flag leaf area, increased leaf rolling, as well as the decrement of yield traits, such as plant height, plant biomass, number of tillers, and 1000-grain yield. Stress also causes the formation of reactive oxygen species (ROS) such as O_2^-, H_2O_2, and OH^-, which promote oxidative stress in plants and cause oxidative damage. The process of oxidative degradation owing to water stress produces cell damage and a reduction in nutrient intake, photosynthetic rate, leaf area, RWC, WUE, and stomatal closure, which may be responsible for the decrement of the transpiration rate and plant dry matter under decreasing soil moisture. Plants have the ability to produce antioxidant species that can either be enzymatic (SOD, POD, CAT, GPX, APX) or non-enzymatic (AsA, GSH) in nature to overcome oxidative stress. During drought, several biochemical osmoprotectants, like proline, polyamines, and sugars, can be accumulated, which can enhance drought tolerance in rice. To meet the demands of an ever-growing population with diminishing water resources, it is necessary to have crop varieties that are highly adapted to dry environments, and it may also involve adopting some mitigation strategies. This study aims to assess the varying morphological, physiological, and biochemical responses of the rice plant to drought, and the various methods for alleviating drought stress.

Keywords: water scarcity; relative water content (RWC); reactive oxygen species (ROS); anti-oxidative enzymes; osmoprotectants; yield attribute; amelioration strategy

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1. Introduction

The term drought is commonly used to describe the lack of water availability, which can have an impact on crop growth and soil moisture storage capacity during periods without significant rainfall [1]. Drought stress is a major challenge to sustainable rice production because it causes a significant loss in productivity [2]. Rice is an essential food crop belonging to the genus *Oryza* of the Poaceae family. Globally, it offers 23% per capita energy, accounting for 65% of total caloric intake. It is primarily grown for its grain, which contains around 80% starch, 7% protein, and 12% water. It stands as the most widely consumed staple food, with the second largest area and productivity following maize worldwide [3]. Global rice consumption has increased in recent years. However, it is expected that rice's annual production gap will expand from 400,000 t in 2016 to 800,000 t by 2030 due to drought stress [4]. Drought reactions include modifications in their physiological and morphological mechanisms, as well as their biochemical mechanisms [5]. Morphological changes in plants are the visible changes that occur in the plant's external structure under different environmental conditions [6]. Leaf rolling is one of rice's acclimatization reactions and is used as a criterion for measuring drought tolerance. Drought stress lowers plant height, leaf area, stem diameter, and biomass output, including spikelet sterility, grain number reduction, unfilled grain number rise, 1000-grain weight reduction, and yield reduction in rice [7].

During drought stress, the osmotic pressure of the cells plays an important role in maintaining the water potential of the plant [8]. Plants respond to water stress by raising the osmotic pressure, which is caused by an increase in solutes. This osmotic adjustment ensures continuous water uptake during drought, allowing the plant to retain turgidity, growth, photosynthesis, and other physiological functions. Water stress leads to the closure of stomata, which decreases the rate of transpiration and CO_2 absorption. To enhance growth and development, higher values of relative water content (RWC), water use efficiency (WUE) and osmotic adjustment are required. RWC, stomatal conductance, photosynthetic active radiation (PAR) and photosynthetic rate all showed strong and positive relations with water use efficiency, although transpiration rate had a negative link. During water stress, there is an increase in reactive oxygen species (ROS), which raises the level of malondialdehyde (MDA). MDA is viewed as a sign of oxidative damage induced by several stressors. ROS promotes lipid peroxidation, protein denaturation, DNA mutation, and other forms of cellular oxidative damage [9]. Plants have evolved several adaption mechanisms, including antioxidant defense systems like superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT). SOD converts superoxide (O_2) to H_2O_2 through catalyzing superoxide anion radical disputation. The POD and CAT reduce H_2O_2 in water, utilizing various substrates as electron donors to maintain the roots and assist the plants in tolerating stress [10].

Proper irrigation is a must for rice cultivation, and more than 80% of freshwater is used for irrigation in emerging Asian countries [11]. Currently, around 1900 to 5000 L of water are required to produce 1 kg of rice grain, and it is estimated that nearly 10% of the irrigated rice will face water scarcity by 2025. To maintain agricultural productivity and environmental sustainability, effective drought mitigation methods are necessary. An overall method for effective drought mitigation includes the use of modified genotypes, the exogenous administration of osmoprotectants, plant growth regulators, and seed priming and breeding. To guarantee food security and sustainable agriculture in water-limited regions it is crucial to prioritize research in this area. Considering the facts, the present study describes the effect of drought stress on the morpho-physiological characteristics of rice as well as the activity of reactive oxygen species, osmolytes and antioxidant enzymes.

2. Rice Consumption and Drought Situation in the World and in Bangladesh

Rice is grown under a wide variety of environmental conditions, including topography, climatic factors, soil type and water regime. The continuous droughts have badly damaged agricultural production systems, with rice production being one of the most hit because the crop is more sensitive to droughts than other crops. Over the past few years, there has been a slight increase in rice consumption worldwide (Figure 1). In the 2021–2022 crop year, rice consumption globally reached approximately 520 million metric tons, compared to 437.18 million metric tons in the 2008/2009 crop year. In 2021, rice production for Bangladesh was 48,667 kg per ha [12]. In Bangladesh, recent rice consumption is 38,200 (1000 MT), which was 24,958 (1000 MT) in 2000 [13]. Day by day, the demand for rice is increasing globally due to the growing population. However, global rice output is severely hampered by drought stress conditions.

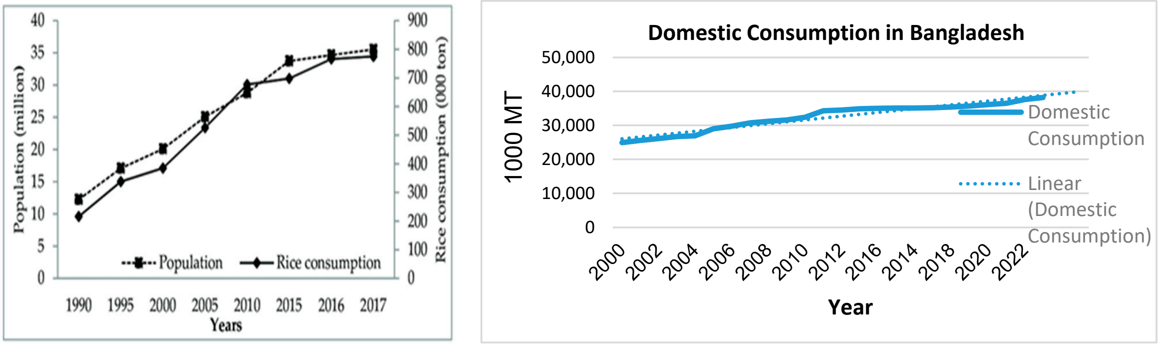

Figure 1. Rice production and consumption in the world and in Bangladesh (Source: [12,13]).

Drought stress affects around one-third of the world's total agricultural area (Figure 2). Within that area, emerging countries account for 33% (9.9 u 107 hm^2), developed countries for 25% (6.0 u 107 hm^2), and underdeveloped countries for 42% (12.6 u 107 hm^2). In Asia alone, over 3.4 u 107 hm^2 of rainfed lowland and 8.0 u 106 hm^2 of highland rice are subject to drought stress [14].

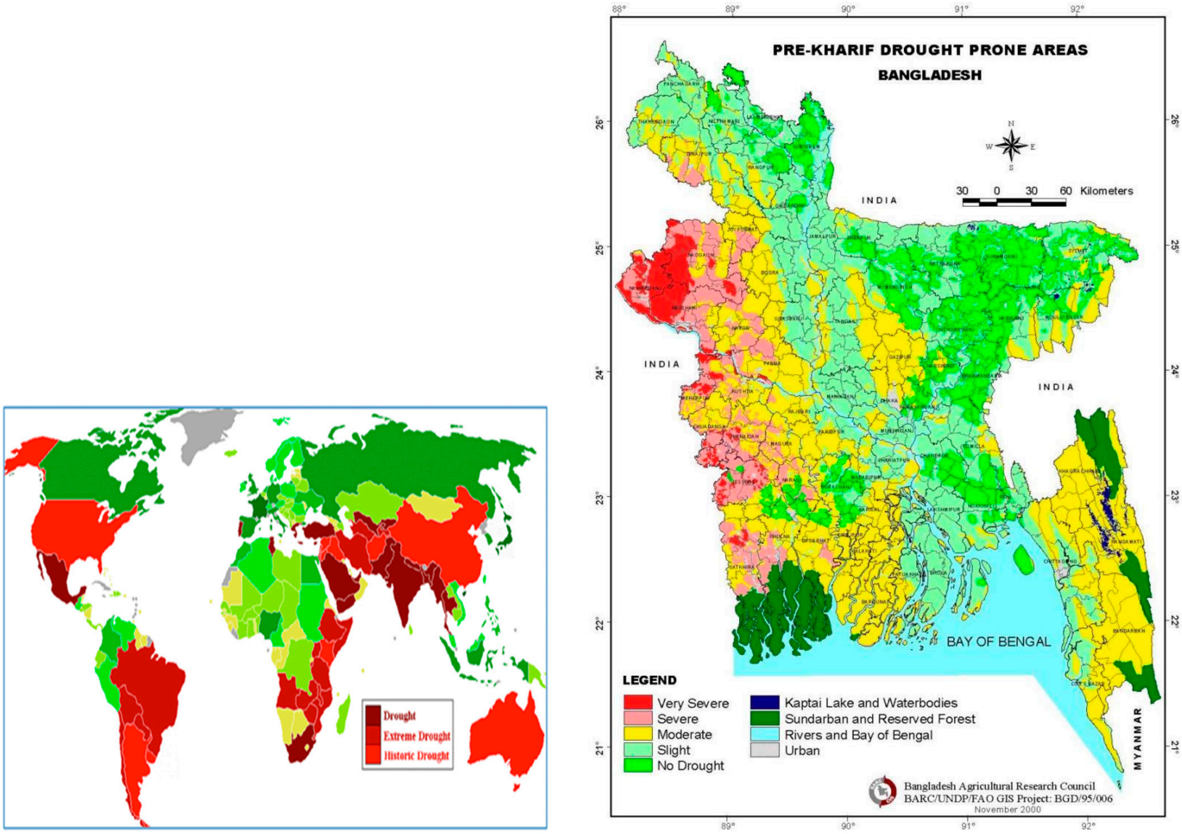

Figure 2. Global and Bangladesh drought map [15].

