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Egypt. J. Agron. **Vol. 44**, No. 2-3, pp. 97-115 (2022)

Egyptian Journal of Agronomy
http://agro.journals.ekb.eg/

Drought Impacts and the Tolerance Mechanisms in Rice (*Oryza sativa* L.): A Review

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RICE (*Oryza sativa* L.) is considered the major source of calories for more than half of the world's population. However, this Asian staple crop is susceptible to abiotic stress, including drought, throughout its life cycle. The main theme covered in this review includes types of drought and its effects on rice morphological, physiological, biochemical, and agronomical levels and their adaptive mechanisms under drought. Drought in the rainfed ecosystem during critical stages (germination and reproductive stages) has seriously undermined rice production, posing a danger to global food supply and sustainable food production worldwide. It caused a reduction in the germination rate, CO_2 assimilation rate, photosynthesis activities, gas exchange via the leaf, plant height, number of panicles, seed weight, biomass, harvest index, and yield. Delayed seed germination, flowering, and maturity of the rice plant are also associated with water stress. Under mild or adverse drought conditions, plants exhibit certain adaptive changes or tolerance mechanisms, including activating antioxidant systems and the production of osmolytes such as proline and polyamine, subsequently enhancing drought tolerance. The role of phytohormones in alleviating stress has been recognized and highlighted in this review. Furthermore, the plant root system also plays a significant role in drought. The information provided in this review will help researchers to have comprehensive knowledge and understanding of the changes and disruptions that occur in rice during water stress and its tolerance mechanisms, subsequently facilitating the selection and development of drought-tolerant rice.

Keywords: Abiotic stress, Antioxidant system, Reproductive stages, Stomata closure, Yield.

Introduction

Rice (*Oryza sativa* L.) is one of the most valuable cereal crops worldwide and has contributed to meeting global food demand (Das et al., 2021). As much as 600 Mt is produced yearly on more than 150 Mha of land (Khush, 2005; Mohd Ikmal et al., 2019). Rice serves as a source of calories (50 to 80%) and protein (15%) for the world's inhabitants (Pandey & Shukla, 2015; Nasrin et al., 2020). Asia continent produces and consumes 90% of the world's rice. Rice belongs to the genus *Oryza* of the family Poaceae. The genus *Oryza* comprises 22 species, including *Oryza sativa* L. and *Oryza glaberrima* Steud, cultivated (Fahad et al., 2019). Due to its semi-aquatic nature, rice can be grown in diverse ecosystems (rainfed upland and rainfed lowland). Concerning rice production, it is projected that for every increase in the world population by 1 billion individuals, an additional 100 Mt of rice will be required to fulfill the demand (Swamy & Kumar, 2013). However, the current production rate is below expectation compared to the quantity needed to achieve the projected demand by 2050 (Yuan et al., 2022) due to various factors such as pest attacks, disease outbreaks, urbanization, and change in climate patterns. More frequent climate changes and a reduction of

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Received 01/07/2022; Accepted 23/10/2022
DOI: 10.21608/AGRO.2022.140551.1321

fertile agricultural land put a lot of pressure on rice production globally. Environmental stress is considered any environmental variable that disrupts plant functionality. These stress include drought, freezing, heat stress, mineral toxicities, salinity, submergence, and other environmental factors. They are more dangerous when they occur simultaneously.

According to Sallam et al. (2019) a drought is a period of lack or shortage of rainfall or irrigation, that causes a decrease in soil water availability resulting in yield loss. The drought has affected 26% of the earth's usable areas, followed by mineral stress with 20% and cold stress with 15% (Tiwari et al., 2021). Due to continuous changes in climatic patterns, a possible increase in the drought scenarios soon is expected. It is projected that by 2050, more than half of the world's agricultural land will be affected by drought (Zia et al., 2021). Rice is prone to water stress because it possesses swift stomatal closure, thin cuticular wax, and a small root system (Manikanta et al., 2022). Due to the drought-induced stress, global rice yield loss was estimated to be USD37 million, which is approximately 34% of the overall rice production (Hosseinifard et al., 2022). Apart from frequent drought scenarios encountered worldwide on the paddy field, there is also the concern of the continuous disappearance of freshwater, with rice making use of more than 50% of the total available freshwater in Asia (Surendran et al., 2021). It was estimated that rice production requires as much as 3000 liters of water to produce 1 kg, which is much compared with the amount of fresh water available for production (Tabassum et al., 2021). Frequent occurrences of drought have triggered and generated various reactions and responses from plants (Fig. 1), which have brought about various adaptive changes in the plant's morpho-physiological and biochemical pathways, including growth rate, plant structure, osmotic potential, and antioxidant defenses (Kanwal et al., 2022). With expected climate change scenarios to worsen, drought occurrence is likely to intensify as time ticks, leading to more complex interactions of drought with other biotic and abiotic stresses (Thomas et al., 2017). From an application perspective, having comprehensive knowledge and understanding of the impact of drought on the rice plant is crucial to aiding the development and selection of cultivars with drought-tolerant traits.

