




Review

The Impact of Drought in Plant Metabolism: How to Exploit Tolerance Mechanisms to Increase Crop Production

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Abstract: Plants are often exposed to unfavorable environmental conditions, for instance abiotic stresses, which dramatically alter distribution of plant species among ecological niches and limit the yields of crop species. Among these, drought stress is one of the most impacting factors which alter seriously the plant physiology, finally leading to the decline of the crop productivity. Drought stress causes in plants a set of morpho-anatomical, physiological and biochemical changes, mainly addressed to limit the loss of water by transpiration with the attempt to increase the plant water use efficiency. The stomata closure, one of the first consistent reactions observed under drought, results in a series of consequent physiological/biochemical adjustments aimed at balancing the photosynthetic process as well as at enhancing the plant defense barriers against drought-promoted stress (e.g., stimulation of antioxidant systems, accumulation of osmolytes and stimulation of aquaporin synthesis), all representing an attempt by the plant to overcome the unfavorable period of limited water availability. In view of the severe changes in water availability imposed by climate change factors and considering the increasing human population, it is therefore of outmost importance to highlight: (i) how plants react to drought; (ii) the mechanisms of tolerance exhibited by some species/cultivars; and (iii) the techniques aimed at increasing the tolerance of crop species against limited water availability. All these aspects are necessary to respond to the continuously increasing demand for food, which unfortunately parallels the loss of arable land due to changes in rainfall dynamics and prolonged period of drought provoked by climate change factors. This review summarizes the most updated findings on the impact of drought stress on plant morphological, biochemical and physiological features and highlights plant mechanisms of tolerance which could be exploited to increase the plant capability to survive under limited water availability. In addition, possible applicative strategies to help the plant in counteracting unfavorable drought periods are also discussed.

Keywords: drought stress; photosynthesis; antioxidant; secondary metabolites

1. Introduction

Plants experience continuous fluctuations of environmental conditions and are often exposed to abiotic stresses, for instance shortage of available water, salinity, excess light, high/low temperatures and nutrient imbalance, all leading to impairment of plant performance [1]. The capability of plants to respond to abiotic stress is associated with their plasticity as well as the adaptableness of plant traits to the fluctuating conditions of water availability [2]. Amongst these limiting abiotic factors, drought (or water deficit) stress is extensively studied given that it is likely the main constraint for crop productivity in many arid and semi-arid areas worldwide [3].

Water deficit occurs when the plant water requirement cannot be fully satisfied and this situation takes place when the level of transpired water exceed the water taken up by the roots, which is caused by inadequate precipitation, decreased ground water level or the retention of water by soil particles [4,5]. As a result of water stress, plants respond with morpho-anatomical, physiological and biochemical adjustments aimed at counteracting the loss of water with the attempt to preserve their hydric status [2].

Being sessile organisms, plants have to face several adverse factors in natural environments, and, for this reason, they possess numerous defense strategies and have evolved several resistance mechanisms through which they cope with abiotic stresses [6]. Enduring severe water deficit periods, which relies on plant-genotype-specific features, also depends upon stress intensity, duration, speed and recovery effectiveness to regulate plant performance [7,8]. In the case of water scarcity, plants need to respond quickly, thus virtually all biological functions are altered by water deficit conditions at whole plant level [9,10]. Plants have to stimulate different strategies that benefit them to absorb water through their roots and to uphold cell turgor, i.e., evade the water loss [11]. Declined frequency of cell division and cell enlargement, root differentiation, foliage dimensions, shoot length, altered stomatal movements, water and mineral nutrition association with decreased plant yield and water usage efficacy are major outcomes of drought in plants [12]. Photosynthesis activity is decreased primarily by closing of stomata, membrane injury and altered functioning of several enzymes, specifically those which are associated with ATP synthesis [12,13]. Drought stress conditions also result in increased generation of reactive oxygen species (ROS) and reactive nitrogen species (RNS), which disturb the cell redox regulatory functioning [8,14].

Plants that are able to tolerate drought stress for extended periods and sustain their vigor and yield represent one of the foremost exploration fields in agriculture studies [15]. As detailed below, tolerant plants may benefit from different features which allow them to tolerate better than others the effect of water scarcity. For example, among morpho-anatomical features, a well-developed root apparatus ensures the plant a deeper exploration of the soil thereby increasing the capability of water uptake [16]. Other physiological (e.g., rapid stomata closure and water use efficiency) and/or biochemical responses (e.g., synthesis of osmolytes, aquaporins and a powerful antioxidant apparatus) may contribute in increasing the drought tolerance of some plant individuals [17], thereby supporting the use of those drought-tolerant genotypes/varieties.

Besides the exploitation of plant tolerant genotypes/varieties based on classic breeding selection, some applicative strategies have also been applied to attempt to overcome drought effects in crop species. For example, under controlled circumstances, regulated deficit irrigation may allow to obtain positive results in plant growth, likely due to a significant overproduction of advantageous moieties such as sugars, organic acids and antioxidant compounds [18,19]. In addition, foliar application of some compounds (including those produced by drought-tolerant genotypes, which are supposed to contribute to plant drought tolerance) may help plants better tolerate a condition of limited water availability. Among these, brassinosteroids [20,21], salicylic acid [22], amino acids [22,23], polyamines [24] and micronutrients (e.g., potassium and phosphorous) [25] are certainly the most efficient with consistent results in different plant species. Knowledge of the morpho-anatomical, physiological and biochemical mechanisms underlying drought tolerance (as discussed in the next

sections) is crucial for conferring drought tolerance to major crops, in order to valorize marginal areas (e.g., semi-arid environments) in which water availability is the major constraint for the plant growth.