Agricultural production and productivity worldwide are affected by drought stress, which is considered one of the most significant environmental stresses and can result in significant yield reductions. Drought stress is regarded to be a loss of water, which leads to stomatal closure, a reduction in gas exchange, lower leaf water potential, turgor pressure, and a diminution in cell enlargement, growth, and the disruption of enzyme-catalyzed reactions, ultimately leading to plant mortality [16]. It inhibits plant growth by affecting various physiological, morphological and biochemical processes, including seedling growth, chlorophyll content, photosynthetic rate and water use efficiency, as well as increasing oxidative stress, which causes cell membrane damage.

Several methodologies commonly used in research to induce drought stress are as follows:

(i) Polyethylene Glycol (PEG) Treatment: PEG-6000 is added to the nutrient solution or growth medium to create an osmotic potential that simulates drought conditions.
(ii) Soil Drying: Gradually reduce irrigation or completely withhold water to induce soil drying. Monitor soil moisture content using sensors, a moisture meter or gravimetric methods.
(iii) Drip Irrigation Control: Use drip irrigation systems to precisely control the amount and timing of the water supplied to plants. Create drought conditions by reducing water supply incrementally.
(iv) Controlled Environment Chambers: Use growth chambers or greenhouses with controlled humidity, temperature, and light to simulate drought conditions.
(v) Sensor-Based Irrigation Control: Use soil moisture sensors to automate and control irrigation based on real-time soil moisture data. Reduce water supply based on sensor feedback to induce drought stress.

3. Morphological Responses to Drought Stress in Rice Plant

Drought stress occurs when the water supply to the roots is limited or when the transpiration rate is extremely high.

However, both factors can happen simultaneously under a limited water supply as well as under a low relative humidity of the air [4]. These have a negative impact on growth, development, and, eventually, rice output (Figure 3). Plants respond to water stress by reducing or halting their growth. This is a normal response to the lack of water and it acts as a survival technique [17]. Plant growth and development is reduced as a result of poor root development, with a decrement of the leaf shape, the composition of cuticular wax, leaf pubescence, and a leaf color that affect the amount of radiation captured into the leaf, delaying or reducing the rate of normal plant senescence as it approaches maturity, and inhibiting the stem reserves [18]. Both elongation and expansion growth are affected by drought, as it also impairs the germination of rice seedlings and reduces the tiller number, plant height and biomass production [19].

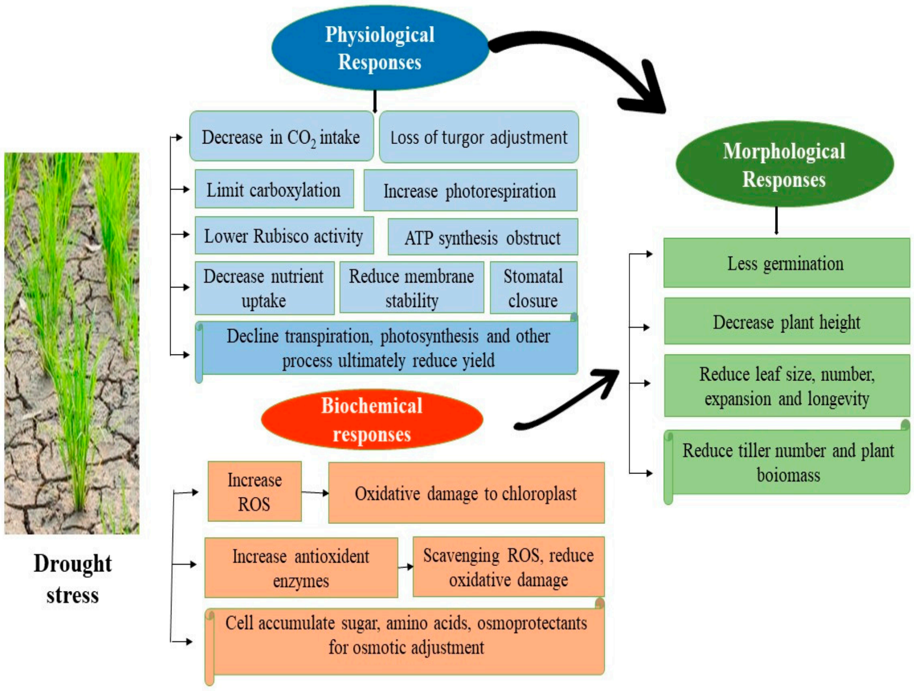

Figure 3. Drought causes various changes to rice plants.

3.1. Effects of Drought Stress on Seed Germination

Drought has the primary consequence of reducing germination and causing poor stand establishment. It causes severe reductions in germination and seedling growth due to water constraints [20]. Seed germination requires proper temperature, oxygen, and soil humidity. Water uptake and imbibition are mostly determined by soil water availability and potential. Drought stress slows down the imbibition process, resulting in lower germination rates and, ultimately, lower seedling vigor [21]. Under water-stressed conditions, development is also linked to ATP (adenosine triphosphate) levels in cells, as seedling establishment requires energy for anabolism in the seed. The drought tolerance process in seedlings comprises the management of ATP energy levels, which results in a reduction in osmotic potential due to the accumulation of osmotic components in growing tissues. This allows for reduced seedling development under water stress circumstances due to ATP. Drought stress reduces plumule length and seedling vigor, resulting in poor stand establishment due to shorter coleoptiles. In this sense, the use of genotypes with longer coleoptiles might be a suitable method to achieve improved stand establishment [22]. Desiccation reduces seed viability and vigor, which is associated with a variety of biochemical changes such as reactive oxygen species (ROS) causing damage and changes in RNA, DNA, and protein structures, membrane ruptures, a decrease in respiratory activity, and thus a decrease in ATP production [23]. Similarly, lower germination rates under water stress could be the reason for a decrease in ATP production. So, drought has a severe impact on the germination process by inhibiting water intake, damaging metabolic pathways at the cell level, impairing membrane transport, and decreasing ATP synthesis and respiration, all of which lead to poor seed germination and, eventually, limit seedling strength [24]. In a research study, the germination and seedling establishment stages were identified as the most sensitive to drought stress. A total of 14 genotypes were tested against five levels of drought stress induced by polyethylene glycol 6000 (PEG-6000) at 0, 5, 10, 15, and 20% [25]. Polyethylene glycol has been used to model water stress in plants [26], and is added to the nutrient solution or growth medium to create an osmotic potential that simulates drought conditions. PEG-6000 reduces the oxygen availability, which hampers the root growth of crops [27]. The highest percentage of germination was recorded under control, while the lowest was at the highest level of drought stress. In general, germination was substantially hampered under the most extreme drought stress, with germination rates of less than 40% for all genotypes tested. Low water content in the soil, along with other environmental conditions, can change germination success [28].

3.2. Effects of Drought Stress on Seedling Growth

The production of root systems during drought is critical, and there is a strong association with yield under low moisture. Water stress has a significant impact on the growth and development of rice roots and shoots, which are crucial components in drought adaptation. Plants obtain water and mineral nutrients from the soil through their roots, so root growth, size and proliferation are key elements in water stress resistance. Deep rooting cultivars are more tolerant than shallow rooting cultivars [3] because a plant's deep root system allows it to obtain water from the depth of the soil. This has a positive correlation with the xylem vessel area, which is important for water conductance from the soil to the higher regions of the plant to meet evaporative demand and promote dry matter accumulation inside the shoots [29]. Xylem vessels are part of the plant's vascular system, responsible for transporting water and nutrients from the roots to the rest of the plant. Water conductance, or hydraulic conductance, refers to the ability of the plant to transport water through its vascular system. It is influenced by factors such as the number and diameter of xylem vessels, as well as their connectivity. The larger the area of xylem vessels (diameter and length), the greater the potential for water conductance within the plant. This is because a larger vessel area provides more pathways for water to move through the plant's vascular system. Therefore, plants with larger xylem vessel areas generally exhibit higher rates of water transport [30]. In ref. [31], Abdullah and his team discovered that crop plants' shoot length decreased because of the increase in drought stress level and duration. The decrease in shoot length is related to decreased cell elongation caused by a lack of water, which reduces the turgor pressure. There are two types of effects of water deficit on root development: the first is a decrease in the rate of meristematic activity and root elongation directly related to the level of internal water deficit, and the second is the effect of suberization on the water and the nutrient uptake proportional to the root system as a whole. Active meristems contribute to the development of root systems that are well adapted to absorb water from soil. When meristematic activity decreases, the production of new cells in roots slows down. This can lead to a reduced root length and surface area available for water and nutrient absorption [32]. A major negative consequence of water stress on crop plants is a lower production of fresh and dry biomass [3]. The ability to produce numerous branches, a deep root system, coarse roots, and a high root to shoot ratio are important traits for rice genotypes, which helps plants to withstand drought. Many studies have shown that plant height and biomass are reduced as a result of water stress [33]. If there is more soil water available, shoot development is often faster. Additionally, plant biomass has shown a considerable drop in both the fresh and dry weight of the root and shoot after scarcity [34]. A reduced leaf surface area, poor root growth, inhibited stem growth, and early maturity are the outcomes of adverse drought stress in rice plants [35]. The four upland rice cultivars responded differently to drought stress in terms of dry matter production [36]. When compared to the control, all upland rice types showed a significant decrease in the dry matter of several organs. For Becor, Kusum, Nabawan, and Bertih, the corresponding shoot length loss percentage under the highest drought stress condition (-8 bar PEG) is 68.97%, 76.84%, 51.72, and 55.56%. For Becor, Kusum, Nabawan, and Bertih, root length% and dry matter% are 100% under control conditions; however, when drought stress increases, decrements occur.

