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Review

Drought Stress Tolerance in Plants: Interplay of Molecular, Biochemical and Physiological Responses in Important Development Stages

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Abstract: Drought is an important abiotic stress factor limiting crop productivity worldwide and its impact is increasing with climate change. Regardless of the plant growth period, drought has a deadly and yield-reducing effect on the plant at every stage of development. As with many environmental stressors, drought-exposed plants trigger a series of molecular, biochemical, and physiological responses to overcome the effect of drought stress. Currently, researchers are trying to determine the complex functioning of drought stress response in plants with different approaches. Plants are more sensitive to drought stress during certain critical stages like germination, seedling formation, flowering, fertilization, and grain formation periods. Plants have high success in reducing the effects of drought stress in vegetative development periods with the activity of tolerance mechanisms. On the other hand, drought stress during the generative period can cause irreversible losses in yield. This review focuses on the progression of molecular, biochemical, and physiological mechanisms involved in the drought stress tolerance in plants and the responses of field crops to drought stress at different development stages.

Keywords: drought stress; important development stages; plant response; adaptation; field crops

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1. Introduction

Agricultural production is directly affected by climatic conditions. The direct or indirect effects of climatic change (e.g., temperature differences to seasonal norms and irregularities in the precipitation regime) limit plant development and yield [1–3]. Water is one of the essential factors for the sustainability of life of all living organisms, including plants. Plants need water for photosynthesis and metabolic activities [4]. Besides, the plants should use the maximum level of water from the environment to continue their growth performance [5]. Drought is a physiological form of water deficiency in which the soil water available to the plant is insufficient and adversely affects its metabolism [6]. Against the negative effects caused by drought, plants manage this process with a complex set of related mechanisms [7]. Physiological and metabolic changes that occur as a result of the interaction of these mechanisms help tolerate the negative effects of stress [8].

Plant stress response mechanisms are controlled by complex networks determined by environmental and genetic factors. Traditional methods are insufficient to control and explain the complex tolerance mechanism [9]. In this respect, omic technologies are promising for improving drought stress tolerance with many biotechnological approaches [8]. The focus of these studies is genome-wide research to discover stress-related candidate regions and genes for stress resilience [2]. Many studies have been carried out on functional genes involved in the stress response, with methods such as QTL (quantitative trait loci) analysis, transcriptomic analysis, and GWAS (genome-wide association study) in important crop species [10–13]. The identified target genes contributed to the improvement of tolerance to stress through gene silencing techniques, transgenic approaches, and genome engineering (CRISPR/Cas9) methods [2,8].

Different defense mechanisms help plants deal with the stress of drought. The plant responds to drought stress with biochemical (antioxidant content, chlorophyll content, proline accumulation, hormonal content, secondary metabolite, etc.), physiological (activity of stomata, photosynthesis, osmotic balance, transpiration, leaf water content, water transmission), and morphological changes (decreased leaf area, number of leaves, increase in root length, leaf aging, early maturation, change in growth stages, etc.). This is due to several molecular mechanisms that are put into action (increased expression of transcription factor genes) [14–17]. Additionally, the plant's stress response and coping mechanisms depend on its growth stage when it experiences drought stress [18]. Depending on the stage of their growth, plants may be more or less sensitive to drought stress. Abnormalities occur in the turgor pressure, leaf water content, stomatal movement, leaf coloration, photosynthesis and respiration, leaf vitality, and ultimately growth activities when drought stress is experienced during the vegetative development cycle. These responses might encourage the plant to keep its vegetative period brief and move quickly through the generative stage [7]. Drought stress exposure during the generative development period causes reductions in flowering rate, fertilization, seed setting and product quality [19,20]. Many researchers have investigated the effects of drought stress in sorghum [21–23], maize [24,25], wheat [19,26,27], rice [20,28], mung bean [29–31], soybean [32,33] and lentil [3]. Nevertheless, depending on the severity and duration of drought stress, the growth period of the plant is an important factor in managing its response to stress [34].

This review focuses on explaining the responses of field crops to drought stress, especially during important developmental stages, by providing information about the interaction between physiological, biochemical and molecular mechanisms underlying drought stress tolerance in plants.

2. Drought Stress Signaling and Molecular Regulation

Drought stress negatively affects plant growth with various physiological and biochemical processes such as respiration, translocation, ion uptake, water potential, stomatal closure, photosynthesis, sugar and nutrient metabolism, antioxidant system, and phytohormones [35]. The activation of numerous genes with different functions causes the plant to undergo physiological and biochemical reactions in response to drought stress [36,37]. Molecular mechanisms related to drought tolerance are studied under two main categories. The first is signal transduction factors, including protein kinases, transcription factors, and ABA receptors. The other is functional factors, including proteins involved in metabolism, osmotic regulation, protein conversion, protein modification, and ROS transport [38].

