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Review

The impact of drought in plant metabolism: how to ameliorate plant performances in arid environments

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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 alters 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 osmolites, 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 raise in human population, it is therefore of outmost importance to highlight: (i) how plant react to drought; (ii) the mechanisms of tolerance exhibited by some species/cultivars; (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 finding on the impact of drought stress on plant morphological, biochemical and physiological features and highlight 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 continuously fluctuations of environmental conditions and are often exposed to abiotic stresses for instance, shortage of available water, salinity, light excess, high/low temperatures, 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 stress is extensively studied given that 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 morhpo-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]. Endurance of the severe water deficit period, that rely upon plant-genotype-specific features, also depends upon stress intensity, duration, speed and recovery effectiveness to regulate plant performance [7,8]. In case of water scarcity, plants required to respond quickly for the reason that virtually biological functions are altered by water deficit conditions at whole plant level [9]. Plant has to stimulate different strategies that benefit plants to absorb water through its roots and to uphold cell turgor i.e. evade the water loss [10]. Declined frequency of cell division and 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 [11]. 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 [11]. Drought stress conditions also results in increased generation of ROS and reactive nitrogen species (RNS) which disturb the cell redox regulatory functioning [8].

Plants that are capable to tolerate drought stress for extended period and sustain their vigor and yield, represent one of the foremost exploration fields in agriculture studies [12]. As detailed below, tolerant plants may benefit of 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 [13]. Other physiological (e.g. rapid stomata closure, water use efficiency) and/or biochemical responses (e.g. synthesis of osmolytes, aquaporins, a powerful antioxidant apparatus) may contribute in increasing the drought tolerance of some plant individuals [14], 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 been also applied with the 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 like sugars, organic acids, and antioxidant compounds [15,16]. 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 the plants to tolerate better a condition of limited water availability. Among these, brassinosteroids [17], salicylic acid [18], amino acids [18,19], polyamines [20] or micronutrients (e.g. silicon, potassium, phosphorous) [21] are certainly the most efficient with consistent results in different plant species. These knowledge of the morpho-anatomical, physiological and biochemical mechanisms underlying drought tolerance (deepen in the next sections) are crucial for conferring drought tolerance to major crops, this 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 stimulates several plant responses, such as morphological, physiological, biochemical and molecular alterations that ultimately results in disturbing plant functioning [22] (Fig. 1). Water deficit conditions alters several activities of plant, declines photosynthetic activity, and the plant yield. During the drought stress conditions, oxidative stress is directly or indirectly generated in plants which results in damage to cell membrane, altering membrane integrity, physiological and biochemical alterations which lead to acute metabolic disorders which eventually alter the plant productivity [23].