3.3. Effect of Drought Stress on Leaf Traits

Since leaves are the source organs that assimilate synthesis for the sink organs to sustain the growth of the entire plant even under stressful conditions, research on leaves is just as important as research on roots and shoots. Due to the limited water potential during drought stress, leaf growth is decreased. Crops that have disrupted water flow from the xylem to another cell, such as when there is a shortage of water, exhibit reduced leaf area and poor cell development. The anatomy and ultrastructure of leaves alter under drought-stress conditions [37]. These alterations include leaf size shrinkage, a decrease in stomatal number, thicker cell walls, cutinization on the leaf surface, and the poor development of the conducting system. A significant symptom of drought in plants is leaf rolling, which is considered an important trait in rice breeding. This leaf rolling phenotype is partially regulated by the formation of specific thin-walled, highly vacuolated cells called bulliform cells, located on the adaxial leaf surface [38]. These specific cell types lose turgor during water stress, leading to a leaf-rolling phenotype. In rice and other field crops, moderate leaf rolling contributes to an erect leaf structure, which improves light capture and gas exchange, thereby enhancing photosynthesis efficiency. This process results in greater dry matter accumulation and increased yield, and it may also help maintain the plant's internal water status [39]. However, severe leaf rolling negatively impacts plant growth, development, and grain yield [38]. Since moderate leaf rolling reduces water loss by lowering the transpiration rate, it aids plant survival during drought conditions [40]. Therefore, manipulating leaf rolling is a crucial strategy for improving rice productivity under drought conditions. Due to its agronomic importance, leaf rolling has garnered significant attention from plant scientists. Under drought conditions requiring grain filling, the flag leaf must sustain the synthesis and transport of photoassimilates [41]. A reduced flag leaf area leads to smaller leaf size, earlier senescence, and slower leaf emergence. Water deficit impacts various other leaf traits, such as reducing the number of leaves per plant [42], leaf area, and leaf area index [43]. Rice plants limit their leaf area under water stress to conserve water, resulting in lower growth rates and biomass production compared to well-watered plants. This decline in growth is likely due to a rapid decrease in cell division and leaf elongation under drought. Studies have shown that rice plants with smaller leaf areas use less water but are also less productive [18]. In Zayed's experiment [44], the leaf area index and flag leaf area were significantly affected by water scarcity over two seasons. The highest values for leaf area index and flag leaf area were observed in the transplanting method with well-watered treatment. Consequently, the leaf area index and flag leaf area decreased in cultivation when there was a shortage of water. The rice cultivar Nagina 22 showed notable reductions in total leaf area caused by drought, as reported in [45]. Remarkable results were documented by [46]. An experiment by Kumar and colleagues (2019–2020) found that the leaf area under irrigation varied from 25.2 cm^2 to 54.5 cm^2. The leaf area dropped dramatically under drought simulation conditions, from 16.63 cm^2 to 40.73 cm^2 [47].

3.4. Effect of Drought Stress on Yield and Its Associated Traits

Yield is the ultimate trait that is heavily influenced by water stress. Water stress has an impact on a variety of yield-regulating factors. Many of these factors affect plant yield in a variety of complex ways. Under drought stress, rice plant yield is determined by drought timing, drought level, and plant growth stages [48]. In ref. [49], Hsiao arranged the drought stress based on the water potential, as shown in Table 1.

Table 1. Drought stress levels as a function of water potential.

Category of Stress	Soil Water Potential	Reduction in Leaf Relative Water Content %
Mild stress	−0.1	8–10
Moderate stress	−1.2–−1.5	>10–20
Severe stress	<−1.5	>20

Drought impacts yield components at various growth stages of a plant, such as the vegetative stage [50], reproductive stage [51], flowering stage [50,52], anther dehiscence stage [53], grain-filling stage [54], and heading stage [55]. For instance, during the vegetative stage, drought reduces plant height, biomass, and the number of tillers, and causes leaf rolling in rice. Drought stress during the tillering stage is caused by a reduced soil moisture uptake, which limits food preparation and decreases cell division in meristem tissues. Under water stress, plants release phytohormones like ethylene, which inhibit leaf and root growth in the initial phase. Water stress occurring up to 12 days before anthesis severely impacts spikelet fertility and significantly reduces grain yield [53]. Water stress during flowering is particularly harmful to the yield, as it disrupts pollination, causes flower abortion and grain abscission, and increases the percentage of unfilled grains. Moisture stress for 20–25 days during the panicle initiation stage can reduce rice yield by 53.7 to 63.5 percent, representing a significant loss for farmers [56]. Drought stress was found to affect 23.2% of flowering and reduce panicle development [52]. Drought interferes with grain development during the reproductive stage, and spikelet infertility leads to unfilled grains. Drought causes leaf shrinkage, which affects tillering capacity and photosynthesis in plants. Grain-filling stages suffer from decreased photosynthesis rates and assimilate transport from source to sink. This leads to poor assimilate translocation to the grains, which increases spikelet sterility and produces empty grains. Water stress during the grain-filling stage causes early senescence in the plant, shortening the filling period and reducing yield [57]. Several other scientists reported a reduction in rice yield under drought stress conditions [58] (Table 2).

Table 2. Yield reduction in rice under drought stress condition.

Stage of Growth	Level of Drought Stress	Reduced Yield (%)	References
Vegetative stage	Mild drought stress	21%	[50]
	Withholding water for 24 days from 21 DAT (Severe stress)	50.6%	[55]
Flowering stage	Withholding water at 60 DAT (−30 ± 5 kPa)	23–24%	[52]
	Short severe stress	54%	[54]
	Severe stress	>70%	[59]
Heading	Severe stress	23%	[55]
Reproductive stage	Moderate stress	51–57%	[60]
	Moderate to severe stress withholding water-70 kPa at 0.2 m depth)	51–60%	[61]
	Severe stress	75–87%	[54]
Grain-filling Stage	Mild stress	19%	[54]
	Prolonged mild stress	52%	[54]
	Grain filling	84%	[54]

Several studies on rice have shown that increasing moisture stress leads to a decrease in the number of grains per panicle, grain weight per panicle, and the weight of 1000 grains [52]. In some cases, a drastic reduction in grain number was observed [50]. The decline in grain production is attributed to water stress reducing the starch accumulation capacity of the endosperm in the grain by inhibiting the photosynthesis rate and nutrient uptake, thereby affecting rice yield, similar to the findings of [58]. Moisture stress at the panicle initiation stage was particularly destructive, reducing the number of panicles per hill, panicle length, panicle dry weight, shoot dry weight, and total grains per panicle, regardless of the cultivar. This results in a significant decrease in paddy yield per hectare. Additionally, plant height is reduced by 49.31% under water-stress conditions [51]. Under soil moisture stress (30% of field capacity), the 1000-grain weight decreases by 1.07% to 7.80%. Stress can reduce the translocation of assimilates to the grains during various growth stages, decreasing grain weight and increasing the number of empty grains [47]. The yield traits of 20 rice genotypes showed significant decreases under both normal and drought conditions, with every parameter significantly lower under drought stress [62]. Plant height, grains per panicle, and tiller number were all reduced under stress, with plant height decreasing by 7–45%, tillers per plant by 13–32%, and spikelet fertility by 12–90%. The 1000-grain weight was reduced by 9–56% under drought stress. A recent study indicated that rice yield showed a 25.4% reduction despite variations in response across different studies [58]. The total number of filled grains per panicle was severely affected when drought occurred during flowering [14]. Though drought causes a decrease in agronomic traits, biomass and yield are the most significantly reduced. Thus, it is clear that drought has a significant impact on the morphological characteristics of rice plants, including yield. Drought has been shown to have a negative effect on yield [63].

Pre-anthesis drought treatment has been reported to decrease grain number and grain size in crops [34]. Studies have shown that yield components, such as panicle length, the number of primary and secondary branches per panicle, seed setting rate, and grain weight per panicle, are significantly reduced during drought in *Oryza sativa* L. During the reproductive phase, key factors for grain yield potential include panicle and spikelet development, and even minor changes induced by drought during panicle development can greatly impact crop yield. In Rwanda, the number of panicles per plant, spike length, spikelet fertility, and the grain yield of rice at Bugarama and Tonga sites were reduced under different drought treatments, confirming similar findings. An evaluation of eighteen rice genotypes showed a reduction in panicle number (72%) and grain yield (12%) [19]. In another experiment [2], researchers evaluated six generations (P1, P2, B1, B2, F1, and F) of six rice crosses under drought and irrigated conditions, observing reductions in several traits, including grain yield, under drought conditions. They found that plant height averaged 107.31 cm under well-irrigated conditions, but only 92.00 cm under drought conditions. Similarly, they recorded various parameters, such as the number of ear-bearing tillers (7), panicle length (24.31 cm), number of grains per panicle (94), number of spikelets per panicle (113), spikelet fertility (84.04%), test weight (21.48 g), grain yield per plant (19.64 g), biological yield per plant (45.24 g), and harvest index (43.33%). However, under drought conditions, these metrics decreased to five ear-bearing tillers, 21.36 cm for panicle length, 59.08 g for the number of grains per panicle, 95.59 for the number of spikelets per panicle, 61.80% for spikelet fertility, 18.97 g for test weight, 8.77 g for grain yield per plant, 25.66 g for biological yield per plant, and 34.28% for harvest index. This highlights the impact of drought stress on grain yield and its associated traits in rice cultivation. Audebert [64] also observed reductions in height, leaf area, biomass production, tiller abortion, changes in rooting pattern, and delayed development [47]. Another study revealed a significant decline in mean grain yield of up to 85.7% in rice genotypes due to cumulative drought stress compared to non-stressed conditions. Xu identified the primary reasons for this yield reduction as the significant decrease in the number of effective panicles, the seed setting rate, and a decrease in the 1000-grain weight under drought stress [65].