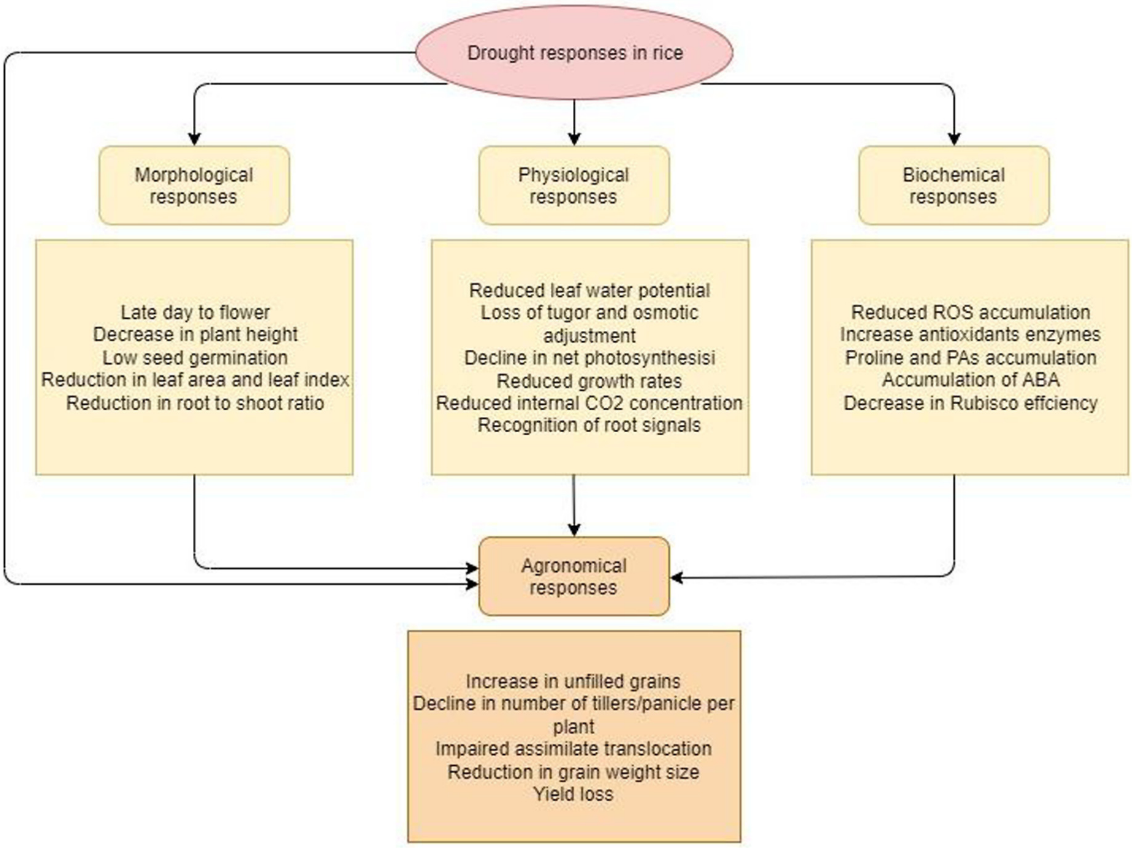

Fig. 1. Drought elicited diverse responses and reactions in rice causing yield loss

Types of drought

The severity of the drought depends upon multiple factors such as the period, time, and extent of exposure, development and growth stage when drought occurs, and the degree of severity (Anjum et al., 2011). A prolonged dry season enhances drought intensity, thereby increasing the evaporation rate, and resulting in crop failure. In the rainfed ecosystem, drought can be categorized into three types; i) early drought stress that ensues during the vegetative growth stage, which is the initial germinating stage, ii) an intermittent drought that occurs at the developmental stage such as the flowering stage, and iii) terminal drought stress that arises before the end of the planting season (Fisher & Fukai, 2003; Kanwal et al., 2022). Just recently, a new classification method was released by the International Rice Research Institute (IRRI) to which there are four major classes of drought-prone rainfed environments; i) drought stress at the beginning of the new cropping season in lowland areas (non-flooded soils and root zones below saturation for at least ten consecutive days before flowering, ii) drought stress at the flowering stage in lowland (non-flooded soils and root zone below saturation for at least seven days around anthesis), iii) drought stress at the end of the cropping season in lowland (non-flooded soils and root zone below saturation for at least ten consecutive days after flowering, and iv) drought stress at the flowering stage in the upland field (without rainfall or irrigation for at least seven days around anthesis and groundwater table below 100cm) (Kumar, 2018).

In the present decade, the occurrence of early-season drought in various rice ecosystems especially shallow rainfed ecosystems has become worrisome. This is triggered by the late arrival of monsoon rains or long gaps between rainfalls (Swain et al., 2017). In Thailand, the occurrence of early-season drought is widespread in several regions, affecting the time of seedling transplanting and direct seeding (Jongdee et al., 2006) which account for 67% of the country's total rice-growing area. This rice system is often characterised by too much and too little water in the same season. Farmers' estimates of their annual losses to drought are as high as 45% in the upper parts of the toposequence. In contrast to irrigated rice systems, gains from crop improvement of rainfed rice have been modest, in part because there has been little effort to breed and select for drought tolerance for the target rainfed environments. The crop improvement strategy being used in Thailand considers three mechanisms that influence yield in the drought prone targets: yield potential as an important mechanism for mild drought (where yield loss is less than 50%. This type of drought occurs mostly within the Southeast region, predominantly in the Mekong area of Cambodia, thereby causing a delay in transplanting; however, in severe cases, planting may not be possible (Kamoshita et al., 2008) and drought frequently reduces yield. This paper reviews drought-resistance traits in rice and their quantitative trait loci (QTLs. Early-season drought delays the maturity process due to prolong vegetative stage, reduces the number of tillers (Novero et al., 1985; Lilley & Fukai, 1994; Boonjung & Fukai, 1996), causes a reduction in the leaf area, appearance, transpiration, and photosynthesis via leaf senescence (Gano et al., 2021). A decrease in the leaf area experienced is considered an avoidance strategy displayed by plants to escape early-season water stress (Gano et al., 2021). Early-season drought has a significant effect impact on yield but is not detrimental compared to terminal drought due to the plant's capability to recover at a certain point of the season (Kamoshita et al., 2008) and drought frequently reduces yield. This paper reviews drought-resistance traits in rice and their quantitative trait loci (QTLs).