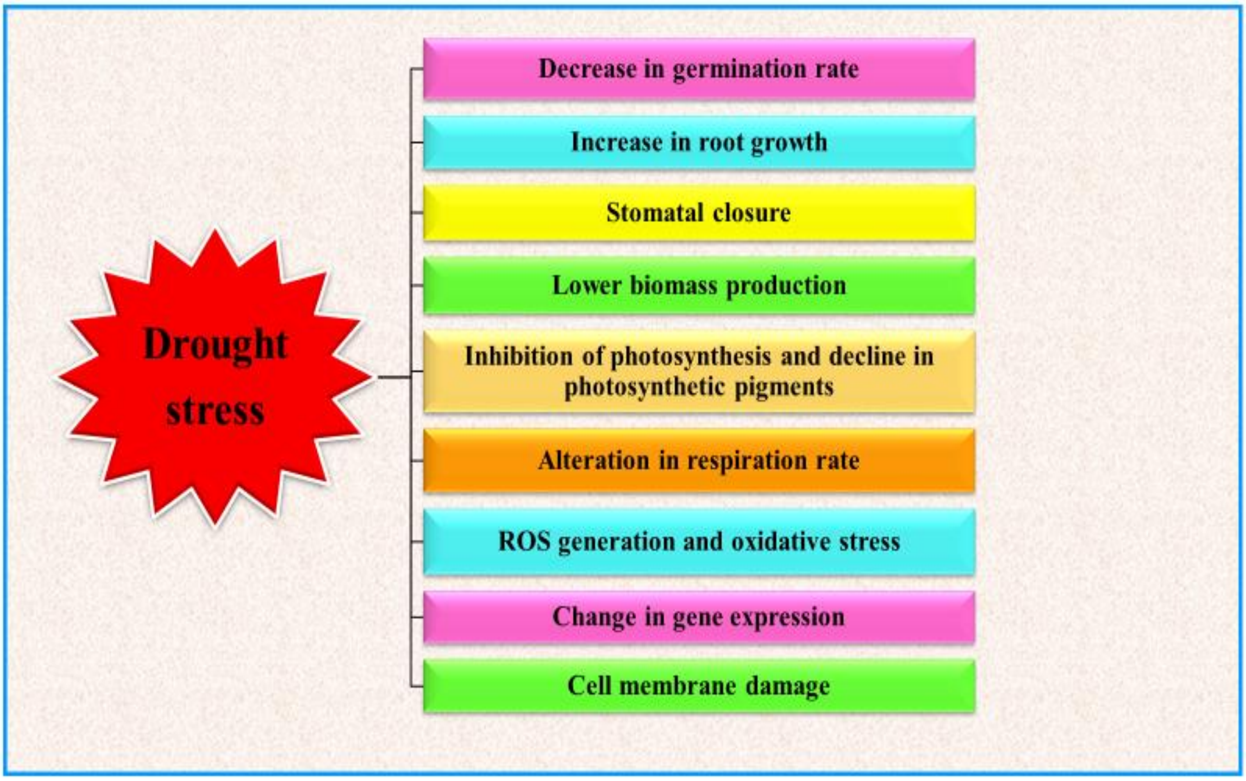

Figure 1. Effect of drought stress on plant growth and development (modified from Ghatak et al. [24]).

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 [25]. Seed germination is the primary aspect of growth which is susceptible to drought stress. Noteworthy alterations are observed in the seed germination of maize and sorghum under drought stress [26]. Observable indication 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 [27]. Drought conditions also limit the uptake of nutrients by the plants due to limited soil moisture, this leading to decreased stem length [28]. Shoot length was also reduced under water deficit conditions in *Lathyrus sativus* L. [29]. In conditions of water deficit circumstances, plants seek to extract water from deeper soil layer by boosting their root architecture [30]. Moreover, water accessibility is primarily recognized by roots, which influences its growth and organization characteristics such as root length, spread, number, and length of lateral roots [31]. Roots are crucial for different biological activities and plant yield, for instance nutrient accumulation and water absorption and also involved in rhizospheres symbiotic association with other microorganisms. Drought stress escalated root length in *Crocus sativus* L. [32]. 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 [33]. Escalation in root length is recognized as a useful strategy to increase soil water retentions and nutrient accumulation to enhance plant biomass production [34]. Under water deficit environment, the plant root to shoot proportion generally improved subsequently, the plant biomass decreased substantially [35].

The leaf is the chief part of the plant where most of the photosynthetic products are synthetized. Number of leaves decreased when subjected to water stress in *Andrographis paniculate* [36]. Optimal leaf development and the maintenance of an adequate leaf area is vital for photosynthesis, which in turn is the main driver of the 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 [37,38]. 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 [39]. Decrease in soil moisture causes a parallel reduction of leaf water content which induces, in turn, a decline of turgor pressure of guard cells due to stomata closure [40]. Of note, rate of premature leaf senescence is enhanced in drought environments [14].

4. Drought stress and photosynthesis

Major consequence of water deficit in plants is the decrease or suppression of photosynthesis [41] (Fig. 2). Reduced leaf area, increased stomata closure and consequent reduced leaf cooling by evapotranspiration, increases of osmotic stress leading to damages to the photosynthetic apparatus are among the major constraints for photosynthesis [42,43]. 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 [44]. Decrease in photosynthetic activity due to drought may also be due to reduced ability of stomatal movement [45,46]. Declined activity of photosynthesis is triggered by the loss of CO_2 [47] uptake, whose drop has been shown to affect Rubisco activity and decrease the function of nitrate reductase and sucrose phosphate synthase and ability for ribulose bisphosphate (RuBP) production.