4. Effects of Drought on Physiological Characteristics

Drought stress impacts various physiological processes in plants, triggering several responses that aid in adapting to such challenging environmental conditions (Figure 4). Optimizing these physiological mechanisms is crucial for enhancing water productivity under water stress [66]. One key response of plants to drought is their ability to maintain turgor pressure by decreasing osmotic potential as a tolerance mechanism. Water deficiency affects rice physiology in numerous ways, including its impact on plant net photosynthesis [67], transpiration rate, intercellular CO_2 concentration, stomatal conductance [42], relative water content (RWC), water use efficiency [68], and membrane stability index. All these parameters decrease under water stress in rice [69].

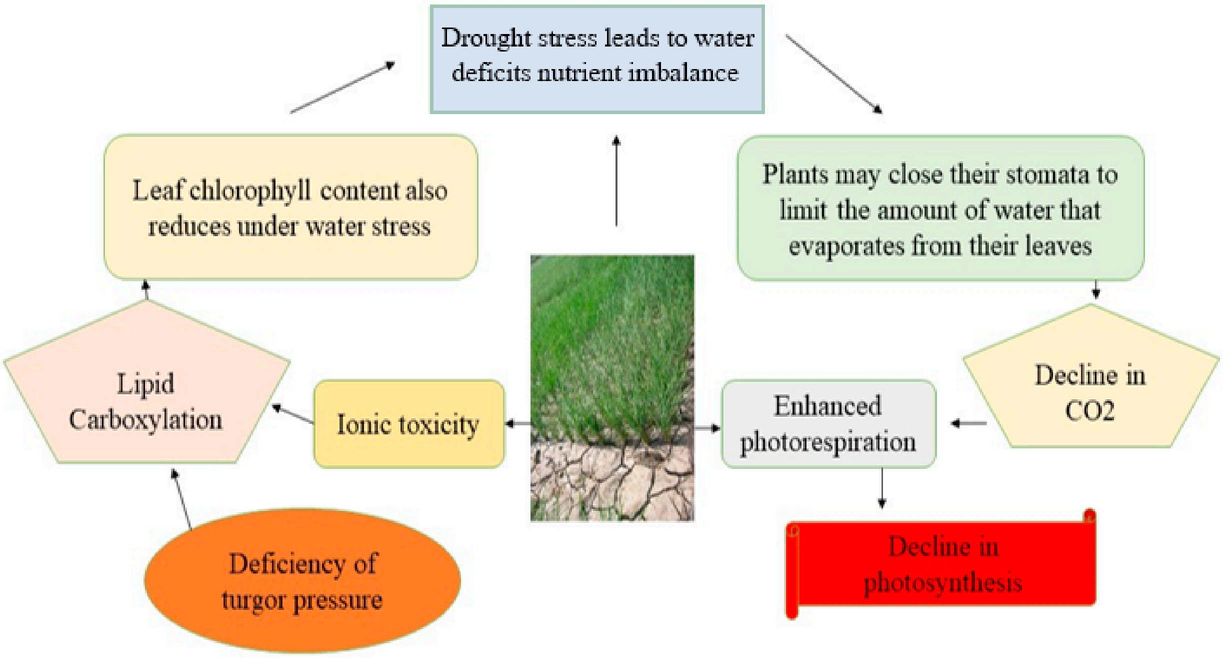

Figure 4. Physiological parameters response under drought.

4.1. Effects of Drought Stress on Chlorophyll Content

Chlorophyll serves as a crucial element of photosynthesis in green plants and is positively correlated with the photosynthetic rate. During drought stress, there is a degradation and oxidation of chlorophyll pigments, a typical symptom of oxidative stress, which leads to a decrease in the plant's chlorophyll content. Drought affects both chlorophyll a and chlorophyll b [3]. The leaves of the plant become aged and yellow as they lose chlorophyll content, due to factors such as the loss of chloroplast membranes, excessive swelling, distortion of the lamellae, vesiculation, and the appearance of lipid droplets. Reduced concentrations of photosynthetic pigments can directly limit the photosynthetic potential and, consequently, primary production. Nevertheless, chlorophyll plays a crucial role in plant adaptation and in maintaining growth and development under drought conditions [70]. Additionally, other pigments like carotenoids contribute to the structure of the chloroplast photosystem, light harvesting, and photoprotection, thereby assisting plants in coping with the challenges of drought. Carotenoids belong to the isoprenoid class of molecules and play a significant role in the antioxidant defense system of plants, although they are susceptible to oxidative stress. Under water stress conditions, both carotenoid and chlorophyll concentrations decrease due to reactive oxygen species (ROS) production in thylakoids [71]. Drought leads to a reduction in carotenoid content ranging from 0.41% to 32.7% between 3 and 12 days of treatment [72]. In an experiment by Saha, leaf pigment content was analyzed after 11 days of treatment [73]. Drought stress significantly decreased chlorophyll-a content in the leaves of BRRI Dhan-30, BRRI Dhan-32, BRRI Dhan-34, BRRI Dhan-38, and BRRI Dhan-56 by 45%, 40.21%, 21.47%, 14.38%, and 7.45%, respectively, and chlorophyll-b content by 29.8%, 29.9%, 17.19%, 17.46%, and 8.97%, respectively. Total chlorophyll content decreased by 46.4%, 45.83%, 43.14%, 38.25%, and 21.31%, and carotenoid content decreased by 25.64%, 19.04%, 16.64%, 15.03%, and 14.09% for BRRI Dhan-30, BRRI Dhan-32, BRRI Dhan-34, BRRI Dhan-38, and BRRI Dhan-56, respectively. Another study carried out by Khan and his team [74] found reduced chlorophyll content in two rice varieties under drought-stressed plants compared to normal plants, similar to other findings [75]. Conversely, another study reported reduced chlorophyll content (SPAD value) in five rice genotypes (Nagina 22, Swarna sub1, NDR 97, Shusk Samrat, and NDR 9830102) at the reproductive stage under drought stress. Drought decreased chlorophyll-a content by 11.2% to 61.6%, chlorophyll-b content by 21.4%, and the chlorophyll-a/b ratio by 18.2% to 58.5% from 3 to 12 days of treatment. It also reduced total chlorophyll content by 9.01% to 66.2% from 3 to 12 days of drought-stressed conditions, consistent with other studies [72,76]. Nithya's study revealed that for rice yield under drought stress, a genotype should possess a high relative water content and chlorophyll stability index, which are severely decreased under water stress conditions [77].

4.2. Effects of Drought Stress on Leaf Photosynthesis, Stomatal Conductance and Transpiration

Drought stress is a critical factor for plant growth, affecting both elongation and expansion growth [78]. Photosynthesis is a critical metabolic process that determines crop growth and production, and it is influenced by water scarcity and drought stress. Plants absorb CO_2 and convert it into sugars, which they then use for growth and energy. Photosynthesis is required for sucrose synthesis, which is a sugar transported by the phloem to various sinks. At the reproductive stage, sucrose is translocated to the grains and then hydrolyzed to provide substrates for starch synthesis, so a decrease in photosynthesis may reduce grain yield. Water stress reduces leaf area, cell size, and intercellular volume. As a result, they capture less sunlight and produce less photosynthesis.