Stress signal activation occurs through protein molecules that are activated by disruption of the cell wall [39]. The diverse signaling pathways of water deficiency stress in plants consist of several proteins, including transcription factor (TFs), enzymes, molecular chaperones, and several metabolites [40]. Many genes have been identified that are differentially expressed in plants in response to drought [41,42]. These genes function in different cellular signaling pathways and cellular responses such as transcriptional regulation [43,44]. Transcriptional factors consist of the DREB, WRKY, bZIP, bHLH, NAC, MYC, MYB gene families and protein kinases (mitogen-activated protein kinases (MAPK), calcium-dependent protein kinases (CDPK), are composed of receptor protein [45,46]. Numerous TF genes associated with stress have been discovered in various plant species [6]. Plants use both pathways categorized as abscisic acid (ABA)-dependent and ABA-independent signaling pathways to sense and respond to drought stress [47]. During signal transduction, ABA-independent TFs serve as molecular switches, directly regulating the expression of associated genes by interacting with cis-elements in the promoter region of genes [48,49]. This is based on the specific nature of the DNA binding sites themselves [41,50]. In this way, TF genes are involved in the expression of a specific gene in the event of drought stress [49,51,52].

Another mechanism implicated in stress signaling is an increase in the generation of reactive oxygen species (ROS). ROS signaling is associated with abscisic acid (ABA) and Ca^{2+} increase under drought stress in plants [53]. Overproduction and accumulation of ROS in different tissues and cells of the plant are considered stress signals [54]. In addition, protective molecules such as low molecular weight osmolytes (sugars, polyols, amino acids such as proline), heat shock proteins, aquaporins, and LEA proteins are involved in the responses to stress in plants [55]. Proteins are synthesized in the plant cell by gene expression as a result of stress signaling. Synthesized proteins are responsible for biochemical, physiological, and morphological activities such as transcriptional regulation, cell membrane protection, antioxidant biosynthesis, initiating or stopping physiological activities, and uptake of water and ions [56].

3. Biochemical Reactions of Plants in Drought Stress

Drought resistance is a complex set of events involving the interaction of different stress-sensitive mechanisms [57]. Arid and semi-arid environmental conditions induce the formation of ROS in plants and cause oxidative damage in plant cells. ROS signaling is involved in the initiation of stress-induced molecular, biochemical, physiological, and morphological responses [58–60]. ABA, a crucial component of stress signaling, is produced when ROS production increases in response to stress [61]. In this way, it can regulate gene expression for biochemical responses by producing superoxide dismutase (SOD) and catalase (CAT) [62].

High levels of ROS production can damage various physiological and metabolic processes such as photosynthesis and the antioxidant defense system in plants [58]. The antioxidant system and osmotic regulation are the main defense systems that provide the tolerance of plants against water deficiency stress conditions. CAT, peroxidase (POD), SOD, glutathione reductase (GR), ascorbate peroxidase (APX), glutathione peroxidase (GPX) are enzymatic antioxidants, and phenolic compounds are non-enzymatic antioxidants (e.g., ascorbic acid, vitamins, carotenoids, phenolic compounds) [63].

SOD is the first line of defense in the presence of ROS. CAT and APX detoxify ROS and prevent its accumulation in cells and tissues [64]. However, non-enzymatic antioxidants such as flavonoids and tannins, which are phenolic compounds, play a significant role in ROS detoxification and mitigate the effects of oxidative stress [65]. Natural antioxidants maintain cellular redox balance by binding and neutralizing free radicals for plant survival under stress conditions [66]. The antioxidant defense system, consisting of the coordinated action of enzymatic and non-enzymatic antioxidants, provides an effective mechanism to control the toxicity induced by ROS. Plants respond to drought stress by accumulating soluble chemicals in the cytoplasm, such as proline, glycine-betaine, glucose, fructose, mannitol, inositol, valine, isoleucine, etc. These metabolites don't interfere with the functioning of metabolic reactions under normal conditions. However, in case of stress conditions, they act as an osmoprotectant to regulate the osmotic balance of the plant, maintain water flow and molecular stability, and prevent the accumulation of stress-related free radicals [51,67]. Among the osmoprotectants, proline is one of the important amino acid that have high antioxidant properties and plays a role in the prevention of cell death [68]. Many researchers consider stress-related proline accumulation as a biochemical marker for tolerant cultivar selection [69]. Glycine-betaine acts as a protective in protein unfolding and denaturation through direct and indirect interaction with macromolecules [70]. Mannitol increases enzymatic antioxidant activities in plants. Exogenous application of mannitol increased catalase and ascorbate peroxidase activities in wheat shoots and roots [71]. Sucrose is another important osmolyte found in abundance in the plant. It supports anthocyanin accumulation to scavenge reactive oxygen species and plays an important role in reducing the effect of ROS [72,73].