Intermittent drought occurs mostly at any period during the developmental and reproductive stages (Nasir & Toth, 2022**)**. Water stress during the reproductive stage may cause delays in several developmental processes, such as panicle initiation and anthesis (Rahman et al., 2002; Singh et al., 2017). This causes a delay in flowering by around two to three weeks and a decrease in spikelet fertility, grain number, and grain yield (Fisher & Fukai, 2003). Water deficit during anthesis or cell division causes pollination abnormality, desiccation of spikelet, inhibition of anthesis (Pinheiro et al., 2000), and an increase in the spikelet sterility (Boonjung & Fukai, 1996). Possession of a deep root system with high root length density may be an essential feature during intermittent drought stress if the germinating conditions favor the root development at depth (Kamoshita et al., 2008) and drought frequently reduces yield. This paper reviews drought-resistance traits in rice and their quantitative trait loci (QTLs. Drought-induced before the end of the planting season, known as terminal drought, results in drastic yield loss (Kanwal et al., 2022) due to the disappearance of water at the root region for the transpiration process and may bring about plant death (Fisher & Fukai, 2003).

Effects of drought on germination and morphological traits

Since water is essential for nearly all aspects of crop development and production, a plant is believed to have developed various approaches to compensate for a restricted water supply (Yadav & Sharma, 2016; Islam et al., 2018). However, the effect of drought stress on specific morpho-physiological changes in rice cultivars varies significantly (Nithya et al., 2020). First and foremost, seed germination, seedling emergence, and early establishment are considered critical stages in plant growth and survival. Germination is regarded as one of the most delicate phases of a plant life cycle, influenced by the moisture content in the growing media. The imposition of drought stress at this stage inhibits the seeds from imbibing a sufficient amount of water, which eventually affects several processes (physiological and biochemical) in the seed, causing a decrease in the germination percentage, rate, and time, a decrease in the growth of the seedling and the total plant number per unit area (Khodarahmpour, 2011; Soleymani & Shahrajabain, 2018; Zia et al., 2021). Additionally, variables such as the seed germination ability, root/shoot biomass, length of hypocotyl, and fresh/dry weight decline progressively in the presence of polyethylene glycol accumulation, whereas the root measurement was expanded (Akram et al., 2019).

Drought stress inhibits cell growth due to a lack of turgor. Since the development of seedlings is dependent on the active meristematic cell division, the initiation of drought restricts cell growth and expansion via water spilling out of the xylem into the surrounding enlarging cells (Akram et al., 2019). Water stress inhibits the plumule elongation and reduces the seedling vigor, resulting in a poor seedling establishment due to shorter coleoptile. Using varieties with long coleoptiles can be considered a good way to achieve improved seedling establishment (Anjum et al., 2017). Seed germination and early seedling growth stage have been documented to be more vulnerable to drought stress, which causes a decrease in plant height. Based on previous literature, water stress has been confirmed to be a major factor that causes a reduction in the height of the seedlings, seed germination, and the number of the tiller (Islam et al., 2018).

Furthermore, adenosine triphosphate (ATP) is essential for cell development under drought circumstances. The seedling establishment needs energy for the anabolic process in the seed. For the seedling to withstand drought stress, the ATP is regulated, which causes a decrease in osmotic potential due to an osmotic compartment accumulation in developing tissues. This allows for reduced seedling growth during drought at the expense of ATP (Anjum et al., 2017). Plant seedlings are hampered by drought, causing a decrease in the leaves' water potential and gas exchange which leads to reduced growth and rate of survival (Poorter & Markesteijn, 2008). Water stress that is induced at the seedling stage may have prolonged consequences on the plant life cycle, including the growth and development phase and, consequently, the grain yield. The drought tolerance and susceptible varieties can be determined at the seedling stage by evaluating the seed germination rate under water stress (Kumar et al., 2015). In addition, seed priming is an effective and environmentally friendly strategy to improve seedling tolerance under drought-stress conditions (Liu et al., 2022) (Table 1).

Days to flowering are affected by several factors which include intensity, water scarcity, and time (Lanceras et al., 2004). In rice, apical morphogenesis is drought-sensitive. Drought experienced during flower induction and inflorescence development causes the flowering to be delayed or even completely inhibited (Barnábas et al., 2008). A reduction of panicle length and development of the floral part in a slow manner is reported to be the primary causes of delayed flowering time under drought. Flowering delay may also be due to impaired vegetative growth of the plant. A plant that flowers late generally uses excessive water at the vegetative stage leading to too much water deficiency at the later stage (Pantuwan et al., 2002; Haque et al., 2016). Many studies documented a negative correlation between day to flowering and the percentage of filled grains, fertile panicle, and yield (Pantuwan et al., 2002; Mohd Ikmal et al., 2019) rainfed lowland rice genotypes to drought stress environments and to examine ways to identify genotypes that confer drought resistance. One hundred and twenty-eight genotypes were grown under non-stress and four different types of drought stress conditions. The relationship of genotypic variation in yield under drought conditions to genetic yield potential, flowering time and flowering delay, and to a drought response index (DRI). Delay in flowering also causes a delay in maturation (Ndjiondjop et al., 2010). Pantuwan et al. (2002) found that plant prone to drought takes a longer time to maturity. This can be utilized to discover tolerant genotypes. To alleviate or escape drought to prevent flower delay, the plant tends to flower as early as possible to minimize yield loss (Seleiman et al., 2021). One of the advantages of this drought escape mechanism is that plant tends to avoid terminal drought stress, which is very detrimental. However, a significant amount of yield is lost, and also the ability of the crop to extend the growing season decreases (Yadav & Sharma, 2016).

Drought has a significant impact on plant cell division, elongation, and expansion (Wahab et al., 2022). Meristematic tissues in cells are essential for plant expansion via active cell division. However, any alteration within the cell water potential reduces cell size and cell division processes, affecting plant growth (Aslam et al., 2015). Plant cell expansion and elongation impaired under drought conditions can be attributed to; (i) poor root growth, (ii) impairment of stem reserves, and (iii) reduction in leaf-surface components such as shape, leaf color, and cuticular composition, consequently affecting the radiation load on the leaf canopy (Ndjiondjop et al., 2010). In addition, water deficit brings about osmotic stress, which affects the turgor pressure causing a decline in cell expansion and growth, ultimately plant productivity (Goche et al., 2020), while osmotic regulation assists in plant growth under severe drought conditions in cereals (Begna, 2020). Cell growth inhibition is frequently accompanied by a decrease in cell wall synthesis (Sikuku et al., 2010). Previous studies documented a decrease in plant height under drought (Mohd Ikmal et al., 2019; Seleiman et al., 2021). This may be due to inhibition of growth and cell enlargement during the booting, flowering, and grain filling stages, thereby affecting plant growth. Water stress can also cause cellular genetic disorders, including impaired mitosis and inhibited cell elongation and expansion, which finally decrease overall plant growth (Lisar & Bakhshayeshan-Agdam, 2020).