The adverse impacts of water deficiency on mineral nutrition (Table 3) and metabolism result in a reduction in leaf area and alterations in the allocation of plant organs [79]. The limited moisture availability induces unfavorable changes in photosynthetic pigments, reduces and impairs Rubisco activity, diminishes nutrient uptake, damages the photosynthetic machinery, and hampers the performance of crucial enzymes, leading to significant losses in plant growth and yield [80]. Water stress disrupts the normal functions of both photosystem I (PSI) and photosystem II (PSII) [81]. The function of PSII is particularly crucial in reduction reactions and ATP generation. Numerous in vivo studies have observed that drought causes a substantial detrimental decrease in centers for oxygen evolution within the photosystem, resulting in the inhibition of the electron transport chain and the subsequent inactivation of PSII [81]. Various other factors contribute to the decline in photosynthesis, including stomatal closure, reduced turgor pressure, decreased leaf gas exchange, and diminished CO_2 assimilation, ultimately causing damage to the photosynthetic apparatus [3]. The decline in soil moisture likely led to decreased water content in the leaves, resulting in a loss of turgor pressure in the guard cells. Consequently, this causes a reduction in the size of stomatal pores or triggers stomatal closure. Additionally, increased stomatal resistance may have contributed to diminished water transport within the leaves, further lowering stomatal conductance. This decrease in stomatal conductance reduces transpiration by facilitating stomatal closure, thereby prolonging plant survival through the extension of essential soil water reserves in the root zone. Stomatal closure also helps maintain high leaf water content and, consequently, a higher leaf water potential. However, it restricts the entry of CO_2 into leaf tissues for photosynthesis in rice [82]. Elevated photosynthetic rates resulting from enhanced stomatal conductance could potentially enhance biomass and crop yields. Prathi noted a reduction in stomatal conductance and transpiration rate under drought stress compared to control conditions, which may account for the decreased yield production in rice [83], consistent with prior research on rice [84]. Zulkarnain [85] observed a decrease in stomatal conductance across all rice varieties as the severity of the water deficit increased over time. The decline in stomatal conductance was more pronounced after 6 days of stress development compared to well-watered conditions. Drought stress not only restricts grain dry weight and chlorophyll content but also diminishes the photosynthetic rate [86]. Da Mata [87] conducted an experiment aimed at evaluating the effects of water deficit on leaf gas exchange parameters (such as net CO_2 assimilation, transpiration, stomatal conductance, intercellular CO_2 concentration, instantaneous water use efficiency, and instantaneous carboxylation efficiency) as well as leaf non-structural carbohydrate contents (including myo-inositol, glucose, fructose, sucrose, and starch) in eight rice genotypes. The results indicated that the water deficit caused a reduction in stomatal conductance, ranging from 28% to 90% across all genotypes. Similarly, transpiration was also decreased by 40.63% to 65.45% in all genotypes under water deficit conditions. Additionally, net CO_2 assimilation showed a reduction in all genotypes by 70.04% to 99.91% due to the water deficit. Myo-inositol, glucose, fructose, and sucrose were found in the leaves of all the studied upland rice genotypes. Under water deficit conditions, the concentration of myo-inositol decreased by 80% ($P < 0.05$), and glucose concentration decreased by 70.43%. The decline in stomatal conductance, observed as the water deficit progressed in this study, suggests a simultaneous reduction in photosynthesis compared to the control condition, which is consistent with findings reported in a previous study [80].

Table 3. Effect of drought stress on rice plant nutrients.

Stress	Process Affected	Nutrient Loss
Water stress	Soil integrity by erosion	Loss of all mineral nutrients
	Transpiration driven mass flow	Specially loss of mobile nutrients such as Ca, Mg, Si, sulfates and nitrates
	Root growth	Almost all nutrients mostly P and K
	Biological nitrogen fixation	Nitrogen
	Soil microbial activity	Nitrogen

4.3. Effect of Water Stress on Relative Water Content (RWC) and Water Use Efficiency (WUE)

The relationship between plants and water is characterized by various indicators, including leaf water potential and relative water content (RWC) [3]. Relative water content, leaf water potential, and water use efficiency (WUE) are pivotal factors influencing plant water relations. Relative water content serves as a marker of plant water status, reflecting metabolic activity in tissues and playing a significant role in assessing dehydration tolerance. Initially, RWC is higher during early leaf development but decreases as leaves mature and accumulate dry matter. RWC is linked to both water uptake by roots and water loss through transpiration. Numerous studies have noted a decline in relative water content (RWC) in response to drought stress across diverse plant species [88]. Water use efficiency (WUE), which measures the amount of biomass or grain produced per unit of water utilized, provides a straightforward and rapid gauge of how efficiently available water can be converted into grain. Hence, it serves as a fundamental metric for evaluating the effectiveness of water-saving agricultural practices [89]. With water becoming increasingly scarce in agriculture, optimizing water use efficiency, often referred to as "more crop per drop," is crucial, representing a strategy to improve crop performance under conditions of water scarcity. The influence of water stress on the relative water content (RWC) of three rice varieties was explored [90]. The findings revealed a similar declining trend in RWC across all three rice varieties as water stress levels increased (T1 = 5 cm standing water, T2 = 3 cm standing water, T3 = saturated condition, T4 = 75%, and T5 = 50% saturation), with T5 exhibiting the lowest RWC. The highest RWC (73.62 ± 1.71, 76.45 ± 1.80, and 76.72 ± 4.44%, respectively) was observed under the T1 condition compared to the other water treatments. The results show that the change in WUE varies with water level and rice variety, and it decreases as water stress increases. Under drought conditions, relative water content decreased significantly, ranging from 36.1 to 75%, whereas in the no moisture stress plots, it ranged from 63.1 to 84% [91]. Under drought stress conditions, Thai lowland rice cultivars' grain productivity and water use efficiency were lower than in the control group. The grain productivity of the cultivars decreased by 21–45% and 21–52% in the first and second seasons, respectively. Similarly, water use efficiency decreased significantly, ranging from 7 to 53% and 21 to 55% in the first and second seasons, respectively [33]. Water use efficiency is reduced by approximately 39% under drought stress, as demonstrated by [52]. Water consumption in the stress treatments was reduced by 51.69–58.78% compared to the control [65].

5. Effects of Drought Stress on Biochemical Characteristics

Plants accumulate different types of organic and inorganic solutes in the cytosol to reduce the osmotic potential, which helps to maintain the turgor pressure [92]. This biochemical mechanism, known as osmotic adjustment, is strongly influenced by the rate of plant water stress. The accumulation of proline, sucrose, glycine betaine and other solutes in the cytoplasm helps to achieve osmotic adjustment, resulting in an increased water uptake capacity from dry soil. The accumulation of soluble sugar and osmoprotectants are also triggered by water stress. An increase in the antioxidant activity, which improves drought tolerance by scavenging reactive oxygen species, is a further biochemical response.

5.1. Production of Reactive Oxygen Species under Drought Stress

Reactive oxygen species (ROS) are produced naturally during aerobic metabolism. However, extreme ROS production, which damages cells and causes plant death, is often stimulated by drought stress [93]. ROS are produced in many parts of the cytosol during photosynthesis and respiratory processes. In adverse conditions, the excessive reduction in the electron transport chain of mitochondria and chloroplasts leads to an increase in ROS production [94]. This imbalance of ROS production has a negative effect in the reaction of rice with proteins, lipids and deoxyribonucleic acid, resulting in oxidative damage and a detrimental effect on the plant's life cycle. During drought, the photorespiratory pathway produces excessive levels of superoxide radical ($O_2\bullet$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($OH\bullet$) (Table 4). These radicals are very toxic and damage numerous cell components under water scarcity, such as lipid peroxidation, protein denaturation, DNA mutation, membrane damage, disrupting cellular homeostasis, and causing oxidative damage that ultimately leads to cell death. So, reducing ROS over production or increasing antioxidant activity in rice organs is thus an effective way of enhancing rice's tolerance to drought [93]. Gusain found that H_2O_2 content was increased under drought conditions [95]. Simchi Levi reported that under drought stress conditions, the O_2^- content and H_2O_2 content in leaves was higher than the control conditions for all cultivars [96].

5.2. Effects of Drought Stress on MDA and Electrolyte Leakage

MDA is a byproduct of lipid peroxidation and the outcome of cell membrane injury. MDA content increases with the increment of water stress. MDA is recognized as a marker for the evaluation of lipid peroxidation, which is associated with the activity of antioxidant enzymes. If antioxidant enzymes such as SOD, POD, CAT, APX, and GR are increased, MDA will be decreased, which enhances the plant's stress tolerance. Changes in cell membrane integrity are strongly linked to membrane lipid peroxidation and electrolyte leakage. The amount of membrane damage was assessed by measuring the conductance of solute leakage from leaf cells [93]. The impact of drought stress on lipid peroxidation was assessed by observing the fluctuations in MDA levels throughout the stress period, which increased significantly by about 6–12% [91], similar to another research study [95]. MDA levels were significantly higher (~48%) in the leaves of IR64, even under control conditions, and increased dramatically (~67%) when drought stress was applied.

However, even after recovery, the MDA level could not return to the normal level. Simchi-Levi conducted an experiment on three rice varieties in control and drought stress conditions. He discovered that MDA content was lower in the control condition, but increased significantly as the growth stage advanced. That was found for all cultivars under water stress. The increase in MDA content might reflect the drought resistance of different cultivars [96]. The seeds of eight rice (*Oryza sativa* L.) varieties (Azucena, Anjali, Buddha, IR-64, IR-20, Moroberekan, Rasi, and Vandana) were collected by Choudhary [97]. Water was gradually withdrawn from the 4-week-old plants to create a dehydration condition. Water stress led to an increase in electrolyte leakage and decreased membrane stability in all rice cultivars.

Table 4. Different sites of ROS production in cellular organelles and their functions.