4. Physiological Responses and Mechanisms of Plants against Drought Stress

The effects of drought stress include decreased plant cell growth, stomatal closure, irregular turgor pressure, decreased leaf water content, accumulation of biochemical substances, poor root-absorption function, reduced photosynthetic activity, impaired metabolism, and plant mortality [74]. Plant response to drought stress is managed by molecular, biochemical and physiological mechanisms (Figure 1).

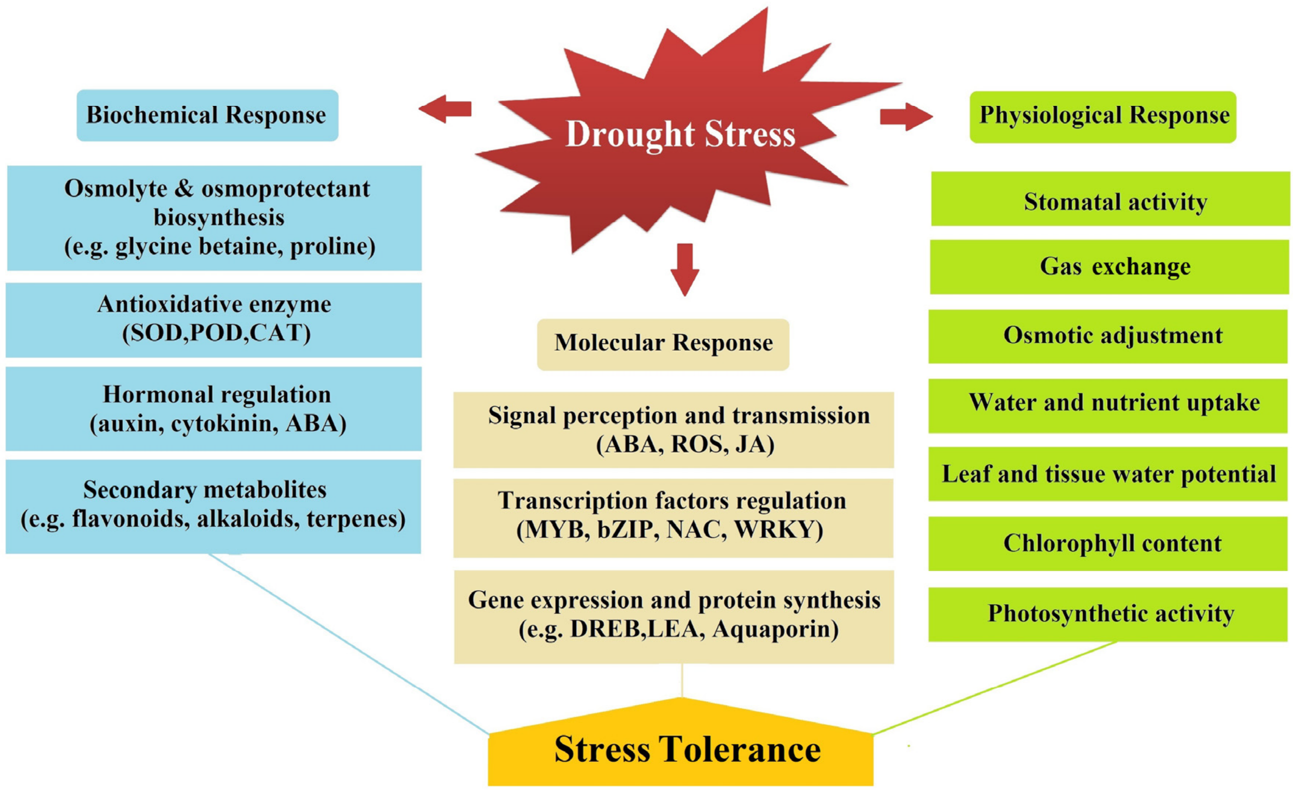

Figure 1. Relation of molecular, biochemical, and physiological responses to drought stress.

The physiological response of plants to drought stress consists of long-term and short-term responses [75]. The long-term negative impact of drought stress on the plant includes processes disruption of leaf/root physiological cycles, changes in maturity times (early productive maturity), and yield losses [76]. Short-term reactions to drought in plants include changes in stomatal conductivity, water potential across tissues, water and nutrient uptake movements of roots, turgor pressure, and biochemical composition [77]. Plants can transmit positive and negative signals between roots and shoots for adaptation to environmental conditions [78]. The stress factor in the environment can cause a reaction in the shoots with the signals transmitted from the roots. As a result, the vital functions of the plant may decrease with some active physiological processes [43,79]. Many factors including abscisic acid (ABA), auxin, cytokinins, ethylene, gibberellins, strigolactone (SL), jasmonic acid (JA), and proline act as signal molecules under variable environmental stresses and play a role in the regulation of physiological processes [39,80–82]. Strigolactone (SL) is a plant hormone that affects physiological processes such as shoot branching, root elongation, and leaf senescence [83]. Besides, SL acts as a signal molecule for drought stress tolerance [84]. The increased level of SL biosynthesis gene expression under drought stress is one of the important regulators in plant response to stress tolerance [85,86].