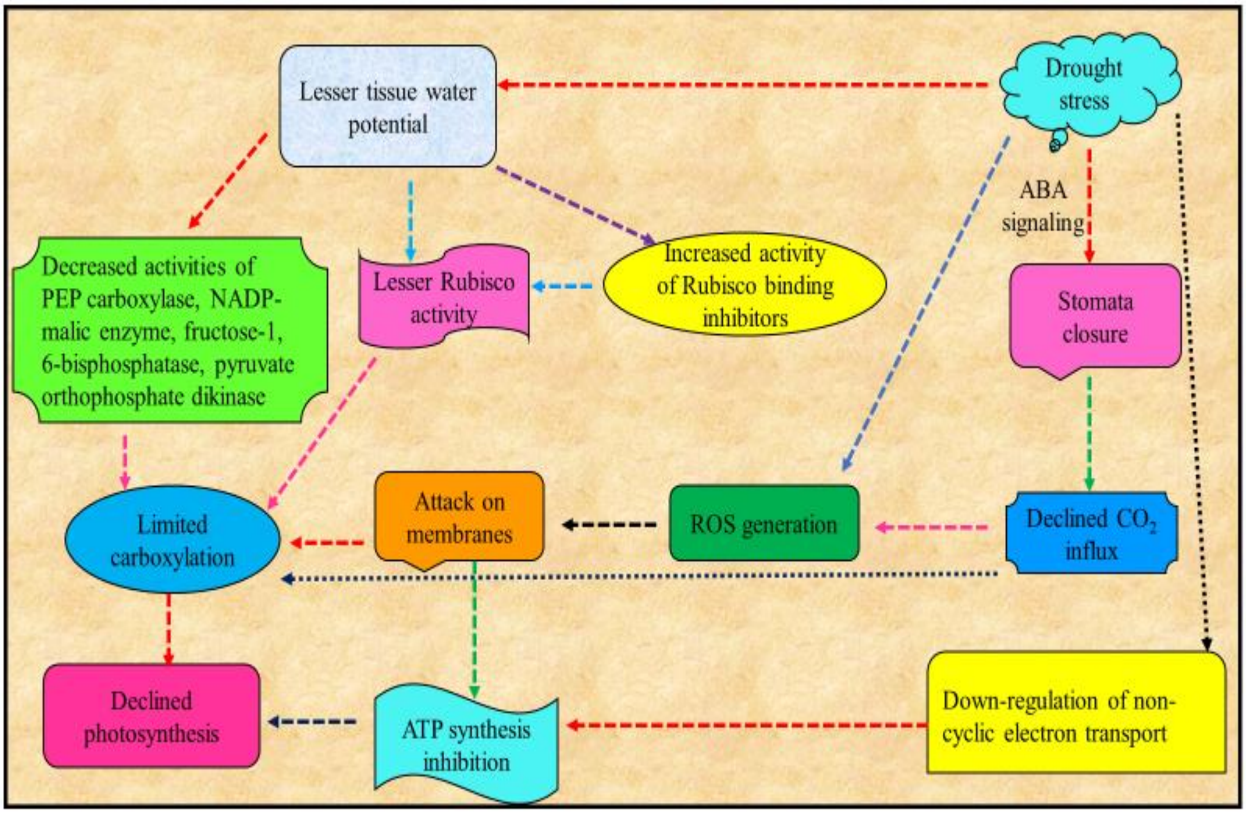

Figure 2. Schematic representation of effect of drought stress on photosynthesis (modified from Farooq et al. [14]).

Chlorophyll content, which is of outmost importance for photosynthesis [48] is another photosynthetic attribute strongly influenced by water deficit which has been recognized as a distinctive indication of photo oxidation and degradation of chlorophylls [49]. Leaf chlorophyll synthesis and chlorophyll *a*/*b* proportion in soybean is altered by drought stress [50]. 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 [51]. Among others, major cause for decline in amount of chlorophyll due to drought stress is as the drought-promoted O_2^- and H_2O_2 which results in lipid peroxidation and ultimately, chlorophyll degradation [52]. 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 [53]. Water deficit alters the action of photosynthetic moieties and chlorophyll pigments, which ultimately results in reduced photosynthetic activities in *Vigna mungo* [54].