The root-to-shoot ratio is frequently utilized to calculate the relative biomass allocation between roots and shoots. Biomass allocation can be influenced by many stressors including nutrients, carbon dioxide, and drought (Xu et al., 2015). Under drought, the root-to-shoot ratio rises, subsequently aiding water absorption and maintaining osmotic pressure. However, the root length and dry weight were reduced (Lisar et al., 2012). A decrease in fresh shoot and root weights and their lengths eventually disrupts the rate of photosynthesis and biochemical pathways (Pandey & Shukla, 2015). The increased root-to-shoot ratio reported may be attributed to the presence of abscisic acid (ABA), in the shoots and roots (Lisar et al., 2012). Also, it causes a reduction of the aerial tissues rather than the roots (Toscano et al., 2019).

The leaf area is determined by traits such as phenology, leaf emergence rates, potential leaf size, and stem morphology. Any alteration in all these traits due to water scarcity affects the overall area of the leaf (Anjum et al., 2017). Wahab et al. (2022) documented that water stress in rice caused a considerable decrease in the leaf area. A decrease in the leaf area under mild water stress is considered a disadvantage to the plant because it decreases nutrient uptake. A decrease in the leaf area can be attributed to a decrease in the leaf number, thereby reducing the transpiration area within the plant. To escape drought, the stomata closure occurs to minimize loss of water, consequently affecting the canopy area (Toscano et al., 2019). Apart from stomata closure, which directly affects the leaf area, slow expansion of leaves and reduction in carbohydrate supply affect the leaf area (Reddy et al., 2003). The leaf area index (LAI) is the amount of foliage in a canopy. It can be used to predict plant growth and the soil condition (whether irrigated or dried) to improve plant productivity. It is considered a simple physiological method that can be used to determine a crop's assimilation rate on the field. A decrease in LAI under drought conditions can be associated with a decrease in the leaf size produced because of a decrease in the elongation of individual leaves. Also, early senescence and inhibition of the emergence of new leaves can bring about a drop in the number of leaves, thus reducing LAI (Mathoboab et al., 2016; Anjum et al., 2017). Improving the leaf morphology using advanced technology such as CRISPR/Cas9 has proven to be critical in enhancing drought tolerance and plant grain yield (Tabassum et al., 2021). Table 1 shows different approaches used to improve drought stress in rice.

TABLE 1. Shows different approaches employed to improve drought stress tolerance in rice

Traits		**Mechanism**	**References**
Morphological Traits Seed Priming	Seed priming	Enhanced production of phenols, flavonoids and antioxidant system	Seleiman et al. (2021)
	Seed priming	Increase proline, antioxidant system and soluble protein content production, reduce soluble sugar and malondialdehyde (MDA) content, and triggers glucose metabolism.	Liu et al. (2022)
	Seed priming	Increase ABA production, regulate water transport, and alters root hydraulic conductivity	Saha et al. (2022)
	Seed priming	Reduce lipid peroxidation and protein oxidation, increase total phenolic content accumulation, enhance the rice drought-responsive genes and Growth and development	Samota et al. (2017)
Physiological Traits	Root plasticity	Increase dry weight accumulation and grain yield	Khan et al. (2021)
	Change in leaf morphology	Increase panicle number, ABA and antioxidant accumulation, and survival rate, curled leaves and decreased stomata number, rate of transpiration, stomatal conductance, and malondialdehyde (MDA) content	Tabassum et al. (2021)
Biochemical Traits (Osmolytes)	Proline	Increase accumulation of antioxidant system and glycine betaine, subsequently improving photosynthetic activities and grain yield	Tomar et al. (2021)
	Proline	It helps to control water loss under drought conditions due action of compatible solutes. It also helps to adjust the osmotic balance	Kanwal et al. (2022)
	Glycine betaine	Helps in adjusting osmotic potential and enhanced root development, subsequently enhancing drought tolerance	Sawahel (2003)
	Glycine betaine	Mitigate drought stress by enhancing the proline level and soluble sugar in leaves and panicles	Aslam et al. (2022)
	Polyamines (putrescine)	Triggers spermine and spermidine synthesis and ultimately confer drought tolerance	Oladosu et al. (2019)
Biochemical Traits (Phytohormone)	Gibberellic Acid (GA)	Enhance WUE, antioxidant system, proline level, photosynthesis activities, and root growth.	Seleiman et al. (2021)
	Ethylene	Improve drought tolerance	Wahab et al. (2022)
	ABA	Enhance antioxidant production system, proline level, ABA, and root growth and decrease stomatal density, size and leaf area	Seleiman et al. (2021)
	Auxins	Induce the formation of new roots, stomata opening and safeguard the spikelet fertility and grain yield	Fahad et al. (2019)
	Jasmonates	Mitigate the impact of drought on WUE, photosynthesis and chlorophyll content.	Jogawat et al. (2021)
	Gibberellin	Improve stomatal conductance, growth of the leaf and net photosynthesis rate.	Wahab et al. (2022)
	ABA	Increase the expression of drought response genes, subsequently enhancing the recovery of stomatal conductance and net photosynthesis rate	Pandey & Shukla (2015)
	ABA	Improve root development for increasing water uptake, soluble sugar production for maintaining leaf water content and osmotic balance	Khan et al. (2021)
Biochemical traits (Antioxidant enzymes)	Superoxide dismutase	Scavenge the production of ROS	Panahabadi & Ahmadikhah (2022), Wang et al. (2021)

Effect of drought on physiological traits

When plants experience drought stress, specific changes occur at the physiological levels including a reduction in photosynthesis, stomatal conductance, and transpiration rate (Kanwal et al., 2022). Photosynthesis is considered the primary determinant of plant development and output during a water shortage. A decrease in photosynthesis could be due to reduced leaf area, damaged or weakened photosynthesis activators or agents, and early leaves senescence (Farooq et al., 2009). Lack of stomatal conductance, which decreases under water stress could also be linked to a decline in the photosynthesis rate. Stomatal closure occurs to reduce plant water loss, preventing CO_2 from entering the plant which could cause a drastic reduction in the photosynthesis rate beyond the compensation point (Sallam et al., 2019). This simply means a decrease in the photosynthesis activity could be associated with a decrease in the transpiration rate, mesophilic changes, and stomatal conductance and subsequently leads to a decrease in the photochemical efficiency of photosystem II (Jafarnia et al., 2017).