Alterations in the cellular ROS due to biochemical response affect various metabolic and physiological reactions in the plant. Certain ROS also acts as a signaling molecule in stress adaptation [87,88] addition, the roots create stress-related hormones and osmoprotectants when they detect a scarcity of water in the soil, and they then direct these substances to the shoot via transpiration current [80]. These substances accumulate in leaf tissues and cause the initiation of molecular, biochemical, and physiological processes. Oğuz et al. [89] stated that under the influence of drought stress, leaf tissues were physiologically more affected than root tissues and also displayed relatively higher TF gene expression.

The first physiological response of plants under the influence of drought stress is to reduce transpiration by stomata [90]. The closure of the stomata and the reduction of water loss by the plant is a physiological response to avoid drought [91,92]. On the other hand, the stomata's closure influences physiological and biochemical processes, such as a reduction in leaf water content, chlorophyll quantity, chloroplast fragmentation, gas interaction, ion exchange between root and shoot, and photosynthesis, while suppressing leaf expansion morphologically [93–97]. As a result, all these processes and physiological events affected photosynthetic activity directly or indirectly [98–100]. Plants control gas and water flow through the stomata in leaf tissue. The closure of stomata due to drought prevents the use of CO_2, which is of great importance for photosynthesis [101]. The reduction of CO_2 uptake by the plant directly causes low photosynthetic activity [102]. Decreased transpiration due to the closure of stomata under water-deficient conditions also limits the absorption of nutrients from the soil through the roots and their translocation to the upper parts of the plant [24,103] (Figure 2). This situation causes a dramatic decrease in the nutrient concentration of plant tissues and ion balance [79,103,104]. Many processes are adversely affected due to the disruption of nutrient, mineral, water, and gas flow in plant tissues [105–107]. Relative water content (RWC) is another important physiological feature that affects leaf water potential, stomatal resistance, transpiration rate, and plant water relations [90]. Relative water content is considered a marker of plant water status, which regulates metabolic activity in tissues. RWC is formed as a result of water loss by transpiration and uptake by roots [18,108,109] (Figure 2). Leaf water potential, which is important for plant survival and photosynthetic processes; turgor pressure is closely related to stomatal closure and cell growth [110,111]. Maintaining the leaf water potential allows for the tolerance of low to moderate water stress. However, the reduced efficiency of photosynthesis is brought on by the rise in leaf water potential loss brought on by increased water stress [112].

Photosynthesis is the most important physiological process directly related to growth, development, and yield in all green plants [113]. Chloroplasts are cellular organelles and are important for photosynthesis. With the help of metabolites synthesized during photosynthesis and key proteins involved in the metabolic process, chloroplasts provide resistance against various abiotic stresses such as drought [114]. Deterioration in the chloroplast structure due to drought adversely affects the synthesis of chlorophyll [113]. Chlorophyll is one of the main chloroplast components for photosynthesis, and chlorophyll content has a positive relationship with the rate of photosynthesis. The decrease in chlorophyll content under drought stress has been considered a typical manifestation of oxidative stress [115]. The reduction in chlorophyll content due to drought stress is the result of pigment photo-oxidation and chlorophyll degradation [18]. The reduction in photosynthetic pigment concentrations such as chlorophyll due to environmental stressors could directly limit the production of photosynthetic activities [79].