Drought stress induces a decreased of net photosynthesis and also changes the plant carbon allocation and metabolism, which ultimately results in energy dissipation and declined yield [55]. For example, drought stress decreased the physiological metabolic disorders by suppressing the photosynthetic products production and also by disrupting the carbon balance in soybean [13]. Drought stress also caused a reduction in the abundance of several Calvin cycle proteins, including Rubisco downregulation in olive [56]. Acute drought stress conditions also cause the damage to Rubisco enzyme and other enzymes associated with photosynthesis and also responsible for the loss of photosynthetic pigment content [57].

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 [58]. This machinery involves enzymatic and non-enzymatic detoxification moieties which lessen, and repair injury triggered by the ROS. Enhancement of the antioxidant apparatus helps in ROS scavenging that decreases electrolyte leakage, lipid peroxidation therefore, maintaining the vitality and integrity of organelles and cell membrane [59].

It is well recognized that drought induces oxidative stress by generating number of ROS for instance $O_2^{\bullet -}$, hydroxyl radicals ($OH^{\bullet}$), singlet oxygen ($^1O_2$), H_2O_2 [60]. 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 [61]. Numerous studies conducted under water deficit conditions found enhanced activities of pivotal antioxidant enzymes, namely CAT, SOD, POD and APX [62]. 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 specially to control H_2O_2 and $O_2^{\cdot -}$ production and diffusion in leaf tissues [63].

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 the drought-tolerant potato genotypes [64]. Ascorbate peroxidase (APX) also participate to excess ROS scavengers (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 [65]. Alteration in APX activity in leaves was more regular 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 [66]. Activities of SOD, POD, CAT and APX were altered and play a key part to protect the peony plants against acute water deficit [67]. 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 [68]. SOD, CAT and POX enzymes activities were stimulated by limited water availability in *Vicia faba* [53]. Increase of SOD, POX and CAT activities was observed in drought-tolerant genotype, in comparison to the drought sensitive plants of faba bean [69]. Amount of enzymatic and non-enzymatic antioxidants improved in drought tolerant plants under mild and moderate water deficit conditions [70]. 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 [71]. Water deficit boosted level SOD and POD in *Vigna mungo* and the authors concluded that increased level of these enzymes stimulate tolerance against drought stress and are vital to reduce its adverse effects [54]. Water deficit improved the CAT, POX, SOD in leaves of *Glycyrrhiza glabra* L., which aimed at counteracting the spread of H_2O_2 [72].

6. Drought stress and secondary metabolites

Secondary metabolites are produced by plants in the attempt to respond to various environmental stresses [73]. It is recognized that the biosynthesis of secondary metabolites is regulated by environmental factors, for instance temperature, light regime and nutrient availability [74]. 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 (Fig. 3) [75].

