Impact of Drought in Plant-Metabolism

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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.

Plant-Metabolism Drought

1. 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 [1] (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 [2]. 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 [3].

Water deficit conditions alter several activities of plant, but one of the main effects is the decline of photosynthetic activity [4][5] and finally the plant yield [6][7]. 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 [8][9].

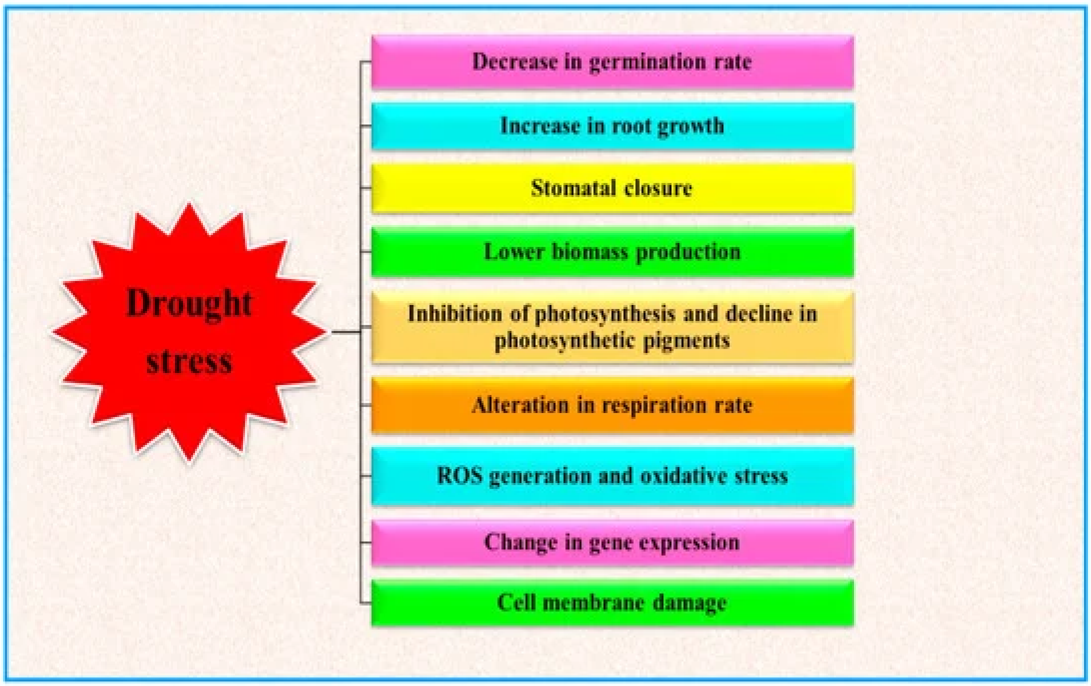

Figure 1. Effect of drought stress on plant growth and development (modified from Ghatak et al. [10]).

2. 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 [11]. 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 [12], sorghum [13] and wheat [14].

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 [15]. Drought conditions also limit the uptake of nutrients by the plants due to limited soil moisture, leading to decreased stem length [16]. Shoot length was also reduced under water deficit conditions in *Lathyrus sativus* L. [17]. In conditions of water deficit, plants seek to extract water from deeper soil layers by boosting their root architecture [18]. 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 [19]. 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. [20]. 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 [21]. Escalation in root length is recognized as a useful strategy to increase soil water retention and nutrient accumulation to enhance plant biomass production [22]. Under water deficit, the plant root to shoot proportion generally improves, and, subsequently, the plant biomass decreases substantially [23].

The leaf is the chief part of the plant where most of the photosynthetic products are synthetized. The number of leaves decreased when subjected to water stress in *Andrographis paniculate* [24]. 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 [25][26]. 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 [27]. 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 [28]. Of note, the rate of premature leaf senescence is enhanced in drought environments .

3. Drought Stress and Photosynthesis

Major consequence of water deficit in plants is the decrease or suppression of photosynthesis [29](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 [30][31]. Among these, the decrease in photosynthetic process in plants under drought is mainly attributable to the decline in CO_2 conductance via stomata and mesophyll limitations [32]. Decrease in photosynthetic activity due to drought may also be due to reduced ability of stomatal movement [33][34]. Declined activity of photosynthesis is triggered by the loss of CO_2 [35] 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 bisphosphate (RuBP) production. Supportively, CO_2 enrichment eliminated many early responses of maize metabolites and transcripts attributable to drought stress [36].