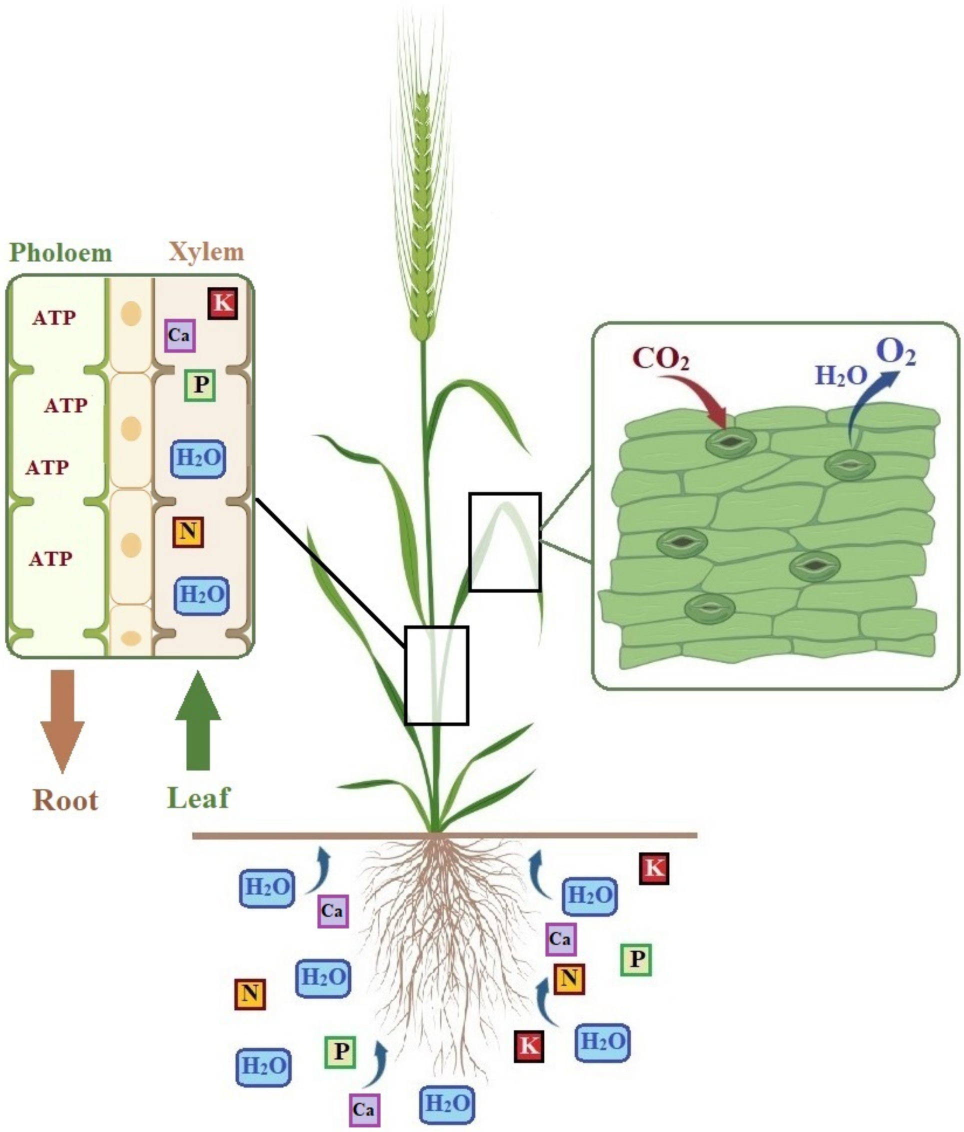

Figure 2. Transpiration through stomata and the movement of water and nutrients from the soil. Leaf transpiration and gas exchange are controlled by stomata. The water movement in the plant is controlled by the loss of water by transpiration from the leaves and the movement of water uptake from the root. Water and dissolved compounds are absorbed from the soil by the roots and transported to the upper parts of the plant through the xylem. The energy (ATP) produced in the upper parts of the plant is moved to the other parts by the phloem. Illustrations such as Ca (calcium), K (potassium), and N (nitrogen) are representative.

5. Management of Drought Stress in Plants

From past to present, a number of important agronomic strategies have been developed to increase plant adaptation to abiotic stress factors caused by climate change [116]. Fertilization and irrigation treatment according to the development periods of the plants and the selection of the appropriate tillage system are of great importance in preventing yield losses in plants under the drought stress [117]. In addition, some strategies such as sowing time, sowing frequency, sowing to stubble, crop rotation, selection of plant varieties with short life cycles, optimum irrigation practices, and use of bio-fertilizers are the key management techniques to obtain higher productivity of crops [118–121]. Except that the methods and practices developed by farmers and researchers for stress management, there are a number of mechanisms that plants have developed to manage drought stress. The effect of drought on the plant depends on the severity of the stress and the developmental stage of the plant [122]. The effects of continuous and intense drought stress and the effects of short-term and low-level drought stress effects different on the plant. The severity and timing of drought stress change the plant's response to drought stress. Stress responses of the plant can be grouped under three different headings as escape, avoidance, and tolerance (Figure 3).