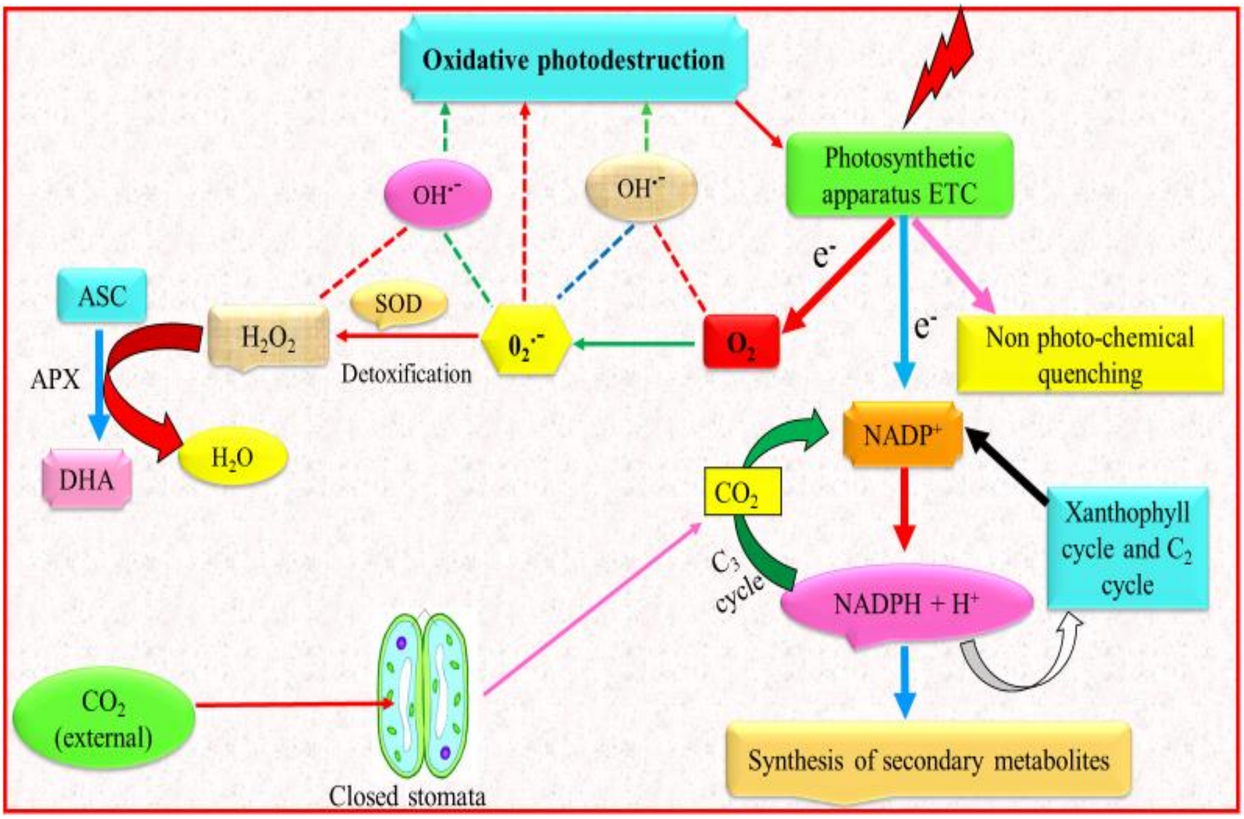

Figure 3. Enhanced synthesis of secondary metabolites under drought stress. Light energy captured by the photosynthetic machinery is considerably greater than the energy essential for the CO2 fixation. Energy dissipation takes place by non-photochemical quenching and re-oxidation of NADPH + H+, i.e. via xanthophyll cycle and C2 cycle. Endogenous CO2 level is low because of the escalated diffusion resistance caused by closing of stomata. Hence smaller amount of NADPH + H+ is utilized in the C3 cycle for the fixation and reduction of CO2, ultimately, greater amount of energy has to be dissipated. Protective activities such as non-photochemical quenching, C2 cycle and xanthophyll cycle are boosted by feedback mechanisms, number of e- are transported to O2 (Mehler reaction). Generation of 02.- ions further produce plethora of ROS. Due to the stress-associated stimulation of SOD and APX, detoxification of the 02.- ions occurs and therefore results in reduction of generation of ROS. Greater enhancement in the reduction potential i.e. to the ratio of NADPH + H+ to NADP+ elevates the plants secondary metabolites synthesis (modified from Kleinwächter and Selmar [73]).

In *Hypericum brasiliense*, concentration of phenolic acids is considerably enhanced when grown in water deficit conditions [76]. In two native sub species of Iranian *Origanum vulgare* i.e. subsp. *gracile* and subsp. *Virens*, content of sesquiterpene (E) β – caryophyllene strongly increased by water limitation [77]. Under mild and mild/severe drought, the content of oleanolic acid and betulin increased in *Betula platyphylla [78] and level of triterpenoid glycyrrhizin in Glycyrrhiza glabra* [79]. Content of lignin is increased in bermudagrass Tifton-85, which is a variety of *Cynodon dactylon* L. under drought conditions [80]. Content of flavonoids was enhanced under stress conditions and high-water deficit conditions improved the medicinal properties of *Labisia pumila [81]. Phaseolus lunatus* under water deficit condition had elevated level of cyanogenic glucosides [74]. In Lamiaceae family, content of essential oils declined in *Lavandula latifolia* and *Salvia sclarea* whereas in *Mentha piperita*, *Salvia lavandulifolia*, *Thymus capitatus* and *Thymus mastichina*, essential oil amount was found to be enhanced under drought conditions and the increase was attributable to a higher concentration of oil glands due to decrease in leaf area [82]. Amount of phenolics and flavonoids increased in *Achillea* species against drought stress [59]. Content of phenolic acids simultaneously improved, while level of flavonoids declined in *Achillea pachycephala* [83].