2. Influence of Drought Stress on Plant Performances: From Morpho-Anatomy to Biochemical Changes

Water deficit conditions stimulate several plant responses, such as morphological, physiological, biochemical and molecular alterations, which ultimately result in disturbing plant functioning [26] (Figure 1). As depicted in Figure 1, drought events limit plant performances in different developmental stages. Limited water availability can indeed reduce the germination rate and the development of young plants [27]. During the progression of plant growth, drought basically influences the plant water relations, which in turn cause severe perturbation to the whole plant metabolism (at physiological, biochemical and molecular levels), depending to the stress severity and duration [14,28]. Water deficit conditions alter several activities of plant, but one of the main effects is the decline of photosynthetic activity [29,30] and finally the plant yield [31,32]. During drought stress conditions, oxidative stress, directly or indirectly generated in plants, is one of the main drivers of plant responses and results in damage to cell membrane, altering membrane integrity, physiological and biochemical alterations which lead to acute metabolic disorders and eventually alter the plant productivity [33,34].

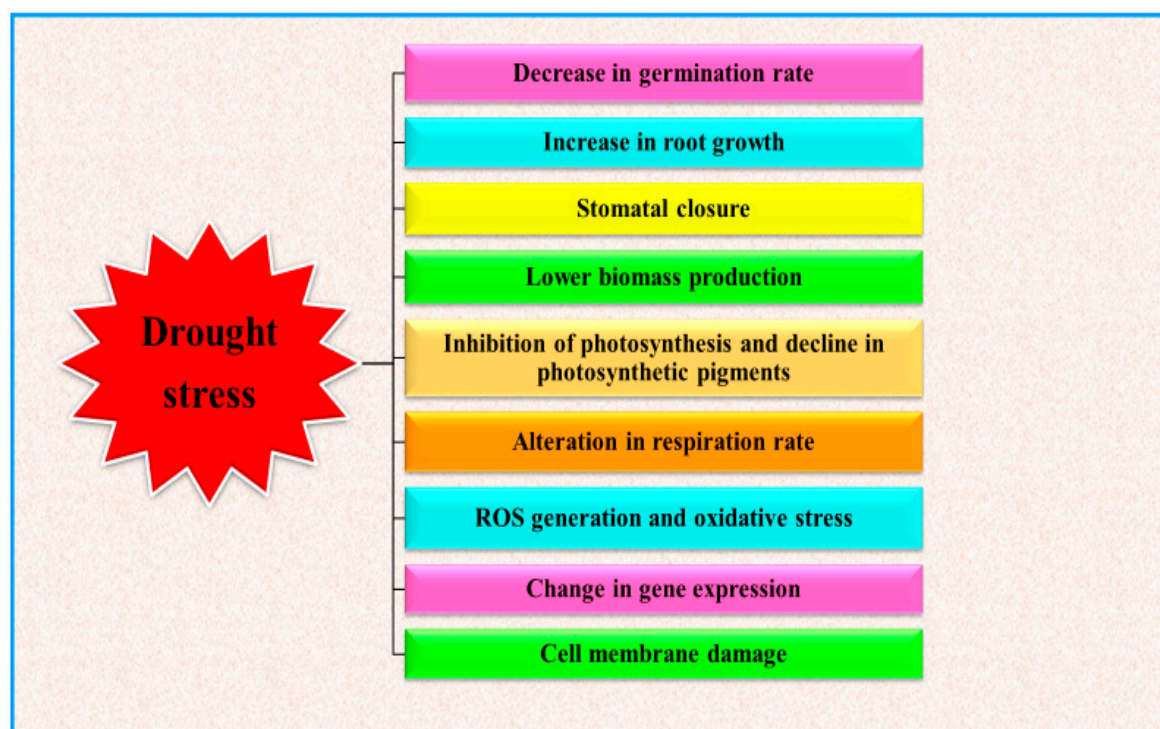


Figure 1. Effect of drought stress on plant growth and development (modified from Ghatak et al. [35]).

3. Drought Stress and Plant Growth

Drought stress is well recognized as a limiting factor which alters multiple aspects of plant growth and development. Germination of seeds, health and coleoptile length are foremost for the plant progression [36]. Seed germination is the primary aspect of growth which is sensitive to drought stress. Noteworthy alterations are observed in the seed germination of a plethora of plant species, including some of the most widely cultivated crops such as maize [37], sorghum [38] and wheat [39].

Visible symptoms of plant exposed to water scarcity in the initial vegetative stage are leaf wilting, decline in plant height and interruption in establishment of buds and flowers [40]. Drought conditions also limit the uptake of nutrients by the plants due to limited soil moisture, leading to decreased stem length [41]. Shoot length was also reduced under water deficit conditions in *Lathyrus sativus* L. [42].

In conditions of water deficit, plants seek to extract water from deeper soil layers by boosting their root architecture [43]. Moreover, water availability is primarily recognized by roots, which in turn regulates its growth and organization characteristics such as root length, spread, number and length of lateral roots [44]. Roots are crucial for different biological activities and plant yield, for instance nutrient accumulation and water absorption, and they are also involved in rhizosphere symbiotic associations with other microorganisms. Drought stress escalated root length in *Crocus sativus* L. [45]. Thus, a healthy root apparatus provides the benefit for sustenance of the escalation of plant growth, especially in the course of primary plant growth phase [46]. Escalation in root length is recognized as a useful strategy to increase soil water retention and nutrient accumulation to enhance plant biomass production [47]. Under water deficit, the plant root to shoot proportion generally improves, and, subsequently, the plant biomass decreases substantially [48].