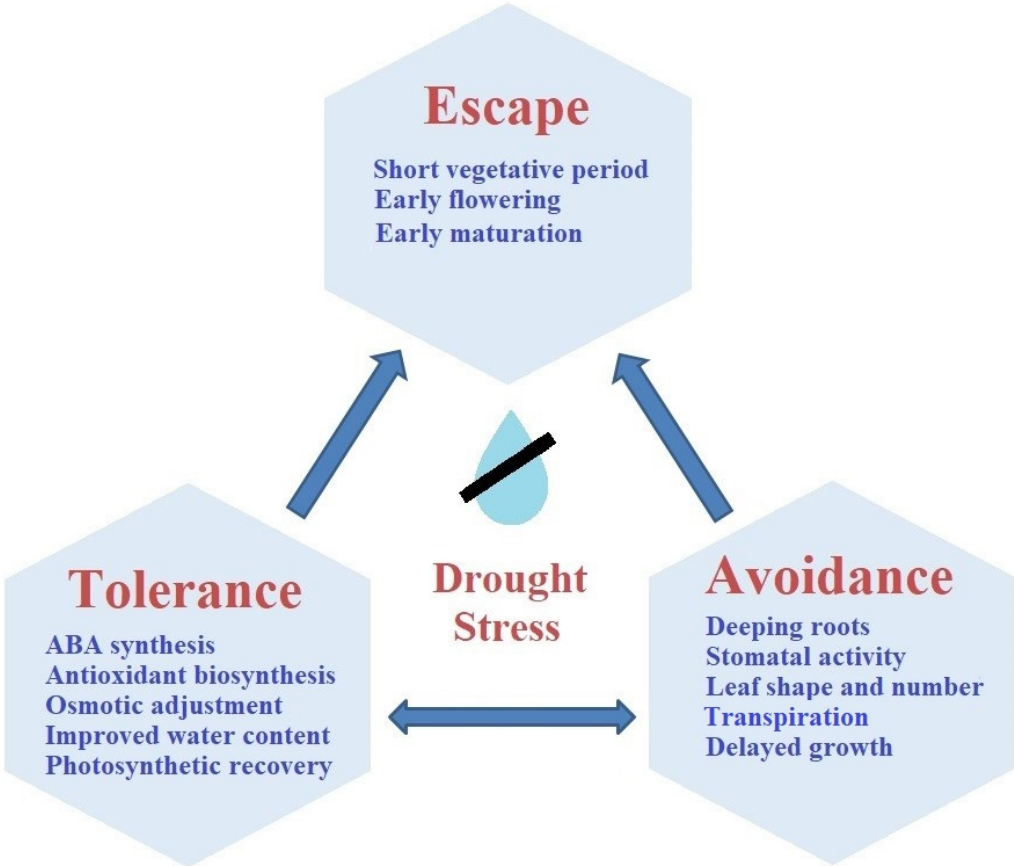

Figure 3. Drought stress management of the plant.

Tolerance includes molecular, biochemical, and physiological responses mediated by osmotic regulation, accumulation of osmoprotectant (e.g., proline), ABA biosynthesis, and stomatal activities [7]. Stress avoidance by plants is the ability of the root to move deeper to reach water, the closing of stomata, leaf rolling, and efficient use of available water by plants [18]. To escape drought the vegetative cycle is completed in a short time. Plants pass the generative stage quickly. This situation leads to early flowering and seed formation [123]. These reactions occur as a result of the effect of multiple stress tolerance mechanisms operating within the plant.

6. Drought Stress Effect on Different Development Stages

Many processes that affect growth and development in plants are impacted by water deficiency stress. Yield is the final stage of these processes. The effect of drought on the plant varies according to the genotype, the intensity and duration of the drought stress, and the growth stage of the plant [14,124].

Growth is established through cell division, cell growth, and differentiation. Low turgor pressure greatly limits cell growth [125]. The mitosis process disrupted by drought causes decreased cell growth and development [126]. Consequently, cell growth is one of the most drought-sensitive physiological processes. It has been stated that cell growth responds to even mild drought stress and can be adversely affected [127]. With the continuation of drought stress and the increase in stress severity, cell death can occur. This situation causes the metabolism to be disrupted and thus the physiological functioning to be damaged [128].

Plants can be exposed to drought stress for many periods from germination to harvest. Drought stress is an important factor that directs germination, seedling formation, root and shoot growth, tillering, flowering initiation, pollination, fertilization, seed yield, and quality [129]. Plants are susceptible to drought stress during all growth periods [130]. The growth and development phases of the plant, such as germination, seedling formation, and tillering constitute the vegetative development stages. Generative growth consists of flowering, fertilization, seed formation, and grain-filling periods. Drought can affect the vegetative and generative stages of the plant differently [14,131]. Researchers focused on examining the effects of drought on yield and quality in crop production during these critical developmental periods [18].