Drought interferes with the carbon fixation process by disrupting enzymatic activities (Nadeem et al., 2019; Srivastava & Kumar, 2020). The early stoma closure is considered an avoidance mechanism to conserve water for future use. Still, it decreases the diffusion of carbon dioxide needed to generate ATP by photosystem II and photosynthetic enzymes (rubisco activase) (Singh et al., 2017) and also affects the photophosphorylation, ribulose-1,5-bisphosphate regeneration, and rubisco activity (Reddy et al., 2004). In addition, photosynthetic metabolism (ribulose bisphosphate regeneration and ATP) inhibition is prevalent under severe water stress events. Flexas et al. (2002) stated that a reduction in the stomatal conductance causes a decrease in the CO_2 concentration but rises again at lower conductance levels, thus restricting photosynthesis primarily during moderate drought stress (Singh et al., 2017). Intensive water stress can result in the impairment of photosynthesis, metabolism aggravation, turgor loss (Anjum et al., 2017), destruction of photosynthetic components, and other pathways, thus bringing about yield loss (Farooq et al., 2009; Tátrai et al., 2016) and reduction in dry matter accumulation (Nadeem et al., 2019).

Intensive water stress disrupts the chlorophyll content, by impairing the chlorophyll compartment and disrupting the photosynthetic apparatus, all of which impairs the rate of photosynthesis (Mafakheri et al., 2010). During drought, chlorophyll fluorescence is used as an effective indicator to determine the extent of damage in the photosystems (Ammar et al., 2014). Previous studies have shown that drought stress in the plant during production causes a significant reduction in the content of chlorophyll a, b, and total chlorophyll (Mohd Ikmal et al., 2019; Wahab et al., 2022). This might be due to the disablement of the biosynthetic pathways, the breakdown of pigments, the disappearance of chloroplast membrane, and increased lipid peroxidation (Pandey & Shukla, 2015; Mohd Ikmal et al., 2019). Changes observed in the leaves' color can also be attributed to the impairment of the chlorophyll, followed by a rise in the visibility of the orange or yellow pigments. An increase in the leaves' senescence is caused by water stress and an increase in the average temperature beyond the optimal (Baharuddin et al., 2019). Due to the significance of chlorophyll during drought events, it is used as a criterion to determine the tolerance level of genotypes, stating that plants with a high mean value of chlorophyll are less susceptible to water stress (Kumar et al., 2014).

One of the crucial and apparent physiological responses to drought stress is leaf rolling. It is regarded as a way plants adapt to water stress to maintain plant water status during diminishing soil moisture (Kumar et al., 2014; Kanwal et al., 2022). Leaf rolling occurs due to several levels of dehydration experienced by the plant in various cross-sections of the rolled leaf, ultimately minimizing the amount of sunlight and transpiration witnessed by the plant. Although leaf rolling is a way of preventing excessive water loss in plants and minimizing transpiration, a higher leaf rolling score during water deficit reflects the incapability of the plant to withstand turgor pressure (Mohd Ikmal et al., 2019). Leaf rolling reduced the exposure of leaves to sunlight and caused a reduction in photosynthesis. Poorter & Markersteijn (2008) also reported that when the turgor pressure is lost, the leaf rolls and then wilts. Wilting is an indication that the plant was not able to sustain high water potential within its tissues during water deficit. Rolling of the leaves under water stress coupled with the drying of leaves tip is hydronasty resulting in a decrease in dehydration of the leaf, an interception of light, and the rate of transpiration. To respond to water stress, the plant's rate of transpiration is reduced by forming a waxy and thick leaf cuticle layer. Also, they develop certain xeromorphic traits and alter their structure, such as developed vascular bundles, tiny and thick leaves, thick palisade tissues, smaller and reduced stomata number, and large trichomes numbers to enhance resistance to drought (Ilyas et al., 2020).

The root is the principal organ that is essential for the plant under water stress because they are known as the primary detectors or sensors of soil drying. In cereals such as rice, wheat, and maize, the entire root system comprises several root components, including nodal, seminal, and lateral roots of different branches. Among these root components, the lateral roots covered more than 90% of the total root system and more than 99.9% in terms of the root number, which are common attributes of plant species grown under both excess and deficit soil moisture environments (Suralta et al., 2008). Factors such the root architecture, size, thickness, depth of penetration, root length density, and root distribution determines the plant's ability to access and absorb water to undergo normal physiological functions in the shoots (Matsui & Singh, 2003; Ascha et al., 2005; Kim et al., 2020; Gano et al., 2021). The roots extract more water from the immediate environment via expansion of their branches into the depth of the soil profile and eventually adapt to plants by reducing the amount of water loss via the stomatal (Seleiman et al., 2021).