The leaf is the chief part of the plant where most of the photosynthetic products are synthesized. The number of leaves decreased when subjected to water stress in *Andrographis paniculate* [49]. Optimal leaf development and the maintenance of an adequate leaf area is vital for photosynthesis, which in turn is the main driver of plant growth. Water stress causes reduction in leaf area, which results in decreased photosynthesis, hence reducing the crop yield. Leaf area declined under water stress conditions in *Petroselinum crispum* L. and in *Stevia rabaudiana* plants to achieve stability among the water absorbed by roots and the water status of various plant parts [50,51]. Reduction in leaf area is a drought avoidance strategy because declining leaf area results in a decreased water loss by the process of transpiration and this reduction in leaf area is attributable to the inhibition of leaf expansion by declined rate of cell division, which results in loss of cell turgidity [52]. Decrease in soil moisture causes a parallel reduction of leaf water content, which, in turn, induces a decline of turgor pressure of guard cells due to stomata closure [53]. Of note, the rate of premature leaf senescence is enhanced in drought environments [17].

4. Drought Stress and Photosynthesis

Major consequence of water deficit in plants is the decrease or suppression of photosynthesis [54] (Figure 2). Reduced leaf area, increased stomata closure and consequent reduced leaf cooling by evapotranspiration increases osmotic stress leading to damages to the photosynthetic apparatus are among the major constraints for photosynthesis [55,56]. Among these, the decrease in photosynthetic process in plants under drought is mainly attributable to the decline in CO₂ conductance via stomata and mesophyll limitations [57]. Decrease in photosynthetic activity due to drought may also be due to reduced ability of stomatal movement [58,59]. Declined activity of photosynthesis is triggered by the loss of CO₂ [60] uptake, whose drop has been shown to affect Rubisco activity and decrease the function of nitrate reductase and sucrose phosphate synthase and the ability for ribulose biphosphate (RuBP) production. Supportively, CO₂ enrichment eliminated many early responses of maize metabolites and transcripts attributable to drought stress [61].

Water deficit also resulted in decreased leaf area per shoot, and, thus, modification in canopy architecture, and this feature can alter gas exchange, water relations, vegetative growth and sink development (e.g., fruits or grains) [62], altering, for example, berry sugar concentration in grape [63] and biomass partition in maize (i.e., kernel number and 100-kernel dry weight decreased with increasing water stress duration) [64].

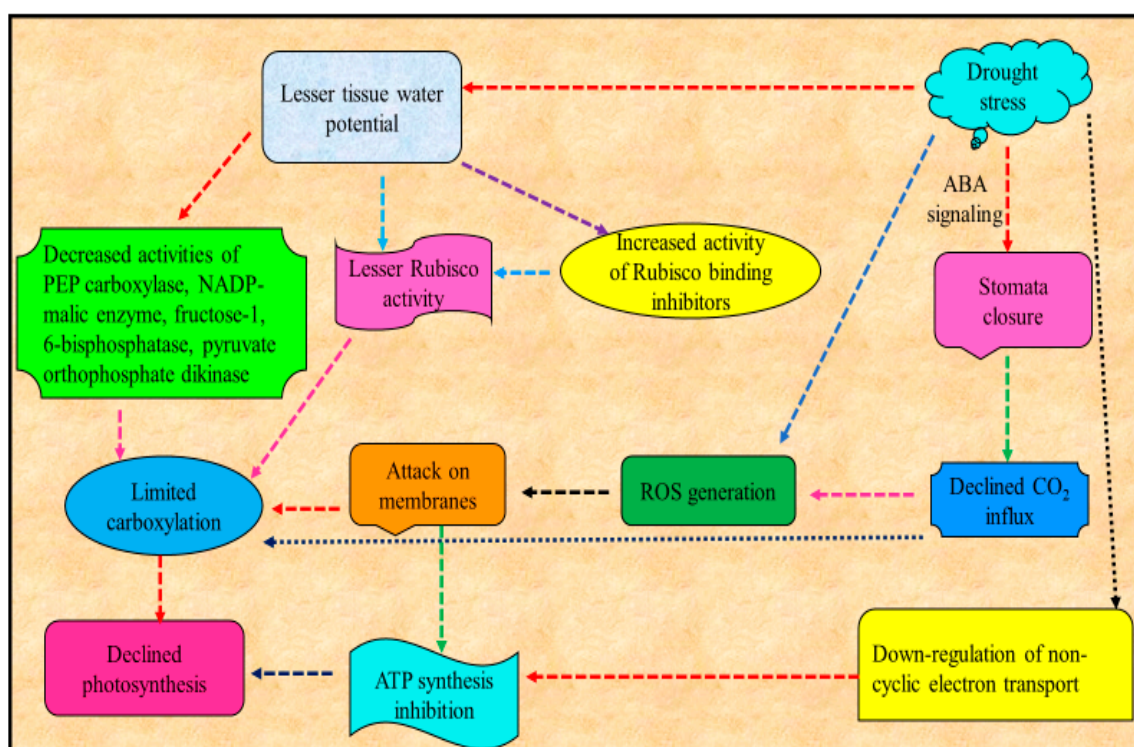


Figure 2. Schematic representation of effect of drought stress on photosynthesis (modified from Farooq et al. [17]).