6.1. Drought Stress in the Vegetative Stage

The germination of plant seeds marks the start of vegetative growth. A complicated series of biochemical and physiological processes occurs inside the seed to start plant development and embryo growth. Seeds undergo biochemical changes quickly after absorbing water. The amount of water in the environment affects how much water is taken in and absorbed [132]. For successful germination, seeds must reach a sufficient level of hydration during the absorption phase to reactivate the metabolic processes and stimulate the growth of the embryonic axis. Under drought stress, more time is needed to adjust the osmotic potential of the seed [133]. Therefore, there is a delay in the absorption process [21]. As the germination rate of seeds that do not reach the required hydration level decreases and the germination delay increases, poor seedling formation occurs [134]. Decreased germination rate and poor seedling growth are early signs of drought stress [132]. The negativities encountered in the early stage of plant growth due to drought stress reduce plant establishment per unit area [135,136]. Many researchers have reported that drought has negative effects on physiological processes in the early development stage such as germination, coleoptile length, shoot, and root length [21,137–141]. Coleoptile length is an important parameter that affects the emergence of the germinated seed in the soil and the success of seedling formation. Under the condition of water deficiency, suppression of coleoptile and root formation may occur due to turgor pressure-induced negativities in early cell division and growth. This has important consequences that affect shoot elongation and root growth in the afterward growth stages of the plant [21,133,142].

Varieties that show long and widespread root development in tolerance to drought stress can have successful seedling formation with advanced root systems that can reach deep for water uptake from the soil [143]. This feature is one of the mechanisms developed by the plant to avoid drought stress. Besides, root characteristics such as the number of roots, diameter, angle, depth, total length, distribution, and biomass of the plant in the later stages of the vegetative growth period are closely related to drought tolerance [144,145].

Physiologically drought-resistant varieties have high water use efficiency. They can produce better photosynthetic activity and energy with low water consumption and low transpiration rate mechanism [146,147]. Mega et al. [148] reported that the phytohormone abscisic acid (ABA) is involved in regulating water use, directly regulating stomatal opening and perspiration. Plant growth is positively affected as a result of decreased transpiration and the accompanying increase in photosynthetic activity and increased water use efficiency.

To maintain a balance between the water received by their roots and the hydration status of plant tissues, plants can restrict leaf elongation when they are under water stress [149]. A reduction in the number of leaves per plant, a reduction in leaf size, and an increase in leaf senescence are only a few of the detrimental effects of drought stress during the vegetative period [150–153]. Another important physiological response that occurs in response to water stress is leaf rolling. It is thought that leaf rolling aims to reduce the transpiration rate of the plant [38,154]. The purpose of the plant with these physiological responses is to keep water loss to a minimum [18]. However, photosynthetic activities may be damaged due to decreased gas assimilation, decreased amount of chlorophyll, and impaired physiological and biochemical balance such as RWC [14,79,155–157].

Drought has a great effect on the intake of minerals and nutrients needed by the plant from the soil. The decrease in soil water content due to drought adversely affects the water content in the cells and tissues of the plant [158,159]. In addition, water is an important factor in dissolving the supplements necessary for plant growth and development in the soil. Due to the decrease in the assimilation of the roots, there are problems in the uptake of these nutrients [160–162]. The effects of drought in the vegetative period are decreased fresh and dry biomass production, delayed tillering, shorter first internodes, early maturity and unexpected plant losses [163]. According to Semerci et al. [164] pointed to a significant reduction in growth, including shoot length, biomass, and leaf number, due to low turgor pressure that drives the plant to stunted growth during drought stress. Panda et al. [165]; reported that drought stress during the vegetative growth period was effective on RWC, the number of siblings, plant biomass, and grain yield. In addition, significant and positive correlations were observed between yield and physiological and biochemical properties such as proline content, relative water content, catalase activity, peroxidase activity, total chlorophyll content, and plant biomass under drought stress conditions [165]. Hossain et al. [166] reported a significant decrease in the number of days to flowering, plant height, seeds, and yield per plant under drought stress. According to Bangar et al. [30] stated that significant decreases in RWC, membrane stability index (MSI), proline content of leaves, leaf area, plant height, and yield occur under drought stress in the vegetative and reproductive stages.

Most of the molecular, physiological, and morphological studies carried out in the explanation of drought stress are generally carried out at the seedling stage (Vegetative period). However, it has been suggested that the most important period for sensitivity to drought is the vegetative and generative phases merge. The physiological merge stage represents vegetative growth ends and flower formation begins, and the transition to the generative stage.

6.2. Drought Stress in the Generative Stage

Drought stress on the vegetative growth and development stages of the plant can affect the yield. However, the plant's exposure to stress in the generative stage has a more severe effect on fertilization and grain yield. The plant vegetative stage takes longer than the generative period. Therefore the plant has more time to respond to stress and improve physiological processes. Conversely, the stresses encountered in the generative stage can cause irreversible results. The period of plants such as pollination, fertilization, grain formation, and grain filling in the generative stage are critical periods when yield losses can be high [22,157,167].