When compared to other crops, especially cereals, Rice possesses poor adaptation to drought conditions. During water scarcity, having a deep root system is a crucial trait and has been shown to have a positive correlation with yield. Genotypes with a deep root system have proved more resilient to limited-water supply Compared to shallow root systems because of the plant's capability to extract in the depth of soil profiles (Ascha et al., 2005). For instance, during limited-water supply, rice grown in upland areas develops thick and deep roots to enhance its root hydraulic properties and uptake water in the depth of soil profiles (Singh et al., 2017). During the plant's early developmental stage, a prolific root system can be beneficial to the plant for promoting rapid growth and extracting water from shallow soil profiles, which are easily lost in legumes through evaporation (Jaleel et al., 2009). Alteration in root development and distribution due to limited water supply causes a reduction in shoot development and functions as an effect of root-to-shoot signaling with the contribution of plant hormones (Begna, 2020).

Plant hormones such as ABA, cytokinin (CK), malate, pH, a precursor of ethylene, and other unspecified issues have all been concerned with root-to-shoot motioning under water stress (Lisar & Bakhshayeshan-Agdam, 2020). Under water stress conditions, a rise in the root to shoot ratio was associated with the presence of ABA in the root and shoots (Jaleel et al., 2009), because an increase in ABA concentration within the root is triggered by dryness of the soil and may help to maintain the root development and improve hydraulic conductivity. These mechanisms improve the uptake of water and delay the impact of drought stress on the shoot (Barnábas et al., 2008). Furthermore, the hydraulic conductivity of the root is also influenced by the size of xylem vessels, which ultimately determines plant productivity under water stress (Gaballah et al., 2021). An increase in the amount of ABA present in the root may restrict ethylene's activities, which may prevent plant growth (Tátrai et al., 2016). There are two problems that the root may encounter during water scarcity. First is the impact of suberization on the water and nutrients uptake proportional to the root system as a whole, and the second is the decrease in the activities of the meristem and elongation of the root, which is directly associated with the level of internal water stress (Singh et al., 2012).

The plant adopts a wide range of defensive systems coupled with controlling plant water status to respond to terminal drought stress. Plant water status comprises osmotic potential, relative water content and leaf water potential are considered simple indicators to evaluate water stress and provide the best stress sensor (Yadav & Sharma, 2016). Relative water content (RWC) is used to determine plant water status, which reflects the metabolic behavior in the cell (Sallam et al., 2019). At the early stage of leaf expansion and growth, the RWC is high but decreases progressively as the leaves mature and accumulate dry matter. Relative water content (RWC) is associated with water absorption via the roots and water loss via the transpiration process (Anjum et al., 2011). A plant subjected to drought experienced a decrease in the RWC and leaf water potential accompanied by a rise in the leaf temperature (Farooq et al., 2009; Wahab et al., 2022). Osmotic adjustment in plants leads to a reduction in leaf water potential without any consequences on the leaf turgor, affecting turgor-dependent processes such as cell expansion and metabolic activity of the tissues. This kind of adaptive feature has proven to be a success by helping to control the rate of photosynthesis and stomatal conductance at low leaf water potential. Also, it helps to prolong leaf senescence under Drought (Tounekti et al., 2018). In response to the reduction in the leaf water potential, the plant osmotically adapts by producing organic and inorganic solutes within the cells. Due to this, the osmotic potential becomes more negative, functioning as a stimulant for water absorption in the roots (Tounekti et al., 2018). In general, plant water status is hindered by decreased water availability, while the stomata are more severely affected. Furthermore, during drought stress, leaf temperature changes may be considered an essential component in regulating leaf water status. Drought tolerant plant maintains water-use efficiency by limiting water loss.

Biochemical responses of rice under drought

Biochemical responses to water stress include mainly stress metabolite production such as glybet, polyamines, proline and glutathione, etc (Table 1). A decline in the effectiveness of photochemical, production of enzymatic and non-enzymatic antioxidant systems, decrease in the efficiency of rubisco and accumulation of reactive oxygen species (ROS) (Nezhadahmadi et al., 2013). In plants, ROS production is referred to as oxidative burst. During adverse environmental challenges such as drought, ROS are generated in plants. Increased ROS production causes several damage within the plant cell due to its activities such as nucleic acids, and membrane lipids, consequently undermining plant growth and productivity (Aslam et al., 2022). ROS are considered very harmful and toxic to plants because they disrupt the normal activities and structure of the biomolecules. Under the stable condition, ROS is assumed to be at an equilibrium state which is not harmful to the plant. However, the introduction of drought disrupts the balance by increasing ROS accumulation within the plant cell (Koyro et al., 2012). Although the accumulation of ROS is hazardous to plant health, if present in an optimal condition, it can help enhance cellular signaling and the development and growth of the plant (Hernández et al., 2012).

The plant generates some defense systems known as antioxidative enzymes and non-enzymes to counteract ROS accumulation and prevent oxidative stress and damage in the plant. The main scavenger is the superoxide dismutase (SOD) enzyme, which converts O_2 to H_2O_2 (Aslam et al., 2022). Under adverse environmental stress conditions, ascorbate peroxidase and carotenes are also important for scavenging ROS in the plant (Tiwari et al., 2021). Furthermore, as the drought becomes more intense, antioxidative enzymes are triggered and produced in multiple folds within the plant cell. This shows the efficiency and effectiveness of plants' antioxidant systems in safeguarding the cell from oxidation stress (Nezhadahmadi et al., 2013; Oladosu et al., 2019). Genetic engineering has also been utilized in enhancing plant defense mechanisms against oxidative stress by up and down-regulating some genes which play a critical role in plant defense. For instance, monodehydroascorbate reductase, dehydroascorbate reductase and SOD genes were reported to confer protection in plants under abiotic stress by counteracting the activities of oxidative agents (Sallam et al., 2019; Verma et al., 2019). Apart from ROS accumulation triggered during drought stress, methylglyoxal is another metabolite produced during an adverse climatic change affecting plant growth and productivity. Production of methylglyoxal is experienced within the cells during physiological activities such as photosynthesis, but its level skyrockets during adverse environmental stress (Sallam et al., 2019). A previous study has shown that under drought stress, methylglyoxal accumulation is high (Sallam et al., 2019).