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 [84]. Water deficit conditions decreased plant potassium (K) uptake [85]. This decline in K was attributable to reduced K mobility, declined transpiration rate and weakened action of root membrane transporters [85,86]. Decreased K amount was also found in drought-stressed plants of *Malus hupehensis* [87]. Resistant genotypes of *Triticum durum* had the maximum amount of K and susceptible genotypes had the maximum amount of sodium (Na) [52]. Genes encoding K transporters were inhibited by water deficit [88] 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 [89]. 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 is reduced in all species except *S. sclarea* whose concentration remained same [82]. This reduction in N was considered as the main responsible factor for photosynthesis decline and leaf senescence [90]. There is significant reduction in leaf P amount in *Ocimum gratissimum* [91] and decline in K level in *Thymus daenensis* under water deficit conditions [92]. K level also decreased in *Ocimum basilicum* and *Ocimum americanum* plants subjected to limited water availability [93]. Principally, decrease of K amount occurs in leaves because water scarcity disturbs stomata movement and guard cell turgidity, which results in decreased photosynthesis and decline in the [94]. Drought-stress conditions increased the accumulation of manganese (Mn), molybdenum (Mo), P, K, copper (Cu), calcium (Ca), and zinc (Zn) in soybean [95].

8. Plant tolerance mechanisms against drought stress: 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 refers to the effective use of water resource in the process of growth and development of plant, thereby increasing crop water use efficiency (WUE) [96]. WUE is defined as the economic production per unit water consumption and it may or may not be related to drought resistance [97]. On the other hand, the main accepted definition of drought resistance is the ability of an individual to survive or grow in water-stressed environment due to dehydration avoidance, dehydration tolerance or drought recovery [97]. Discerning between drought tolerance or drought resistance can be very complex and this is out of the scope of the present review, aware that there are already excellent papers dealing with this topic [98,99]. Therefore, in the next paragraphs of the present review, plants able to tolerate better than other drought stress conditions are referred as "tolerant" without any distinctions between drought tolerant or drought resistant.

Plant drought tolerance encompasses alterations at morphological, biochemical and molecular levels (Fig. 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 will be described with the attempt to propose some of them as suitable features for crop selection in the context of reduced water availability.