Chlorophyll content, which is of outmost importance for photosynthesis [65], is another photosynthetic attribute strongly influenced by water deficit that has been recognized as a distinctive indication of photo oxidation and degradation of chlorophylls [66]. For example, leaf chlorophyll synthesis and chlorophyll *a/b* proportion in soybean is altered by drought stress [67]. Decline in photosynthetic activity, amount of chlorophylls, loss of photosystem II photochemical efficiency, alteration in stomatal movement and disturbance in water status of plants resulted in declined plant productivity [68]. Among others, a major cause for decline in amount of chlorophyll due to drought stress is the drought-promoted O_2^- and H_2O_2 , which results in lipid peroxidation and ultimately chlorophyll degradation [69]. The decrease of plant development and yield in several plant species under water deficit is often associated with decline in photosynthetic action and chlorophyll content impairment [70]. Water deficit alters the action of photosynthetic moieties and chlorophyll pigments, which ultimately resulted in reduced photosynthetic activities in *Vigna mungo* [71].

Drought stress induces a decreased net photosynthesis and also changes the plant carbon allocation and metabolism, which ultimately results in energy dissipation and declined yield [72]. For example, drought stress decreased the physiological metabolic disorders by suppressing the photosynthetic products production and disrupting the carbon balance in soybean [16]. Drought stress also caused a reduction in the abundance of several Calvin cycle proteins, including Rubisco downregulation in olive [73]. Acute drought stress conditions also cause the damage to Rubisco enzyme and other enzymes associated with photosynthesis and are responsible for the loss of photosynthetic pigment content [74].

5. Drought Stress and Antioxidant Defense System

Most of the plant defensive system is devoted to contrast the adverse consequences of drought-triggered ROS. In this context, a prompt, powerful and efficient antioxidant system is of pivotal importance to provide drought tolerance [75]. This machinery involves enzymatic and non-enzymatic detoxification moieties, which lessen and repair injury triggered by ROS. Enhancement

of the antioxidant apparatus helps in ROS scavenging that decreases electrolyte leakage and lipid peroxidation, therefore maintaining the vitality and integrity of organelles and cell membrane [76].

It is well recognized that drought induces oxidative stress by generating ROS, for instance $O_2^{\bullet-}$, hydroxyl radicals (OH^\bullet), singlet oxygen (1O_2) and H_2O_2 [77]. The proportion of ROS generation and antioxidant enzyme activities regulates the cell redox state, thereby resulting in ROS control or cell injury and cell death when ROS exceed the physiological levels [78]. Numerous studies conducted under water deficit conditions found enhanced activities of pivotal antioxidant enzymes, namely CAT, SOD, POD and APX [79]. Usually, tolerant species/varieties/genotypes have an enhanced antioxidant enzymes activity in comparison to non-tolerant plants, which is supportive for their essential role in drought tolerance, especially to control H_2O_2 and $O_2^{\bullet-}$ production and diffusion in leaf tissues [80].

Production of $O_2^{\bullet-}$ and H_2O_2 were controlled by superoxide dismutase (SOD), peroxidase (POX) and catalase (CAT) action, whose activity was enhanced for example in drought-tolerant potato genotypes [81]. Ascorbate peroxidase (APX) also participates as excess ROS scavenger (APX uses ascorbate as a substrate to stimulate the conversion of H_2O_2 to H_2O), and its activity is usually elevated under stress conditions [82]. Alteration in APX activity in leaves is more common than in fibrous roots because APX mainly occurs in the chloroplast and cytoplasm and is a crucial enzyme for scavenging H_2O_2 in chloroplasts [83]. Activities of SOD, POD, CAT and APX were altered and played a key role in protecting peony plants against acute water deficit [84]. The amount of non-enzymatic antioxidants (ascorbic acid, reduced glutathione and α -tocopherol) and antioxidant enzymes (SOD, CAT and APX) activities were simultaneously enhanced in *Coleus plectranthus* in drought stress conditions [85]. SOD, CAT and POX enzymes activities were stimulated by limited water availability in *Vicia faba* [70]. Increase of SOD, POX and CAT activities was observed in drought-tolerant genotype, in comparison to the drought sensitive plants of faba bean [86]. The amount of enzymatic and non-enzymatic antioxidants improved in drought tolerant plants under mild and moderate water deficit conditions [87]. CAT, SOD, POD and APX activities increased in *Adonis amurensis* and *Adonis pseudoamurensis* subjected to drought, indicating that improved functioning of these enzymes helps to lower the level of ROS and mitigate the drought generated oxidative stress [88]. Water deficit boosted the levels of SOD and POD in *Vigna mungo* and the authors concluded that increased levels of these enzymes stimulate tolerance against drought stress and are vital to reduce its adverse effects [71]. Water deficit increased the CAT, POX and SOD levels in leaves of *Glycyrrhiza glabra* L., which aimed at counteracting the spread of H_2O_2 [89].

6. Drought Stress and Secondary Metabolites

Secondary metabolites are produced by plants in the attempt to respond to various environmental stresses [90,91]. It is recognized that the biosynthesis of secondary metabolites is regulated by environmental factors, for instance temperature, light regime and nutrient availability [92]. Improved production of secondary metabolites is usually observed under water deficit conditions, which is caused by reduction in biomass formation and destination of assimilated CO_2 to C-based secondary metabolites to avoid sugar-promoted feedback of photosynthesis (Figure 3) [93].

