

Responses and Mechanisms of Plants against Drought Stress

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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.

drought stress

important development stages

plant response

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][2][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][11][12][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 defence 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 ageing, 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][15][16][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 colouration, 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][22][23], maize [24][25], wheat [19][26][27], rice [20][28], mung bean [29][30][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].

2. 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 [35]. Plant response to drought stress is managed by molecular, biochemical and physiological mechanisms (**Figure 1**).

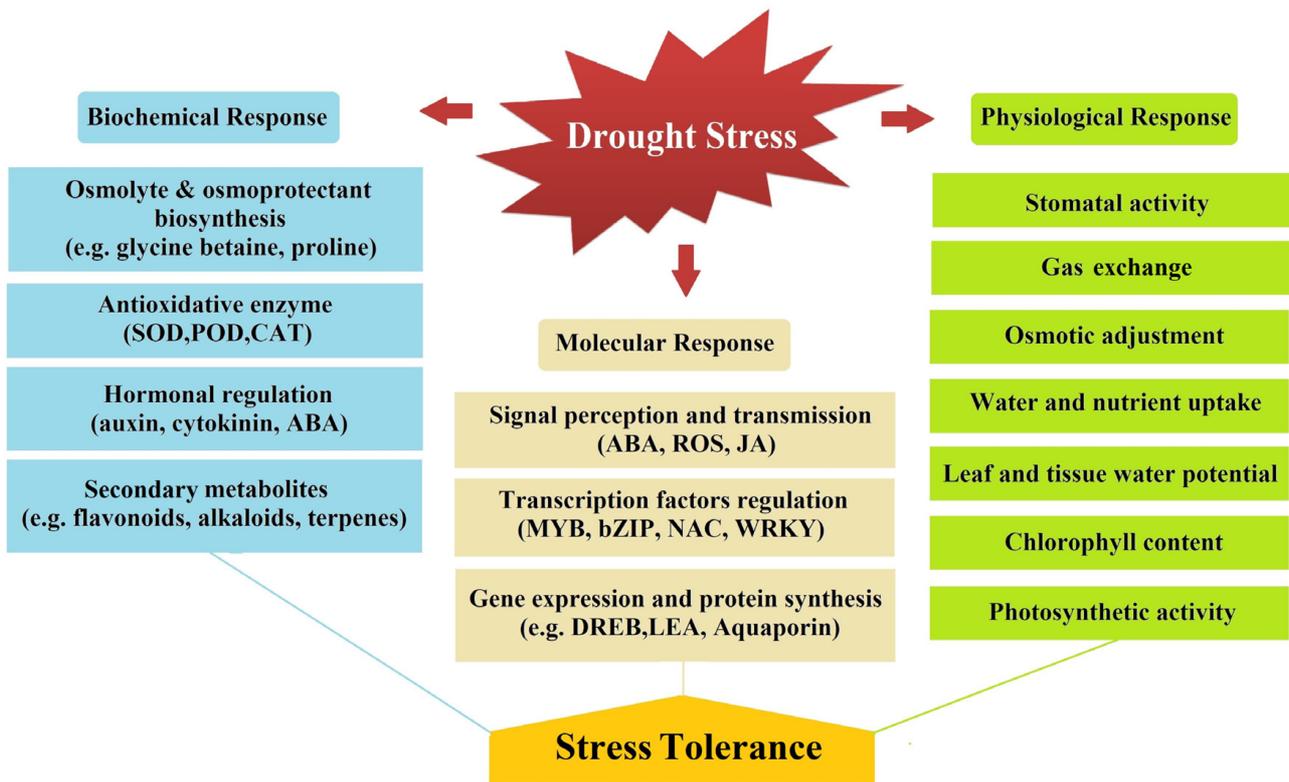


Figure 1. Relation of molecular, biochemical, and physiological responses to drought stress.

The physiological response of plants to drought stress consists of long-term and short-term responses [36]. 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 [37]. 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 [38]. Plants can transmit positive and negative signals between roots and shoots for adaptation to environmental conditions [39]. 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 [40][41]. 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 [42][43][44][45]. Strigolactone (SL) is a plant hormone that affects physiological processes such as shoot branching, root elongation, and leaf senescence [46]. Besides, SL acts as a signal molecule for drought stress tolerance [47]. The increased level of SL biosynthesis gene expression under drought stress is one of the important regulators in plant response to stress tolerance [48][49].

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 [50][51] 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 [43]. These substances accumulate in leaf tissues and cause the initiation of molecular, biochemical, and physiological processes. Oğuz et al. [52] 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 [53]. The closure of the stomata and the reduction of water loss by the plant is a physiological response to avoid drought [54][55]. 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 [56][57][58][59][60]. As a result, all these processes and physiological events affected photosynthetic activity directly or indirectly [61][62][63]. Plants control gas and water flow through the stomata in leaf tissue. The closure of stomata due to drought prevents the use of CO₂, which is of great importance for photosynthesis [64]. The reduction of CO₂ uptake by the plant directly causes low photosynthetic activity [65]. 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][66] (**Figure 2**). This situation causes a dramatic decrease in the nutrient concentration of plant tissues and ion balance [41][66][67]. Many processes are adversely affected due to the disruption of nutrient, mineral, water, and gas flow in plant tissues [68][69][70]. Relative water content (RWC) is another important physiological feature that affects leaf water potential, stomatal resistance, transpiration rate, and plant water relations [53]. 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][71][72] (**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 [73][74]. 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 [75].