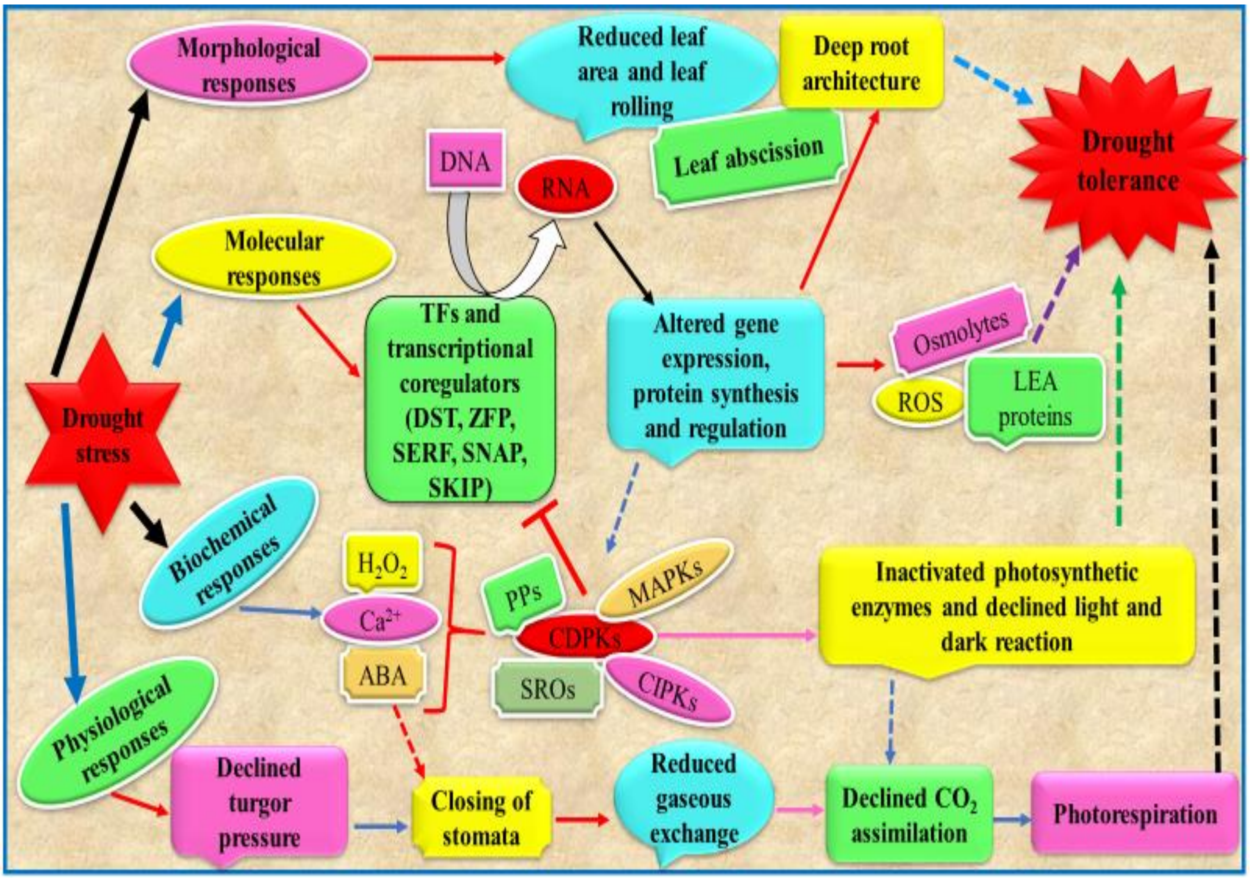

Figure 4. Diagram showing plants drought tolerance mechanism. TFs: transcription factors, DST: drought and salt tolerance, SERF: serum response factor, SKIP: ski-interacting protein, ZFP: zinc finger TF, SNAC: stress responsive NAC TF, LEA: late embryogenesis abundant, ABA: abscisic acid, SROs: similar to RCD-ONE, CDPKs: Ca2+ dependent protein kinases, MAPKs: mitogen activated protein kinases, PPs: protein phosphatases, CIPKs: CBL interacting protein kinases (modified from Zargar et al. [100]).

9. Morphological and biochemical mechanisms involved in drought tolerance

Plants survival to drought encompasses two main strategies, i.e. drought avoidance and drought tolerance [40]. 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 after or later a drought period while some other plants displayed adaptations to escalate water absorption and decrease water loss to circumvent its adverse consequences [1].

At morphological level, root is one the major driver of water therefore, the root size, its progression rate, density, and root proliferation are important features which prompt plant responses to drought stress [5]. Plants with adeep root organization and a perennial development system showed more ability to cope with drought in comparison to plants with shallow-root system [101]. In view of above, the selection of genotypes with a more developed root apparatus resulted in increased plant yield, as demonstrated for example in rice seedlings [102] and in tobacco [103].

When drought stress occurs at initial phases of plant growth, drought-avoidance plants gradually changes 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 increasing the water use efficiency [104]. Satisha et al. [105] 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 [106], therefore stomata regulation is of outmost importance in increasing WUE. Both drought tolerance, water use efficiency and K^+ content has a close association in plants as sufficient level of K^+ can improve the plant total dry mass and photosynthetic rate; K^+ also regulates the SOD enzyme activity to mitigate cell membrane injury which is caused by drought-triggered ROS [107].