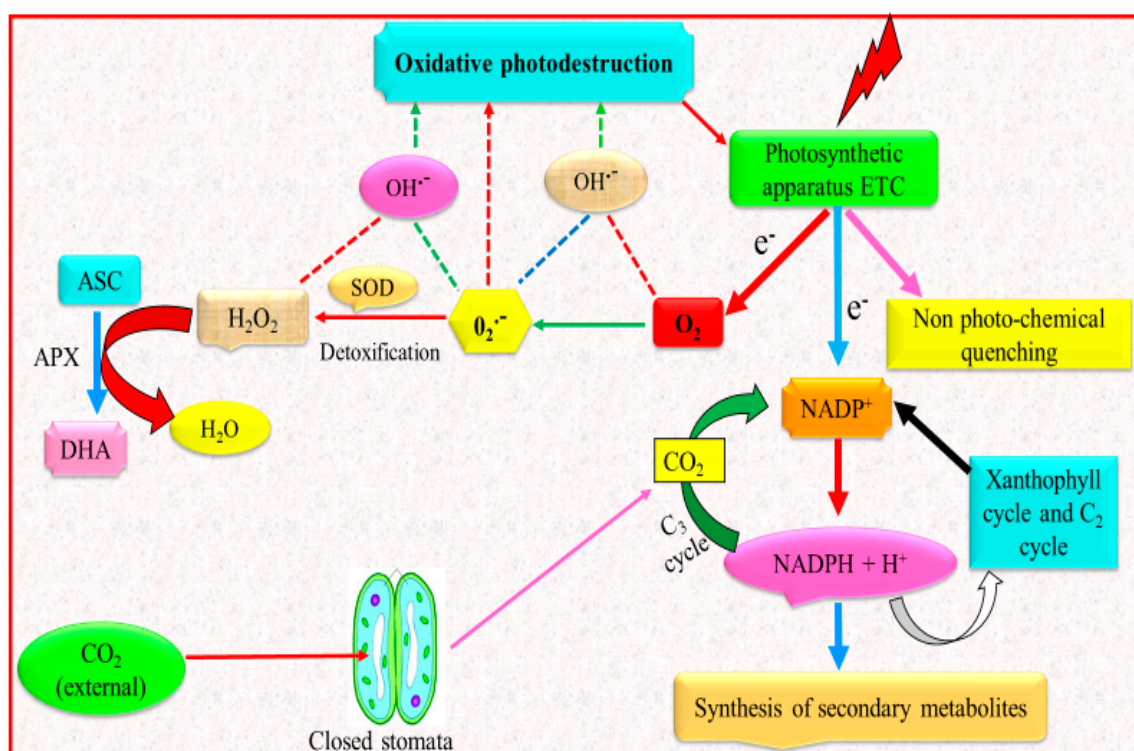


Figure 3. Enhanced synthesis of secondary metabolites under drought stress. Light energy captured by the photosynthetic machinery is considerably greater than the energy essential for the CO_2 fixation. Energy dissipation takes place by non-photochemical quenching and re-oxidation of $\text{NADPH} + \text{H}^+$, i.e., via xanthophyll cycle and C_2 cycle. Endogenous CO_2 level is low because of the escalated diffusion resistance caused by closing of stomata. Hence, a smaller amount of $\text{NADPH} + \text{H}^+$ is utilized in the C_3 cycle for the fixation and reduction of CO_2 , and, ultimately, a greater amount of energy has to be dissipated. Protective activities such as non-photochemical quenching, C_2 cycle and xanthophyll cycle are boosted by feedback mechanisms; a number of e^- is transported to O_2 (Mehler reaction). Generation of $\text{O}_2^{\bullet-}$ ions further produce various ROS. Due to the stress-associated stimulation of SOD and APX, detoxification of the $\text{O}_2^{\bullet-}$ ions occurs and therefore results in reduction of generation of ROS. Greater enhancement in the reduction potential, i.e., the ratio of $\text{NADPH} + \text{H}^+$ to NADP^+ , elevates the plants secondary metabolites synthesis (modified from Kleinwächter and Selmar [90]).

In *Hypericum brasiliense*, concentration of phenolic acids is considerably enhanced when grown in water deficit conditions [94]. In two native sub species of Iranian *Origanum vulgare*, i.e., subsp. *gracile* and subsp. *Virens*, the content of sesquiterpene (E) β -caryophyllene strongly increased by water limitation [95]. Under mild and mild/severe drought, the content of oleanolic acid and betulin increased in *Betula platyphylla* [96] and level of triterpenoid glycyrrhizin in *Glycyrrhiza glabra* [97]. The lignin content was increased in bermudagrass Tifton-85, which is a variety of *Cynodon dactylon* L., under drought conditions [98]. The flavonoids content was enhanced under stress conditions and high-water deficit conditions improved the medicinal properties of *Labisia pumila* [99]. *Phaseolus lunatus* under water deficit condition had an elevated level of cyanogenic glucosides [92]. In Lamiaceae family, the content of essential oils declined in *Lavandula latifolia* and *Salvia sclarea*, whereas, in *Mentha piperita*, *Salvia lavandulifolia*, *Thymus capitatus* and *Thymus mastichina*, the essential oil amount was enhanced under drought conditions and the increase was attributable to a higher concentration oil glands due to decrease in leaf area [100]. The amount of phenolics and flavonoids increased in *Achillea* species against drought stress [76]. The content of phenolic acids simultaneously improved, while the level of flavonoids declined in *Achillea pachycephala* [101].