Figure 2. Schematic representation of effect of drought stress on photosynthesis .

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) [37], altering, for example, berry sugar concentration in grape [38] and biomass partition in maize (i.e., kernel number and 100-kernel dry weight decreased with increasing water stress duration) [39].

Chlorophyll content, which is of outmost importance for photosynthesis [40], is another photosynthetic attribute strongly influenced by water deficit that has been recognized as a distinctive indication of photo oxidation and degradation of chlorophylls [41]. For example, leaf chlorophyll synthesis and chlorophyll *a*/*b* proportion in soybean is altered by drought stress [42]. 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 [43]. 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 [44]. 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 [45]. Water deficit alters the action of photosynthetic moieties and chlorophyll pigments, which ultimately resulted in reduced photosynthetic activities in *Vigna mungo* [46].

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 [47]. For example, drought stress decreased the physiological metabolic disorders by suppressing the photosynthetic products production and disrupting the carbon balance in soybean. Drought stress also caused a reduction in the abundance of several Calvin cycle proteins, including Rubisco downregulation in olive [48]. 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 [49].

4. 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].

5. 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].

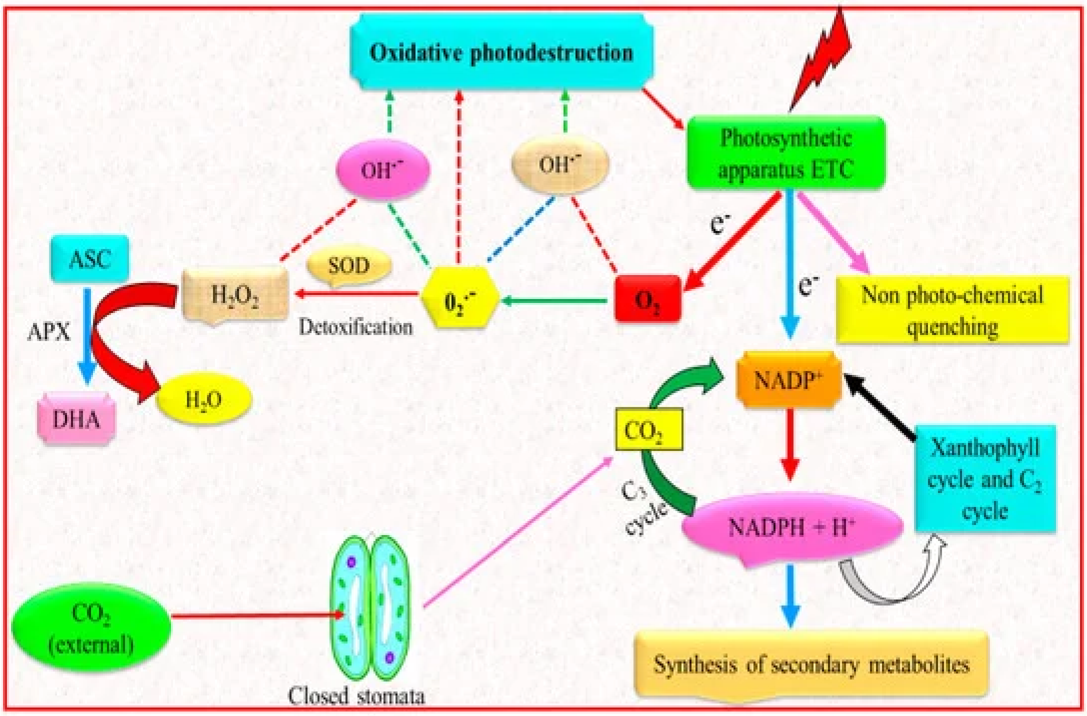

Figure 3. Enhanced synthesis of secondary metabolites under drought stress. Light energy captured by the photosynthetic machinery is considerably greater than the energy essential for the CO_2 fixation. Energy dissipation takes place by non-photochemical quenching and re-oxidation of $NADPH + H^+$, i.e., 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 $NADPH + H^+$ 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 $O_2^{\bullet-}$ ions further produce various ROS. Due to the stress-associated stimulation of SOD and APX, detoxification of the $O_2^{\bullet-}$ ions occurs and therefore results in reduction of generation of ROS. Greater enhancement in the reduction potential, i.e., the ratio of $NADPH + H^+$ 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].

6. 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].

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