At biochemical level, plant hormones, secondary metabolites and other key molecules such as carbohydrate, amino acid, polyamines play a crucial role 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 by reducing ion leakage [108]. 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 act as an important signaling moiety against drought stress to stimulate mitochondria functioning and alter cell proliferation stimulating particular drought stress recovery genes [109]. Proline accumulation helps to maintain membrane integrity by diminishing lipids peroxidation by defending cell redox potential and declining ROS level [110]. It has been shown that plants which accumulates higher levels of proline exhibit higher rate of plant survival (*Triticum aestivum*; [111], biomass production [112] and grain yield [113]. Similarly, genotypes which accumulates higher level of glycine betaine [114], mannitol and other non-structural carbohydrates [115] 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 [116,117]. Besides the selection of overproducing osmolite-producing 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 [118].

Increased antioxidant defenses also assist to increase drought tolerance by defending plants from oxidative stress triggered by limited water availability (see details in section "Drought stress and antioxidant defense system").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 [119] for which the enhanced activities of superoxide dismutase, ascorbate peroxidase, and glutathione reductase was essential to plant drought tolerance. Shamin et al. [120] 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 [121] which was essential to tolerate prolonged drought.

10. Molecular and phytohormone-mediated signaling mechanisms of drought tolerance

Molecular responses to adverse stress conditions involves highly regulated genes and signal transduction processes that aid plants to confront the stress conditions. CBF/DREB, MYB, CUC (NAC) TFs, and zinc-finger proteins (ZFPs) are recognized as significant moieties in conferring plant drought tolerance [122]. *GsZFP1* gene improved *Medicago sativa* drought tolerance, suggesting that the GsZFP1 is effective to promote drought tolerant plants in genetic engineering breeding practices [123]. 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 useful in drought resistance breeding [124]. *BdWRKY36* gene stimulates transcription of stress-related genes and reduced electrolyte leakage and decreased ROS level, but elevates chlorophyll amount, plant water status and antioxidant enzyme activities to enhance the drought tolerance [125]. MpCYS4 boosted closing of stomata and triggers the transcription activity of abscisic acid (ABA) and water-deficit-associated genes to confer drought tolerance and also associated with ABA induced stress signal transduction [126]. *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 [127]. In drought-tolerant *Malus domestica*, foremost stimulatory strategy for high water use efficiency involves maintenance of C_3 cycle activity by enhancing the function of photosynthetic enzymes, alleviating e^- transfer, and diminishing ROS amount by controlling the photosynthetic e^- transport chain, C_2 cycle and ROS mitigation ability to inhibit photoinhibition, and improving photosynthetic activity [128].

Against water deficit stress, resulting signal transduction induced the generation of different constituents including phytohormones to respond and adapt to drought stress. ABA useful in plant drought tolerance by triggering diverse signaling mechanisms [129]. 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 [130]. 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 [31,131]. ABA mitigates drought stress and increase the wheat tolerance ability by improving stem lengths and plant biomass, declining the level of H_2O_2 and MDA [132]. Increased level of cytokinin amount in xylem sap induced stomata opening by diminishing its sensitivity to ABA [133]. Jasmonic acid (JA) synthesis-related genes were stimulated in the overexpressing lines of *VaNAC26* which increased ROS scavenging and also stimulating stomata closure and root growth thereby promoting higher drought tolerance [134]. JA enhances plants drought tolerance by stimulating root growth, decreasing level of ROS, and stomatal closure [135]. Auxin regulates root development, functioning of ABA related genes and ROS metabolism to improve drought-tolerance [136]. Ethylene mediates synthesis of guard cell antioxidant flavanols in an EIN2 dependent manner and adversely affects stomata closing by suppressing drought mediated ROS formation [137], resulting thereby another possible target for genetically engineered plants tolerant to drought.

In view of above, obtainment of transgenic plants results a promise approach to improve 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 filed, 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 occurs. Thus, much more has to be done from this point of view to establish the real values 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 approach over the classical breeding.

11. Conclusion

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 of upmost importance factor to be considered in the attempt to select drought-tolerant species in particular environments. Drought stress negatively affects various biological processes of plants i.e. from the embryo phase to the reproductive stage and maturity phase. 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 deep 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 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, despite their validation cannot preclude from real field experiments.

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