Sites	Majorly Produce	Extent of Reactivity	Chemical Functions Occurred by Reactive Oxygen Species	References
Peroxisomes	O_2^-, H_2O_2	Both are moderately reactive	Xanthine oxidase (XOD) produces O_2^- in peroxisomes, which is then transformed to O_2^- and H_2O_2 by SOD.	[98]
Mitochondria	H_2O_2, O_2^-, OH^-	Moderately reactive, Very highly reactive	Over-reduction in ETC and ubiquinone (UQ). O_2^- is produced at two major sites: complex I (NADH dehydrogenase) and complex III (ubisemiquinone).	[99]
Chloroplasts	O_2, H_2O_2, O_2^-	Highly reactive, Moderately reactive	Production of ROS is caused by an excess decrease in ETC in photosystems I and II (PSII) due to electron leakage from QA and QB.	[99]
Endoplasmic reticulum (ER)	O_2^-	Moderately reactive	Superoxide is produced when cytochrome P450 combines with an organic substrate.	[99]
Apoplast	H_2O_2	Moderately reactive	The enzymes oxidases, peroxidases, polyamine oxidases, and oxalate oxidase helps to create apoplastic ROS.	[100]
Cell wall	H_2O_2, OH^-	Moderately reactive, Very highly reactive	ROS are produced by diamine oxidases and malate dehydrogenases, which are found in the cell wall.	[100]

5.3. Drought Stress Effects on Proline and Total Sugar Content of Rice Plants

When a plant is facing a water scarcity, proline formation is an early reaction that lessens cell damage. Proline is an osmoprotectant, a source of food, an energy sink to control the redox potential, and a scavenger of radical hydroxyls. Proline decreases cell acidity and protects the macromolecules from denaturation. It has three major functions during stress, namely as a metal chelator, an antioxidant defense molecule and a signal molecule, rather than acting as an excellent osmolyte. Proline, according to Szabados and Savoure [101], can act as a molecular marker for mitochondrial function, affecting cell proliferation, initiating some gene expressions that play an important role in the protection of plants from stress. By enhancing antioxidant activity during drought stress, the buildup of proline can improve a plant's damage repair capacity. Proline acts as a compatible osmolyte and serves as a reservoir for carbon and nitrogen. It helps maintain osmotic balance and leaf water potential, preventing dehydration by preserving turgor pressure. When rice experiences drought stress, proline levels increase, enhancing stress resilience. Drought-tolerant varieties accumulate more proline and maintain higher root water content (RWC) compared to susceptible ones [102]. Abdula's team [103] found that an increased proline biosynthesis improves drought tolerance in rice genotypes. The ability to accumulate proline can be used as a criterion for assessing drought resistance potential in rice crops [102]. Proline supports drought stress adaptation by promoting cellular synthesis, stabilizing membranes, scavenging reactive oxygen species (ROS), and regulating osmoregulation. Its synthesis, degradation, and transport collectively control its levels in plants under water stress, making it a biochemical marker for selecting drought-resistant varieties. Proline content rises in all rice cultivars under drought stress compared to controls [76]. Rice strain 51 shows a higher proline level under drought stress than under normal conditions [104]. Although the basal proline content in rice varieties is lower under unstressed conditions, the increase during drought stress is significant (over 24%) [91]. Besides proline accumulation, drought stress also leads to an increase in total sugar accumulation. Total sugars contribute to substrate hydrolysis in biosynthetic processes, providing energy and acting as sensors and signals. They function as typical osmoprotectants to maintain cell stability and turgor pressure. During drought stress, total sugar levels increase especially in the stem, helping plants tolerate drought. The results [105] showed that under drought stress, all experimented cultivars had a higher proline content and total sugar accumulation than the control group. Tolerant varieties (Jatiluhur, Ciherang) have a tolerance mechanism based on the accumulation of proline over a longer period of time during drought stress, resulting in total sugar levels that are 2–3 times higher than the control. The phenolic content increased by 100% under drought stress conditions [106]. Proline and total sugar levels were high during drought stress but rapidly decreased after re-watering [107]. According to Ghorbanzadeh [108], the greater accumulation of sugars and amino acids in the roots of the Azucena genotype (drought tolerant) under drought stress may have promoted the absorption of micro- and macronutrients, resulting in improved root growth. Specific sugars and amino acids in roots enhance nutrient absorption through complex biochemical and ecological interactions involving root exudates, microbial communities, and symbiotic relationships. These mechanisms collectively enhance nutrient availability, solubility, and transport, contributing to improved plant nutrition. Sugars secreted by plant roots, such as glucose, fructose, and sucrose, act as root exudates. These sugars serve as a food source for soil microorganisms, promoting a thriving microbial community in the rhizosphere. Beneficial microbes, in turn, enhance nutrient solubilization and availability to plants. Amino acids such as histidine and nicotianamine act as chelating agents. They form complexes with metal ions like iron and zinc, facilitating their transport across root cell membranes and improving their solubility and availability. Sugars and amino acids can modify the rhizosphere pH and redox conditions, improving the solubility of nutrients. Mycorrhizal fungi and nitrogen-fixing bacteria (such as rhizobia in legumes) are supported by root-derived sugars and amino acids. These symbionts significantly enhance nutrient acquisition, particularly for phosphorus and nitrogen [109–111].

6. Role of Antioxidants under Drought Stress

Plants have an antioxidant defense system to guard against oxidative damage (Figure 5), comprising both enzymatic and non-enzymatic antioxidants [93]. Enzymatic antioxidants include superoxide dismutase (SOD), peroxidase dismutase (POD), catalase (CAT), guaiacol peroxidase (GPX), and ascorbate peroxidase (APX), while non-enzymatic antioxidants encompass ascorbate (AsA) and glutathione (GSH). These antioxidants are vital for the reactive oxygen species (ROS) scavenging system in plants, boosting drought tolerance in rice [112]. Detailed information on the cellular locations, characteristics, and roles of these antioxidants in ROS scavenging can be found in Table 5. SOD, a group of metalloenzymes, acts as the first defense against ROS in most subcellular compartments by converting superoxide anion (O_2^-) into O_2 and H_2O_2. Elevated SOD levels under drought stress have been noted in various plants, including rice, peas, wheat, sunflowers, beans, and sweet potatoes [81,94]. CAT, a heme-containing enzyme found in peroxisomes, remains active for extended periods during drought stress and catalyzes the conversion of H_2O_2 into H_2O and O_2, thereby reducing oxidative stress. POD plays a key role in scavenging the H_2O_2 produced by the SOD-catalyzed dismutation of O_2. The primary enzyme in the AsA-GSH pathway that detoxifies H_2O_2 by using AsA as an electron donor is APX. APX and POD are most likely involved in the precise regulation of reactive oxygen species (ROS) for signaling purposes, whereas CAT removes excess ROS during stress. When ROS levels become too high and inhibit APX activity, CAT steps in to neutralize the ROS. Unlike APX, which is found in a variety of cellular organelles, CAT is found only in peroxisomes and eliminates the large amounts of ROS produced during stress, indicating variable activity [113]. APX is essential for rice development, particularly during the seedling and reproductive stages, as it scavenges H_2O_2 in response to drought and other abiotic stresses [58].

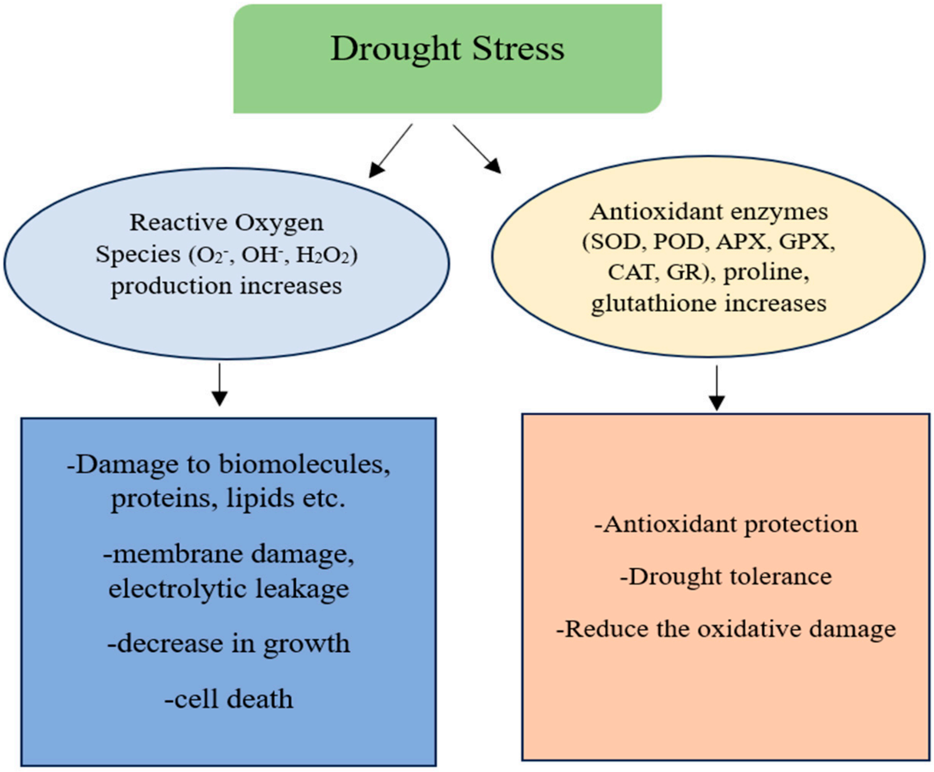

Figure 5. A schematic illustration of reactive oxygen species (ROS) damage and antioxidant defense process during drought stress in rice.

Table 5. Enzymatic and non-enzymatic antioxidants under drought stress their location and features in Rice plants.