Extensive production of various forms of compatible organic solutes (highly soluble compounds) is considered one of the conventional strategies to escape drought stress in the plant. They protect against drought stress by contributing to osmotic adjustment, membrane stabilization, and reduced ROS accumulation. During osmotic stress, osmotic adjustment is regarded as a process that helps to maintain water relations. It entails gathering a wide range of active osmotic molecules such as proline, soluble sugars, and betaine (Omprakash et al., 2017). In the cytosol, a decrease in osmotic potential was attributed to an organic and inorganic solute accumulation, which maintains turgor pressure during water stress (Oladosu et al., 2019). Proline is among the organic solutes accumulated and one of the most investigated solutes that provide cellular defense against drought. Proline oxidative metabolism allows the cell to use it as a source of nitrogen and carbon, which helps in plant development and energy requirement (Christgen & Becker, 2019). It also helps to restrict water loss in plant cells during stress (Kanwal et al., 2022). In addition, under stress conditions, it serves as antioxidative protection, cellular signaling, and metal chelator. Due to the role of proline in enhancing drought tolerance, it has been widely used as a biochemical marker to determine drought-tolerant rice genotypes. Under drought stress, proline accumulation can be enhanced in two ways; (i) by increasing proline synthesis enzyme activities and (ii) by decreasing proline degradation enzyme activities (Riasat et al., 2020).

Polyamines (PAs) are small molecules that are positively charged at a physiological state required for life in most eukaryotic organisms. Under drought stress, PAs play a role in the completion of membranes and nucleic acid. A study reported that increased PAs concentration in plants under drought stress enhances plant growth and development (Nezhadahmadi et al., 2013). In plants, common PAs found include diamine putrescine, triamine spermidine, tetramine spermine, thermospermine, and cadaverine (González-Hernández et al., 2022). Putrescine is the simplest form of PAs derived either directly from ornithine by ornithine decarboxylase or from arginine through several steps catalyzed by arginine decarboxylase, agmatine iminohydrolase, and N-carbamoylputrescine amidohydrolase (González-Hernández et al., 2022). Under drought stress, a higher concentration of putrescine is produced in rice, which facilitates the synthesis of spermine and spermidine, thereby protecting the plant from detrimental consequences induced by Drought (Oladosu et al., 2019).

Phytohormones which include CK, ethylene, and ABA, play an important role in plant response to drought. Water stress is perceived as a hydraulic force induced by a pressure gradient by the soil to the crop due to soil drying. When the hydraulic pull occurs, it shifts the concentration of the signal hormone Abscisic acid (ABA) (Oladosu et al., 2019). Under drought conditions, exogenous ABA application in rice helps to up-regulate drought response genes, thereby facilitating the recovery of stomatal conductance, net photosynthesis rate, and transpiration rate (Pandey & Shukla, 2015) (Table 1). ABA accumulation and decrease in the concentration of 1-aminocyclopropane-1-carboxylic acid and ethylene help to increase the rate of grain filling under mild drought. Accumulation of ABA in the root, stem, and leaves is observed upon drought emergence, while the amount of CK presence in the leaf region is decreased (Sallam et al., 2019). Furthermore, ABA aid in regulating the expression of a significant number of the gene involved in stress response (Danquah et al., 2013). ABA cannot penetrate the plasma membrane and translocate toward the guard cell by the water stream in the leaf apoplast. Increased ABA production around the guard cell causes the stomata to close and permits water to be conserved (Lisar et al., 2012).

Effects of drought on yield and yield components

The ultimate goal of every plant breeding program is to achieve a high yield irrespective of the environmental challenges encountered. Grain yield is a complex polygenic quantitative trait where its outcome (yield) is highly dependent on environmental conditions (Sadia et al., 2020). The effect of drought on yield is primarily determined by the severity of the stress and the stage of plant development when the stress occurs. A significant drop in yield has been documented in rice fields due to drought occurrence at various plant developmental stages (Table 2). In the vegetative phase, the occurrence of drought stress is characterized by a reduction in morphological attributes such as the rate of photosynthesis, spike in the ratio of root to shoot biomass, and root length density (Das et al., 2020). It also disrupts leaf formation, tillering, and panicle development, subsequently causing a decline in grain yield (Kanwal et al., 2022). Drought occurrence at the vegetative stage in rice causes a decline in yield to about 20-27% (Yang et al., 2019; Zia et al., 2021). A decrease in the plant development experienced in the vegetative phase has implications on the reproductive stage and, ultimately, overall plant productivity (Lisar & Bakhshayeshan-Agdam, 2020). Drought occurrence at the early stage of plant growth can trigger a switch to the next growth phase (reproductive), which ultimately can cause early flowering and consequently a considerable drop in yield (Bukhari et al., 2019).

During the rice developmental cycle, the reproductive stage is considered more vulnerable to limited water supply than the vegetative stage. Drought-induced during the reproductive phase hurts the reproductive physiology of plants by disrupting the reproductive processes such as pollination, fertilization, and grain filling, as well as a reduction in spikelet fertility which consequently results in lower yield (Kanwal et al., 2022). Water stress during this critical stage causes a delay in the silking. However, anthesis is not affected but brings about yield loss due to an increased interval between the silking and anthesis stages (Anjum et al., 2017). The emergence of drought during flowering is considered detrimental effect on the entire plant output due to a shrink in the size of the anther and loss of pollen viability resulting in flower abortion, grain abscission, and a decline in the number of filled grains (Das et al., 2020). Drought occurrences at the post-anthesis can cause a decrease in the photo-assimilates production and the sink power to absorb photo-assimilates while later results in grain weight and yield reductions (Saeidi et al., 2010; Saeidi & Abdoli, 2015). Plant exposure to drought stress at the post-anthesis brings about shortened grain-filling period and a reduction in yield (Khatun et al., 2021).