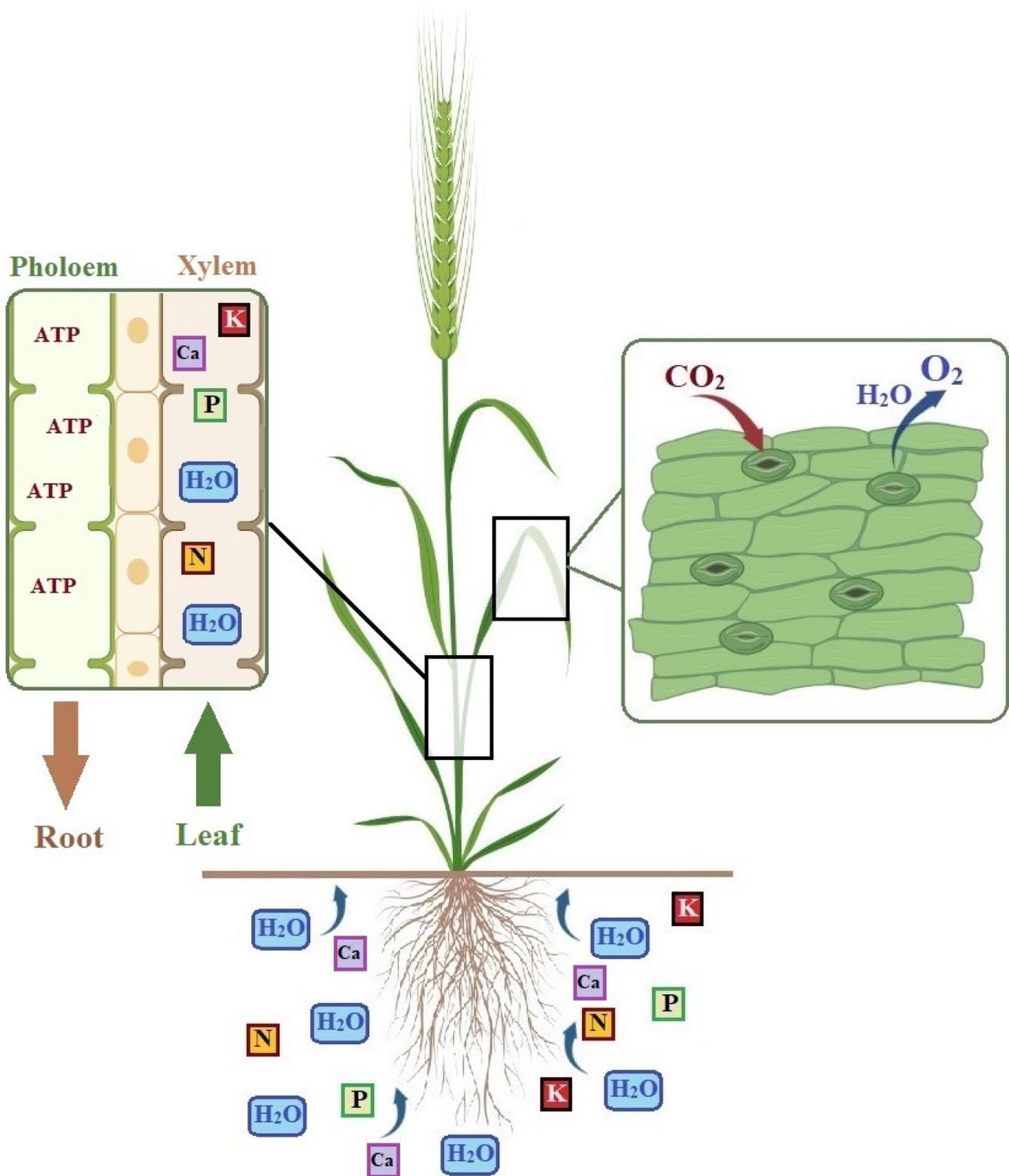


Figure 2. Transpiration through stomata and the movement of water and nutrients from the soil. Leaf transpiration and gas exchange are controlled by stomata. The water movement in the plant is controlled by the loss of water by transpiration from the leaves and the movement of water uptake from the root. 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.

Photosynthesis is the most important physiological process directly related to growth, development, and yield in all green plants [76]. 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 [77]. Deterioration in the chloroplast structure due to drought adversely affects the synthesis of chlorophyll [76]. 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 [78]. 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 [41].

3. 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 [79]. 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 [80]. 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 [81][82][83][84]. 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 [85]. 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 an escape, avoidance, and tolerance.

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