Plants undergo substantial changes during their flowering phase after the vegetative phase has ended. Both the beginning and the duration of these crucial developmental stages are impacted by drought. Plants typically reduce the amount of time between the start of flowering and blooming when there is a moderate drought, in an effort to avoid it. However, under the effect of a severe drought, this time frame could be extended [168].

Arid conditions decrease the development progress as a result of the decrease in the amount of photosynthesis resulting in a loss in flowering formation, grain filling, and yield [102]. Drought during flowering often results in sterility. One of the most important causes of sterility is the insufficient flow of nutrients and minerals to the developing generative area [79,169,170]. On the other hand, drought stress causes anthesis (blooming and dying of the flower bud). The reproductive phase shortened by anthesis occurs as a result of the tendency of plants to escape from stress [171]. Ranawake et al. [172] stated that water stress significantly affects the flowering and pod-filling period.

Vadez et al. [173] stated that the plant's tolerance to drought stress increases as a result of the improvement of physiological activities such as transpiration rate and water use efficiency in the pre-blooming period. Physiological adaptations such as efficient use of water during the vegetative process, low stomatal movement, and maintaining the balance in turgor pressure ensure the preservation of the water needed by the plant during the grain filling phase [174]. Besides, high chlorophyll content positively influences flowering and reproduction periods with increased photosynthetic activities [175]. On the other hand, plants are more sensitive to drought stress during the flowering period [176]. Drought stress delays the flower formation stage and negatively affects fertilization, cluster development, and seed formation processes [177]. Therefore, drought stress at the flowering stage has a strong irreversible effect on yield [28].

During the generative period, drought stress significantly affects grain yield and quality by reducing seed size, number, and seed weight per plant [22,157]. The decrease in grain filling rate occurs due to inactivation in energy synthesis, carbohydrate metabolism, sucrose and starch production as a result of disruptions in the photosynthesis process [19,161]. Drought stress at the stage of fertilization and cob formation in maize led to a significant decrease in components such as grain order, grain number, 1000 grain weight, grain yield per plant, biological yield, and harvest index [14]. Cakir [34] reported that water stress during the cob formation period causes yield loss of up to 40% in maize. Rizza et al. [152] reported that drought in the reproductive growth stage of wheat reduced the yield in the number of grains by up to 72% due to anthesis. One of the adaptation mechanisms that plants have developed to escape from drought stress is the short seed-filling period. However, losses in seed yield occur as a result of the shortening of seed filling time and reduced seed size due to drought stress [178]. Felisberto et al. [32] stated that the lack of water encountered in the grain-filling stage of soybean is of critical importance for yield.

7. Future Scope of Research for Agricultural Sustainability of Crops

In order to meet the increasing food demand of the world population, preventing yield losses due to abiotic stresses in agricultural production is crucial. A prerequisite for increasing plant stress tolerance is an understanding of plant response mechanisms to stress. Innovative and biotechnological methods are of great importance in increasing tolerance to abiotic stress [8]. In this respect, researchers use different omic approaches to develop plant stress tolerance [2].

Local populations are important resources that should be used in plant breeding and selection studies that are resistant to drought stress thanks to their wide genetic variety [117,179]. Especially, agronomic plant traits of local plant populations used in drought-resistant cultivar breeding and their performance under stress conditions should be considered. Because the yield in field crops depends on some agronomic plant traits such as plant height, number of spikes, grain weight, harvest index, thousand seed weight and grain yield [180].

In recent years, researchers have focused to prevent yield losses in plants with environmentally friendly innovative approaches. In changing climatic conditions and under abiotic stress factors, the use of bio-fertilizers, bio-stimulants and agro-industrial wastes as a compost is important for sustainable agriculture [181–183].

Most of the studies to increase stress tolerance target a specific developmental period of the plant. However, the reactions of plants vary according to the developmental stages. For this reason, the responses of plants to stress in different growth periods should be targeted. These approaches need to be integrated into agronomy and supported by field trials. Furthermore, conducting field trials in different locations and climatic conditions will make a significant contribution to supporting the arguments.

8. Conclusions

It is obvious that, as it is today and will continue to be in the future owing to global climate change, dryness will be the primary factor restricting crop production. Drought stress affects plant growth and yield. The timing, duration, severity, and speed of stress undoubtedly play an important role in determining a plant's response to a lack of water.

However, drought is a difficult situation to control under natural conditions. The response of plants to stress at different growth stages is an important criterion for the development of varieties with high-stress tolerance. The response of plants to stress occurs as a result of the cooperation of molecular, biochemical, physiological, and morphological mechanisms. Each of these mechanisms is very complex to be considered separately. Focusing on the differences in the activation and regulation of these mechanisms during important development stages of the plant may lead to new approaches. In this review, we tried to explain the response to drought stress in the critical vegetative and generative periods. Consequently, determining the effect of drought on the critical growth stages will guide the studies to be carried out to prevent yield losses.

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