Grain filling is considered the last growth phase in most cereals, including rice. In this stage, the ovaries are fully mature into caryopses (Mi et al., 2002). The process of grain filling is controlled mainly by four key enzymes: adenosine diphosphate-glucose-pyrophosphorylase, starch synthase, starch branching enzyme, and sucrose synthase. Disruption in the activities of these key enzymes during stress events will lead to a severe decline in grain yield (Peng et al., 2022) because starch accounts for 60 - 80% of cereals' grain weight (Lv et al., 2021). This implies that any changes in the environment dynamic directly affects the grain filling. According to previous studies, grain filling is involved in the senescence process of cereals (Liang et al., 2021). Limited water supply during the grain filling induced early senescence, shortened grain filling time and increased remobilization of assimilates from the straw to the grains (Mostajeran & Rahimi-Eichi, 2009). Drought experienced at the early grain filling stage causes a decline in grain weight due to fewer endosperm cells. In contrast, drought-induced at the later period could cause starch synthesis to be impaired due to restriction in assimilation supply for the grain (Barnábas et al., 2008). When water stress occurs during the flowering and grain filling stages, the photosynthesis and translocation processes are greatly affected, resulting in a decrease in yield. The total reduction in yield experienced under drought can be attributed to a decline in yield traits such as grain number per spike and individual grain weight (Alqudah et al., 2011). Recently, Salleh et al., (2022) reported a decrease in the yield of rice due to the occurrence of drought at the heading which was attributed to a drastic reduction in leaf relative water content, consequently bringing about the suspension of the anthesis process and then yield loss. Based on the study result, the spikelet moisture content must be above 80% for the optimum anthesis process to occur.

TABLE 2. Reduction in grain yield in rice due to drought at different growth stages

Growth stage	Yield reduction (%)	References
Vegetative stage	20	Zhang et al. (2018)
Vegetative stage	21	Sarvestani et al. (2008)
Vegetative stage	21- 50.6	Shrestha (2022)
Flowering stage	23.2	Rasheed et al. (2020)
Flowering stage	42-83.7	Shrestha (2022)
Flowering stage	23.2	Yang et al. (2019)
Flowering stage	24	Yang et al. (2019)
Flowering stage	15.0-20.5	Gui et al. (2022)
Reproductive stage	19.47	Withanawasam et al. (2022)
Reproductive stage	51-90.6	Shrestha (2022)
Reproductive stage	31.5	Zhang et al. (2018)
Reproductive stage	42.9	Mohamed et al. (2019)
Ripening stage	55	Mohamed et al. (2019)
Reproductive stage	56.2	Dixit et al. (2020)
Reproductive stage	12-46	Foomani et al. (2021)
Reproductive stage	51-70	Dixit et al. (2014)
Reproductive stage	65.9	Ghimire et al. (2012)
Reproductive stage	78.5-86.5	Singh et al. (2022)
Reproductive stage	32.9	Dwivedi et al. (2021)
Reproductive stage	15-58	Majumder et al. (2021)
Reproductive stage	79-99	Shamsudin et al. (2016b)
Reproductive stage	86-93	Shamsudin et al. (2016a)
Grain filling	60	Rasheed et al. (2020)

The incidence of drought stress at the grain filling hurts the harvest index compared to stress-induced at the tillering stage, although the occurrence of drought at all stages causes a reduction in rice productivity (Sokoto & Muhammad, 2014). Grain yield under drought is highly correlated with biomass production and harvest index at the vegetative and reproductive stages. The harvest index is said to be the capability of the plant to assign photosynthetic assimilates to produce economic yield. Under drought, a decline in the harvest index is observed probably due to the factors such as a reduction in the assimilate translocation of grains (Sokoto & Muhammad, 2014). Moreover, the decline in the harvest index can be due to a grain reduction than biomass production reduction (Saeidi & Abdoli, 2015). In summary, the occurrence of drought at the reproductive stage brings about a decline in the rates of CO_2 assimilation, disrupt the photosynthesis pathways, decrease plant growth and development, affects the production of flower, disrupt the activities of starch and sucrose biosynthetic enzymes, consequently shortened the grain filling stage, thus decrease in rice productivity.

Conclusion

Water stress interferes with the total plant functionality, bringing about a decrease in the leaf water potential, net photosynthesis, growth rates, dry matter, biomass production, harvest index, and subsequently the yield. However, factors such as the period, time, and extent of exposure to drought, development and growth stage when drought is witnessed, and severity play a crucial role in plant reaction to drought stress. Therefore, the development of drought-tolerant high-yielding rice cultivars becomes a necessity to curb food insecurity. The integration and enhancement of traits such as leaf rolling and a deep root system which is crucial for rice plant survival under drought should be considered. Furthermore, developed varieties should also be subjected to stringent evaluation in different drought-susceptible ecosystems to determine and understand the genotype response to a wide range of drought frequencies. Since the root is considered the most important organ, more research should focus on the discovery of more useful microbes within the root region which can help plants alleviate the impact of drought on plant metabolic and physiological activities. The increased production of biochemical variables such as polyamine, proline, and antioxidant systems should also be intensified to confer drought resistance of genotypes under drought conditions.

Although, several progress has been made in identifying quantitative trait locus (QTL) responsible for drought tolerance in rice. However, research on the incorporation of two or more different drought-tolerant QTLs and their interactions under drought conditions are limited and need to be intensified. Finally, incorporating biotechnological approaches such as genome editing, omics, and speeding breeding should be employed to enhance plant traits and confer tolerance, and speed up breeding programs.

Acknowledgments: All authors would like to thank Universiti Kebangsaan Malaysia (UKM) for the research university grants, GP-2021-K017409 and TAP-K017409. The first author would also like to thank UKM for the Zamalah Scholarship Scheme Award.

Acronyms

ABA = abscisic acid
ATP = adenosine triphosphate
CK = cytokinin
CO_2 = carbon dioxide
DNA = deoxyribonucleic acid
H_2O_2 = hydrogen peroxide
LAI = leaf area index
O_2 = oxygen
PAs = polyamines
RWC = relative water content
ROS = reactive oxygen species
SOD = superoxide dismutase
UKM = Universiti Kebangsaan Malaysia
WUE = water use efficiency

Unit and currencies

Mt = metric ton
Mha = million hectare
USD = United States dollar

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