7. Drought Stress and Mineral Nutrition

Water deficit situations usually reduce the overall soil nutrient accessibility, root nutrient translocation and ultimately lessen the ion content in various plant tissues [102]. Water deficit conditions decreased plant potassium (K) uptake [103]. This decline in K was attributable to reduced K mobility, declined transpiration rate and weakened action of root membrane transporters [103,104]. Decreased K amount was also found in drought-stressed plants of *Malus hupehensis* [105]. Resistant genotypes of *Triticum durum* had the maximum amount of K and susceptible genotypes had the maximum amount of sodium (Na) [69]. Genes encoding K transporters were inhibited by water deficit [106] and inner K channels are stimulated by a protein kinase, CIPK23, which in turn cooperates with calcineurin B-like calcium sensors. This K channel was inhibited in roots but activated in leaves of grapevine [107]. Leaf nitrogen (N) level did not change in drought-stressed *Mentha piperita*, *Salvia lavandulifolia*, *Salvia sclarea* and *Thymus capitatus*, whereas, in *Lavandula latifolia* and *Thymus mastichina* plants, N content decreased while leaf phosphorus (P) level reduced in all species except *S. sclarea* whose concentration remained the same [100]. This reduction in N was considered as the main responsible factor for photosynthesis decline and leaf senescence [108]. There was a significant reduction in leaf P amount in *Ocimum gratissimum* [109] and decline in K level in *Thymus daenensis* under water deficit conditions [110]. K level also decreased in *Ocimum basilicum* and *Ocimum americanum* plants subjected to limited water availability [111]. Principally, decrease of K amount occurs in leaves because water scarcity disturbs stomata movement and guard cell turgidity, which results in decreased photosynthesis and, finally, the plant biomass production [112]. Drought-stress conditions increased the accumulation of manganese (Mn), molybdenum (Mo), P, K, copper (Cu), calcium (Ca) and zinc (Zn) in soybean [113].

8. Plant Tolerance Mechanisms Against Drought Stress to Increase Crop Tolerance: How to Exploit These Mechanisms to Increase Crop Tolerance

The intimal meaning of drought tolerance or drought resistance is still under debate. It is conceivable that water-saving plants mainly refer to the effective use of water resource in the process of growth and development of plants, thereby increasing crop water use efficiency (WUE) [114]. WUE is defined as the economic production per unit water consumption and it may or may not be related to drought resistance [115]. On the other hand, the main accepted definition of drought resistance is the ability of an individual to survive or grow in a water-stressed environment due to dehydration avoidance, dehydration tolerance or drought recovery, where dehydration is considered as the progressive loss of water content in plant tissue [115]. Discerning between drought tolerance or drought resistance can be very complex and is out of the scope of the present review, as there are already excellent papers dealing with this topic [116,117]. Therefore, in the next paragraphs of the present review, plants able to tolerate drought stress conditions better than others are referred to as “tolerant” without any distinctions between drought tolerant or drought resistant.

Plant drought tolerance encompasses alterations at morphological, biochemical and molecular levels (Figure 4). Exhibition of single or multiple tolerance factors governs the plant capability to survive under adverse drought conditions. From an applicative point of view, an in-depth knowledge of these mechanism can be exploited to select crop species/varieties/genotypes with a lower degree of sensitivity to limited water availability. Below, physiological, biochemical and molecular mechanisms which allow tolerant plants to tolerate better drought conditions are described with the attempt to propose some of them as suitable features for crop selection in the context of reduced water availability.