Enzymatic Antioxidants	Location	Features and Their Role	References
Superoxide dismutase (SOD)	Cytosol, Chloroplasts, Peroxisomes and Mitochondria	Dismutate O_2^- and are reduced to H_2O_2 and oxidized to O_2. Enhanced drought tolerance.	[93]
Guaiacol peroxidase (GPX)	Chloroplasts, Cytosol, Mitochondria and Endoplasmic reticulum	Many biosynthetic processes involving GPX include cell wall lignification, wound healing, ethylene synthesis, IAA degradation, and drought resistance.	[114]
Ascorbate peroxidase (APX)	Cytosol, Peroxisomes, Chloroplasts, and Mitochondria	APX maintains the ROS levels and reduces H_2O_2 to water.	[93]
Dehydroascorbate reductase	Chloroplasts, Mitochondria, and Cytosol	It catalyzes the reduction in DHA by GSH to AsA and plays an important role in the maintenance of AsA (in its reduced form).	[115]
Glutathione reductase (GR)	Cytosol, Chloroplasts, and Mitochondria	GR reduces GSSG to GSH, thereby maintaining the cellular GSH/GSSG ratio. It contains a crucial disulfide group and also detoxifies the H_2O_2 produced in the Mehler reaction.	[115]
Catalase (CAT)	Peroxisomes, Glyoxisomes, and Mitochondria	H_2O_2 generated in peroxisomes is primarily neutralized by CAT, which specifically targets H_2O_2. CAT increases tolerance to abiotic stress in transgenic plants.	[114]
Ascorbic acid (AsA)	Cytosol, Chloroplasts, Peroxisomes, Mitochondria, Vacuoles and Apoplast	Ascorbate plays an important role in protecting against oxidative stress caused by excessive ROS production. AsA is essential for many physiological processes in plants, including growth, differentiation, and metabolism.	[115]
Glutathione (GSH)	Cytosol, Chloroplasts, Peroxisomes, Mitochondria, Vacuoles and Apoplast	O_2^- is a non-protein thiol crucial for intracellular defense against oxidative damage induced by ROS. GSH is integral to various biological processes, such as cell growth and division, signal transduction, protein and nucleic acid synthesis, and the activation of stress-responsive genes.	[115]

Another potent antioxidant pivotal in rice under drought stress is GPX, which functions effectively to scavenge ROS and produce related compounds like lignin, guaiacol, and payragallol, which act as electron donors for eliminating hydrogen peroxide both inside and outside the cell. The heightened GPX activity in rice under drought stress is extensively studied and acknowledged as a reliable method for identifying tolerance traits [57]. As for the effect of drought treatment on enzyme activity, it is noted that SOD and POD activities increase over the duration of drought, peaking approximately 21 days after drought onset [112]. Comparatively, the SJ6 variety (drought-sensitive) displayed SOD activity increases of 31.1%, 52.2%, and 62.5%, while the DN25 variety (drought-tolerant) showed increases of 48.7%, 65.5%, and 74.8% with escalating drought intensity. POD and APX activities surged rapidly after the drought onset, reaching peaks on the 9th and 12th days of the drought in both cultivars, respectively. However, their activities declined swiftly during the re-watering stage. Enhanced SOD activity has also been documented in rice plants during drought conditions [94]. Kamarudin examined how drought stress impacts the key mechanisms for detoxifying reactive oxygen species (ROS) in advanced mutant rice varieties, focusing on antioxidant enzymes such as CAT and GPX [116]. During the initial season, drought stress led to higher CAT and GPX activity compared to the control group. Moreover, in both seasons, drought stress induced the highest GPX activity compared to the control. Specifically, drought stress increased catalase activity in the leaves of BRRI Dhan-30, BRRI Dhan-32, BRRI Dhan-34, BRRI Dhan-38, and BRRI Dhan-56 by varying percentages (7.65%, 13%, 15.5%, 22.59%, and 37.67%, respectively) after 15 days of treatment. BRRI Dhan-56 displayed the most substantial increase in CAT activity under stress conditions [73]. Additionally, the Fen experiment observed increased CAT activity in drought-tolerant rice varieties (*Oryza sativa* L.) [117]. Furthermore, it enhanced superoxide dismutase (SOD) activity in the leaves of BRRI Dhan-30, BRRI Dhan-32, BRRI Dhan-34, BRRI Dhan-38, and BRRI Dhan-56 by varying percentages (15.38%, 24.26%, 68.12%, 70.59%, and 94.17%, respectively) after 15 days of treatment. Once more, BRRI Dhan-56 showed the most significant increase in SOD activity under stress conditions. These findings corroborate Lum's research [36], indicating heightened SOD activity in seedlings subjected to drought stress, particularly in upland rice varieties (*Oryza sativa* L.).

The AsA-GSH (Halliwell–Asada) pathway holds significant importance in antioxidant function, operating primarily within the chloroplast to provide photoprotection by neutralizing hydrogen peroxide. This pathway involves a sequential process where H_2O_2 is reduced by APX, utilizing AsA as the electron donor. In rice plants, heightened enzyme activities within this pathway serve as crucial protective mechanisms against oxidative stress during drought periods. Additionally, an increase in the activity of the AsA-GSH cycle directly correlates with elevated levels of both ascorbic acid and GSH in rice plants experiencing drought conditions [93]. AsA and GSH are essential in combating drought stress and excessive ROS production, with GSH acting as a direct scavenger of free radicals, protecting proteins, lipids, and DNA. The accumulation of glutathione serves to shield plants from the detrimental effects of stress. Various studies highlight the importance of the AsA-GSH cycle in mitigating the drought responses caused by water scarcity in rice [94]. Glutathione plays an indispensable role in scavenging ROS, thus preventing oxidative damage throughout all physiological compartments of plant cells. After 15 days of drought treatment, catalase activity in rice leaves surged by 74.70%, and superoxide dismutase activity rose by 1.1 times [72]. Additionally, a range of antioxidant enzymes—catalase (CAT), superoxide dismutase (SOD), glutathione peroxidase (GPX), ascorbate peroxidase (APX), and glutathione reductase (GR)—exhibited significant increases in both shoots and roots across various rice varieties under drought stress compared to control plants. These enhancements ranged from approximately 25% to 155% in shoots and 28.57% to 140% in roots. Consistent findings were also noted in Kumar's study [47], who observed notable increases in superoxide dismutase, catalase, and glutathione reductase activities under drought stress. Furthermore, Wang reported that the activity of SOD, peroxidase (POD), and CAT, critical for hydrogen peroxide scavenging, increased with prolonged and intensified drought stress in rice [112]. Thus, boosting the production of natural antioxidant enzymes presents a promising strategy for shielding plants from oxidative damage and bolstering their resilience to drought [106].

7. Drought Mitigation Approaches

Water stress altered the crop's morphology and physiology, resulting in a reduction in grain yield. As a result, we must develop varieties that can withstand water stress and produce more. The following mitigation strategies could be useful:

1. Development of early maturing rice varieties to mitigate the drought.
2. Development of drought tolerance varieties that perform better under water scarcity conditions.
3. Improving and incorporating essential characteristics for rice plants to survive in water-stressed environments is crucial. These traits encompass deep root systems, leaf rolling, cuticle wax, stomatal positioning, and activity, alongside attributes like high tissue water potential, membrane stability, and quick recovery from water stress. Root features are vital for plant adaptation to drought, particularly their depth and extension into deeper soil layers, which boost crop performance under limited water availability, especially when moisture exists at deeper soil levels [42]. Leaf rolling is a key criterion for selecting drought-resistant rice varieties. Varieties with strong drought tolerance exhibit leaf rolling during stress to minimize water loss, and they recover rapidly once stress subsides. This is essential in rice farming, since the flag

leaf, crucial for grain filling and development in cereal crops, plays a significant role [42,43].

4. Crop management strategies involve a series of steps, beginning with the careful selection of suitable crop types and planting locations. These strategies include tasks such as preparing the seedbed, choosing the best production system, deciding when and how to plant, managing pests and diseases, and efficiently handling nutrients until harvest. Soil type, weed management, irrigation methods, and land preparation are all important factors in rice farming when aiming to maximize water productivity. Minimizing land preparation time to reduce evaporation is a practical method for increasing water productivity. Furthermore, encouraging early canopy closure through optimal plant density and selecting rice varieties with high seedling vigor can reduce evaporation after planting [118]. These efforts not only conserve water but also improve weed competition, thereby reducing non-beneficial transpiration and increasing yield. Besides agronomic techniques, ongoing crop enhancement remains crucial for maintaining productivity and profitability in rice cultivation.
5. Breeding approaches for drought tolerance in rice.

The exploration of natural variations within rice genotypes offers an avenue to discover new strains possessing valuable drought-resistant characteristics, along with the genes and specific locations linked to these traits. Utilizing these newfound genotypes in traditional breeding endeavors and employing marker-assisted selection techniques facilitates the development of drought-tolerant rice varieties. This breeding initiative aims to yield robust lines with enhanced quality attributes, subsequently introducing these cultivars into agricultural practices. Genetic engineering and conventional breeding methodologies stand out as prevalent and efficient approaches for addressing drought-induced stress in rice cultivation.

Breeders are facing various challenges to improve the drought resistance trait in rice. Genes related with drought tolerance mechanisms have been identified by fine mapping and characterized as mendelian factors. In rice, the *drought-induced 19* (*Di19*) gene family contains seven members. Wang et al. [112] found that *OsDi19-4* overexpression rice shows drought tolerance in the decreased water loss from leaves and enhanced ROS-scavenging activity under drought conditions. Wu et al. [119] characterized a new gene, *EHANCED DROUGHT TOLERANCE 1* (*EDT1*), a member of group E of bZIP transcription factor family in rice, which plays a positive role in drought tolerance and provides valuable targets for breeding drought-tolerant rice genotypes. To improve different traits in rice under water scarcity, the identification of genes is important [35]. Several other scientists reported different traits which were induced under drought stress conditions (Table 6).

Table 6. Different traits which were induced under drought stress conditions.