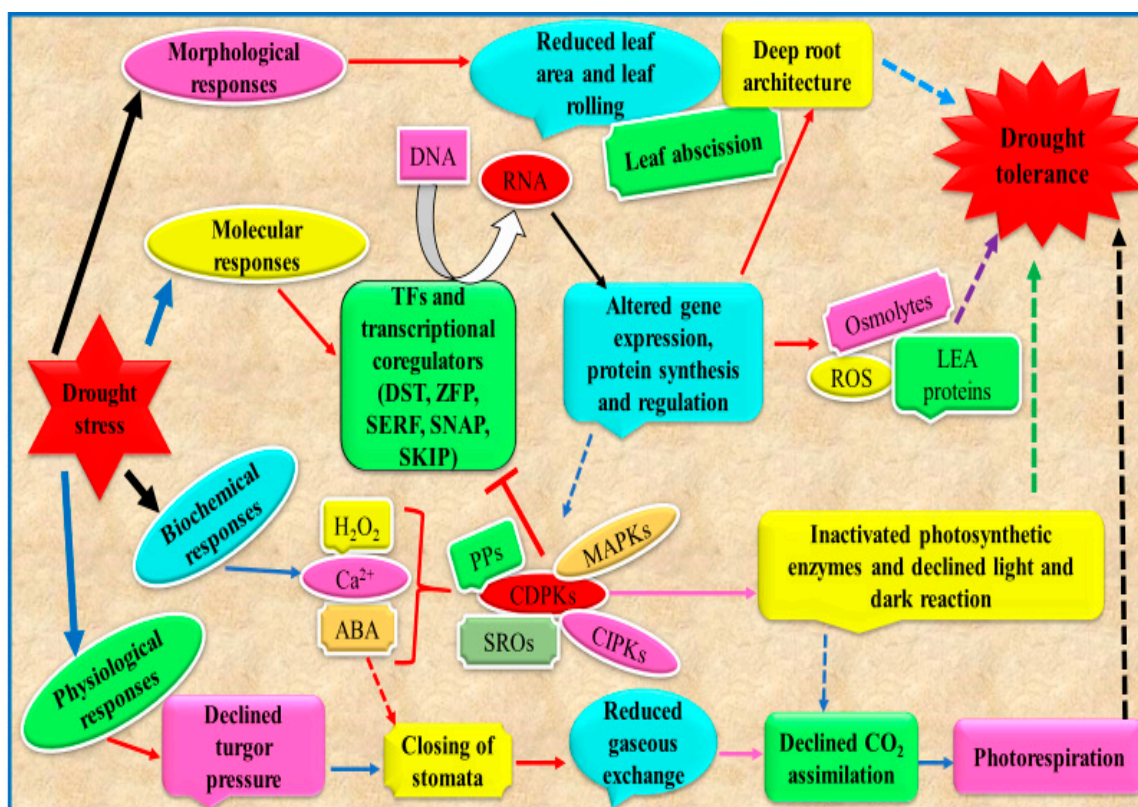


Figure 4. Diagram showing plants drought tolerance mechanism. TFs, transcription factors; DST, drought and salt tolerance; SERF, serum response factor; SKIP, ski-interacting protein; ZFP, zinc finger TF; SNAC, stress responsive NAC TF; LEA, late embryogenesis abundant; ABA, abscisic acid; SROs, similar to RCD-ONE; CDPKs, Ca^{2+} dependent protein kinases; MAPKs, mitogen activated protein kinases; PPs, protein phosphatases; CIPKs, CBL interacting protein kinases (modified from Zargar et al. [118]).

8.1. Morphological and Biochemical Mechanisms Involved in Drought Tolerance

Plants survival to drought encompasses two main strategies: drought avoidance and drought tolerance [53]. Plants have adopted several strategies to increase their drought tolerance at different levels, morphological, physiological, biochemical, and molecular. Conversely, some plant species avoid water deficit situations by accomplishing, for example, their life cycle before or after a drought period while some other plants displayed adaptations to escalate water absorption and decrease water loss to circumvent its adverse consequences [1].

At the morphological level, root is one the major drivers of water; therefore, the root size, its progression rate and density and root proliferation are important features which prompt plant responses to drought stress [5]. Plants with a deep root organization and a perennial development system showed more ability to cope with drought in comparison to plants with shallow-root system [119]. In view of the above, the selection of genotypes with a more developed root apparatus resulted in increased plant yield, as demonstrated for example in rice seedlings [120] and tobacco [121].

When drought stress occurs at initial phases of plant growth, drought-avoidance plants gradually change to succulent types or develop advanced drought tolerance strategies such as generation of compatible solutes, enhancement of antioxidant apparatus and other physiological responses aimed at increase the water use efficiency [122]. Satisha et al. [123] demonstrated indeed, that selection of grape varieties with drought tolerance should follow the analyses of water use efficiency increased for example by the proper selection of rootstocks. Plants avoid water loss by stomata closure, thus decreasing evapotranspiration and increasing water use efficiency [124], therefore stomata regulation is of outmost importance in increasing WUE. Drought tolerance, water use efficiency and K^+ content have close

associations in plants as a sufficient level of K^+ can improve the plant total dry mass and photosynthetic rate; K^+ also regulates the SOD enzyme activity to mitigate the cell membrane injury which is caused by drought-triggered ROS [125]. Besides stomatal movement, drought stress may promote changes of leaf morpho-anatomical traits including vascular bundle per unit leaf area [126], stomata density and leaf thickness [127]. For leaf thickness, especially palisade parenchyma could contain larger numbers of CO_2 -fixation sites [128]. On the other hand, increases of epidermis thickness represent a way to contrast water loss under water limitation and both palisade and epidermis thicknesses can be used to select more tolerant olive genotypes [128]. However, despite drought-promoted morpho-anatomical traits, biochemical limitations might have a greater impact on plant performances [129].

At the biochemical level, plant hormones, secondary metabolites and other key molecules such as carbohydrate, amino acid and polyamines play crucial roles in stress tolerance mechanism and improving the capability of plant adaptation by altering their membrane stabilization, osmoregulation, ROS scavenging, lessening leaf area and its abscission, promoting root development and reducing ion leakage [130]. Osmolytes accumulation is essential for osmo-protection and osmotic adjustment against water deficit conditions which can lead to loss of cell turgor and dehydration. Among others, proline acts as an important signaling moiety against drought stress to stimulate mitochondria functioning and alter cell proliferation, stimulating particular drought stress recovery genes [131]. Proline accumulation helps to maintain membrane integrity by diminishing lipids peroxidation by defending cell redox potential and declining ROS level [132]. It has been shown that plants which accumulate higher levels of proline exhibit higher rates of plant survival (*Triticum aestivum*) [133], biomass production [134] and grain yield [135]. Similarly, genotypes which accumulate higher level of glycine betaine [136], mannitol and other non-structural carbohydrates [137] have greater drought tolerance. Likewise, trehalose under drought stress aids to stabilize macromolecules such as lipids, protein and other biological moieties to enhance photosynthetic functioning, thereby conferring drought tolerance [138,139]. Besides the selection of osmolite-overproducing genotypes/varieties, another promising strategy is the exogenous supplementation of these compatible solutes, which have exerted positive results in different crop species (for a review, see [140]).

Increased antioxidant defenses also assist to increase drought tolerance by defending plants from oxidative stress triggered by limited water availability (see Section 5). Therefore, selection of varieties/individuals with an enhanced antioxidant apparatus allow to select individual with greater possibility to survive and perform better in water-limiting conditions, e.g., in peanut [141] for which the enhanced activities of superoxide dismutase, ascorbate peroxidase and glutathione reductase were essential to plant drought tolerance. Shamin et al. [142] also observed that higher antioxidant capacity protects photosynthetic activities in drought tolerant tomato genotypes. In sugarcane, the tolerant genotype RB867515 exhibited a powerful antioxidant apparatus when compared to the more sensitive RB855536 [143], which was essential to tolerate prolonged drought.

8.2. Molecular and Phytohormone-Mediated Signaling Mechanisms of Drought Tolerance

Molecular responses to adverse stress conditions involve highly regulated genes and signal transduction processes that aid plants to confront the stress conditions. C-repeat/dehydration-responsive element binding factors (CBF/DREB), mitogen-activated protein (MYB), cup-shaped cotyledon CUC, no apical meristem NAC TFs and zinc-finger proteins (ZFPs) are recognized as significant moieties in conferring plant drought tolerance [144]. *GsZFP1* gene improved *Medicago sativa* drought tolerance, suggesting that the *GsZFP1* is effective to promote drought tolerant plants in genetic engineering breeding practices [145]. The overexpression of *SNAC1* in *Gossypium hirsutum* elevates its ability to cope with water deficit and also escalates its root growth, which shows that bigger roots are useful in drought resistance breeding [146]. *BdWRKY36* gene stimulated transcription of stress-related genes, reduced electrolyte leakage, decreased ROS level and elevated chlorophyll amount, plant water status and antioxidant enzyme activities to enhance the drought tolerance [147]. *MpCYS4* boosted closing of stomata, triggered the transcription activity of abscisic acid

(ABA) and water-deficit-associated genes to confer drought tolerance and was associated with ABA induced stress signal transduction [148]. *Late embryogenesis associate (LEA)* gene expression declined photosynthetic activity and boosted the plant antioxidant defense system to improve drought stress tolerance in three Linderniaceae species differing in desiccation tolerance [149]. In drought-tolerant *Malus domestica*, the foremost stimulatory strategy for high water use efficiency involves maintenance of C₃ cycle activity by enhancing the function of photosynthetic enzymes, alleviating e⁻ transfer, diminishing ROS amount by controlling the photosynthetic e⁻ transport chain, C₂ cycle and ROS mitigation ability to inhibit photoinhibition and improving photosynthetic activity [150].

Against water deficit stress, resulting signal transduction induced the generation of different constituents including phytohormones to respond and adapt to drought stress. ABA is useful in plant drought tolerance by triggering diverse signaling mechanisms [151]. Beside stimulating stomatal movement, root architecture and regulating photosynthesis, ABA-induced genes encoding drought-related proteins such as dehydrins, ROS-detoxifying enzymes, regulatory proteins and phospholipid signaling enzymes can improve drought stress tolerance [152]. Improved amount of ABA induced a signaling pathway in guard cells which results in outflow of guard cells K⁺ and reduced turgor pressure, ultimately causing stomata closure [44,153]. ABA mitigated drought stress and increased the wheat tolerance ability by improving stem lengths and plant biomass, declining the level of H₂O₂ and malondialdehyde (MDA) [154]. Increased level of cytokinin amount in xylem sap induced stomata opening by diminishing its sensitivity to ABA [155]. Jasmonic acid (JA) synthesis-related genes were stimulated in the overexpressing lines of *VaNAC26* which increased ROS scavenging and stimulated stomata closure and root growth, thereby promoting higher drought tolerance [156]. JA enhances plants drought tolerance by stimulating root growth, decreasing level of ROS and promoting stomatal closure [157]. Auxin regulates root development, functioning of ABA related genes and ROS metabolism to improve drought-tolerance [158]. Ethylene mediates synthesis of guard cell antioxidant flavanols in an EIN2 dependent manner and adversely affects stomata closing by suppressing drought mediated ROS formation [159], thereby resulting in another possible target for genetically engineered plants tolerant to drought.

In view of the above, obtaining transgenic plants is a promising approach to improving drought tolerance traits in a shorter time as compared to classical breeding programs. However, in view of the legal limitations which exist to cultivate transgenic plants in field, it remains arguable whether or not transgenic plants produced under controlled conditions to enhance drought tolerance really perform in field experiments in which other confounding variables may occur. Thus, much more has to be done from this point of view to establish the real value of the transgenic approach in conferring drought tolerance. For this goal, it is essential for environmentally-controlled experiments to be validated in long-term field experiments, thereby reducing the real advantage between the genetic approaches over the classical breeding.

9. Conclusions

Drought is a widespread adverse limiting factor which alters various characteristics of plant growth, physiology and metabolism. Timing, duration, severity and speed of growth are important factors to be considered in the attempt to select drought-tolerant species in particular environments. Drought stress negatively affects various biological processes of plants, from the embryo phase to the reproductive and maturity phases. Drought stress affects plants morphological, physiological, biochemical and metabolic pathways, ultimately declining plant productivity. The drought tolerance strategies adopted by plants include several biological mechanisms at cell, organ and entire plant levels, when stimulated at various phases of plant growth. Water loss declined by improving stomatal functioning, elevated water transport by emerging bigger and deeper rooting structures and production of compatible solutes. ROS scavenging by antioxidant defense system, maintenance of membrane integrity, usage of precise plant genotypes, treatment with plant growth regulators, production of compatible solutes, stress-related proteins and aquaporins activity are also helpful in generating

drought tolerance in plants. Selection of individuals with increased water use efficiency, enhanced antioxidant apparatus and production of key osmolites and secondary metabolites represent some possible promising strategies to obtain higher drought tolerance plants. In addition, exogenous supply of compounds which are able to promote the drought tolerance in plants could be exploited in water-limiting environments. Biotechnological strategies should also be taken into consideration to generate transgenic plants able to tolerate water scarcity, although their validation cannot precede real field experiments.

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