Crop	Traits for Drought Tolerance	Gene	Reference
Rice	Increased germination efficiency.	*SAPK2*	[120]
	Lower stomatal density transpires less water.	*OsEPF1*	[35]
	Enhances the drought tolerance at the vegetative stage and the reproductive stage, promoting grain yield by approximately 20% through root development.	OsERF71	[121]
	ABA is a key hormone in drought response, regulating stomatal closure and expression of stress-responsive genes.	OsNCED3, SVP, CYP707A1/3 and AtBG1,	[112,122]
	Changing H_2O_2 concentration to enhance drought tolerance.	*OsGRXS17* gene	[123]
	Transcriptional factors in rice.	OsNAC006	[41]

Table 6. *Cont.*

Crop	Traits for Drought Tolerance	Gene	Reference
	Increases grain yield under stress.	*OsPYL9*	[35]
	ROS (reactive oxygen species) scavenging gene, reduces oxidative damage under drought stress.	OsSOD1	[93]
	Accumulation of proline to protect cellular structures and maintain osmotic balance.	P5CS, δ-OAT, OsP5CS1 and OsP5CS2	[38]
	Regulates drought response through the ABA pathway.	JERF1	[124]
	The accumulation of sugar increases drought tolerance.	JERF3	[58]

6. Osmoprotectants are involved in signaling and controlling plant reactions to various stresses, such as diminished growth, which could serve as a stress adaptation mechanism (Table 7). Proline, trehalose, fructan, mannitol, glycinebetaine, and similar compounds are common osmoprotectants found in plants [17]. These substances act as adaptive agents, facilitating osmotic regulation and safeguarding subcellular components in stressed plants [125]. According to Yang's proposition, rice varieties exhibiting elevated levels of free spermidine, spermine, and insoluble-conjugated putrescine are likely to demonstrate superior performance when subjected to drought stress. Polyamines, including spermidine, spermine, and putrescine, play significant roles in plant responses to drought stress through osmotic adjustment, membrane stabilization, antioxidant defense and the promotion of root growth. Polyamines contribute to osmotic adjustment by accumulating in plant cells, which helps maintain cell turgor and hydration during drought. Spermidine, spermine, and putrescine stabilize cell membranes by interacting with phospholipids and proteins, reducing membrane permeability and preventing cellular damage under drought stress. They also enhance the antioxidant defense system by scavenging reactive oxygen species (ROS) directly or by upregulating antioxidant enzyme activities, thereby protecting plants from oxidative damage induced by drought. Polyamines promote root growth and development, enhancing water and nutrient uptake during drought conditions [3,126].

Table 7. Several adaptations of osmoprotectants to induce drought tolerance in rice.

Traits	Function	Reference
Proline	Exogenous application of proline in plants under stress conditions increases the accumulation of proline, which helps the plant to repair the damage under stress by improving the antioxidant activity in plants.	[92]
Sugar contents	Increased under drought.	[107]
Glycinebetaine (GB)	Seed priming and foliar spray of GB improved growth under well-watered and water deficit conditions due to enhanced water potential, an antioxidant system, the integrity of cellular membranes, and photosynthesis.	[3]
Leaf starch regulation	Improved osmotic stress tolerance.	[127]
Starch contents	Increases in starch content protect the plant.	[107]

7. The utilization of silicon when plants are experiencing water scarcity results in heightened plant stature, leaf coverage, biomass, and rice production [42]. Numerous investigations have demonstrated that applying silicon directly to leaves has a beneficial impact on controlling foliar diseases in different crops, including rice. Using a

silicon solution at a concentration of 0.50% led to the largest grain size and protein content. Various research findings have also indicated that the application of silicon enhances drought tolerance in key crops like rice by promoting root development, stomatal conductance, photosynthesis, and antioxidant mechanisms.

8. It is possible to save between 50 and 110 kg N ha^{-1} by applying compost in addition to ascobein without sacrificing grain quality. The compost has a high percentage of organic matter (26.7%), carbon (15.3%), total solids (45%), and nitrogen (1.36%). Incorporating soil compost enhances the soil's physio-chemical and biological characteristics while potentially lowering the use of pesticides and fertilizers.
9. SA helps to regulate important metabolic responses in plants and has led to an increase in their relevance [74]. Rice seeds primed with salicylic acid (1.0 and 2.5 mmol/L) improves the development characteristics of seedlings under drought stress, including emergence rate, biomass accumulation, plumule, and root length. Furthermore, SA primed rice seedlings under drought stress exhibit increased contents of chlorophyll, carbohydrates, total soluble sugar, and protein, as well as lower MDA levels because of the improved activities of CAT, APX, and SOD.
10. Pink pigmented facultative methylotrophic (PPFM) bacteria serve as a versatile and beneficial factor in enhancing the growth and productivity of rice in conditions of moisture deficiency. This innovation was pioneered by Tamil Nadu Agricultural University (TNAU) as a measure to alleviate drought effects. It is offered in a commercial formulation that can be diluted with water (at a rate of 10 mL per liter of water) and applied across the field at a rate of 500 L per hectare using a boom sprayer. Application can be carried out during periods of stress, encompassing both the vegetative and reproductive stages of the rice crop [56]. PPFMs are involved in phosphorous mineralization, siderophore, ACC deaminase, phytohormone production, and assimilation of greenhouse gasses. Additionally, these organisms can also resist harmful UV radiations effectively, as they possess polyketide synthases that could serve as a source of novel bioactives that can protect plants from abiotic stress, such as drought [128].
11. Role of plant growth regulators (PGRs) in drought tolerance

Plant growth regulators (PGRs) play vital roles in a multitude of metabolic pathways essential for plant growth and development, regardless of environmental conditions (Table 8). They function as signaling molecules to govern various processes and genes associated with plant growth and development, including their ability to adapt to drought stress. Key PGRs like auxins, gibberellins (GAs), cytokinins (which promote growth), abscisic acid (ABA, a growth inhibitor), and ethylene (a gaseous hormone involved in plant maturation) are directly involved in regulating water transport within plant roots and shoots by modulating cell membrane permeability and, consequently, cell turgor [129]. The growing importance of plant hormones in bolstering tolerance to abiotic stress in rice plants is briefly summarized here (Table 8).

Table 8. Exogenous application of various plant growth regulators and their effect on drought stress mitigation in rice.

Plant Hormone	Mode of Application	Level of Drought Stress Used	Morpho-Physiological and Biochemical Effects on Rice	Reference
Auxin	Foliar spray	Water stress SMC between 7.3% ± 0.5% and 6.7% ± 0.2%	Reduces lipid peroxidation and ROS accumulation while enhancing membrane stability; improves chlorophyll content and sustain greenness; improves spikelet fertility, number of grains per panicle, and weight of grains per panicle.	[115]
Gibberellic acid (GA)	Foliar spray	Water stress (PEG6000, 15%)	Boosts the soluble sugar content, and enhances shoot and root lengths, as well as germination percentage.	[38]

Table 8. *Cont.*

Plant Hormone	Mode of Application	Level of Drought Stress Used	Morpho-Physiological and Biochemical Effects on Rice	Reference
Abscisic acid (ABA)	Foliar spray	Water stress (PEG6000, 15%)	Boosts the expression of several drought-responsive genes, which in turn improves the recovery of the net photosynthesis, stomatal conductance, and transpiration rate during drought.	[130]
Glycinebetaine (GB)	Seed priming and foliar spray	Drought stress (50% field capacity)	GB enhanced plant growth in well-watered and drought conditions because of an enhanced water potential, antioxidant system, and integrity of cellular membranes	[3]
Polyamines	Seed priming and foliar spray	50% of field capacity	Enhanced levels of free proline, anthocyanins, phenolics and photosynthesis. Increased water use efficiency, and leaf moisture status, as well as reduced oxidative damage	[3]
Jasmonic Acid	Foliar spray	Severe drought stress	JA improves drought tolerance in a number of ways, such as by scavenging reactive oxygen species (ROS), lowering oxidative stress, closing stomata, and promoting root development.	[131]
Cytokinin (CK)	exogenously apply through foliar spray	50% of field capacity	Plant hormone called cytokinin (CK) stimulates cell proliferation, roots nodule formation, and postpones leaf senescence. Cytokinin contributes to drought tolerance through five different mechanisms: it protects the photosynthetic system, increases antioxidant levels, controls water balance, regulates plant development, and controls hormones associated with stress.	[132]

8. Conclusions

Drought stress is a major problem for rice cultivation which causes a range of morphological, physiological and biochemical changes that greatly hamper plant growth and yield. According to the findings, drought stress reduced plant height, leaf area, root length, shoot length, chlorophyll content, photosynthetic value, RWC, WUE, and light interception, and increased membrane injury, which led decreased plant outputs. Drought also increase ROS, antioxidant enzymes activity, proline and soluble sugar content. The enhanced activity of SOD, CAT, POD, GR, DHAR, as well as a higher sugar and proline accumulation and a better GSH/GSSG ratio, indicate a strong anti-oxidative defense mechanism that reduces oxidative stress and prevents lipid peroxidation, which in turn increases photosynthetic activity and improves rice yield. Several remediation processes have been proposed to ameliorate the negative effects of drought stress, including the foliar application of exogenous substances like proline, salicylic acid, and seed treatment with silicon and plant hormones (PGRs), as well as using a tolerant variety and water management to improve plant height, spike length, number of grains per spike, grain yield, physiological parameters like photosynthesis, transpiration, relative water content, and biochemical characteristics.

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Abbreviation

LAI	Leaf area index
ROS	Reactive oxygen species
RWC	Relative water content
WUE	Water use efficiency
SC	Stomatal conductance
SOD	Superoxide dismutase
POD	Peroxidase
CAT	Catalase
GPX	Guaiacol peroxidase
APX	Ascorbate peroxidase
AsA	Ascorbate
GSH	Glutathione
GR	Glutathione reductase
XOD	Xanthine oxidase
PAR	Photosynthetic Active Radiation
MDA	Melondialdehyde
H_2O_2	Hydrogen peroxide
O_2^-	Superoxide radicle
OH^-	Hydroxyl radical
GB	Glycinebetaine
CK	Cytokinin
JA	Jasmonic Acid
GSSG	Glutathione disulfide
DHAR	*Dehydroascorbate reductase*
MDHAR	*Monodehydroasorbate reductase*
SA	Salicylic Acid
PGRs	Plant Growth Regulators
GA	Gibberellic Acid
ABA	Abscisic acid
ATP	Adenosine triphosphate
MSI	Membrane Stability Index
PSI	Photosystem I
PSII	Photosystem II
CO_2	Carbon dioxide

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