Anatomical, Morphological and Physiological Responses of Plants to Drought Stress

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Abstract: In the conditions of changing climate, plants are continuously subject to several abiotic stresses. Among these stresses, drought is the most environmental constraint to plant production and productivity. Plants subjected to water deficit suffers from substantial yield losses. Drought-induced loss in crop yield probably exceeds losses from all other causes, since both the severity and duration of the stress are critical. Drought triggers a wide variety of plant responses, ranging from cellular metabolism to changes in growth development including roots, shoots and final yield. Anatomical and morphological alterations occur in plants under water deficit to protect and adapt the plants to this stress. Drought stress reduces leaf size, number of leaves, number of stomata, stomatal size, stem extension and root proliferation, disturbs plant water relations and improves water-use efficiency. Moreover, plants display a variety of physiological responses at cellular and whole-organism levels towards prevailing drought stress, thus making it a complex phenomenon. Carbon dioxide assimilation by leaves is reduced mainly by stomatal closure, membrane damage and disturbing activity of various enzymes, especially those of CO_2 fixation and adenosine triphosphate synthesis. Therefore, this review describes some aspects of drought-induced alterations in anatomical, morphological and physiological responses in higher plants.

Key words: Anatomy · Drought Stress · Morphology · Physiology · Plant Response

INTRODUCTION

Under both natural and agricultural conditions plants are often exposed to various environmental stresses. Among these, drought is one of the most important environmental factors inhibiting photosynthesis and decreasing the growth and productivity of plants [1]. It is one of the major causes of crop loss worldwide, reducing average yields for most major crop plants by more than 50% [2]. A water deficit stress causes stomatal closure, available water reductions and impaired physiological reactions, reducing the photosynthetic rate, growth and yield [3]. Moreover, excess water or floods can also negatively influence agricultural yields by delaying planting, reducing vigor, altering development and increasing susceptibility to diseases. Drought is generally a common adverse environmental factor that affects the growth of plants and is considered as the main factor determining the global geographic distribution of vegetation and restriction of crop yields in agriculture [4]. The symptoms of drought stress include photosynthesis decline, protein degradation, slower leaf expansion, decreases in respiration and biomass production and stomatal closure, among others [5].

Seedlings under limited watering regimes developed longer roots to uptake limited water available in the soil. The rapid development of a deep root system that can access water stored lower in the soil profile may be essential for successful seedling establishment [6]. Increment in the vessel wall thickness was more in seedlings under water stress as compared to the control. Multiple characteristics of the vascular structure have been investigated, such as modifications to the wall architecture and alteration of xylem/phloem ratio, which are thought to be involved in the resistance of the plant to environmental stresses [7]. However, under drought, many species respond by increasing the proportion of assimilates diverted to root growth with the concomitant root/shoot ratio increase [8]. In this condition, soil nutrients can be available to plants [9]. Also, drought has been associated with cell osmotic adjustment which is accomplished by an accumulation of different compounds

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such as soluble sugars, proline, glycine betaine, polyols and other organic compounds [10]. Soluble sugars (sucrose, glucose and fructose) play a key role in osmotic adjustment in many species; however, proline only plays an important role in a few species, such as potato and tomato [11].

Generally, plant responses to abiotic stresses comprise morphological, physiological and biochemical changes that either decrease plant's stress exposure and/or limit damage and facilitate recovery of impaired systems [12]. However, understanding abiotic stress responses in plants is difficult due to the complexity, interrelationship and variability of mechanisms and molecules involved a fact that consists of their evaluation of an important and challenging topic in plant research. Therefore, this review paper was summarized to investigate anatomical, morphological and physiological responses of higher plants to drought stress.

Anatomical Response of Plants to Drought Stress: Plant tissue responses to water stress depend on the anatomic characteristics that regulate the transmission of the water stress effect on the cells [13]. Tissues exposed to environments with low water availability have generally shown a reduction in cell size and an increase in vascular tissue and cell wall thickness [14]. When water availability is limited, the root: shoot ratio of plants increases because roots are less sensitive than shoots to growth inhibition by low water potentials [15]. Roots are the primary sites of water and nutrient uptake by plants. Roots also have a remarkable capacity to sense and respond to most of the physicochemical parameters of the soil by adjusting their growth and water transport properties accordingly; these functions being tightly linked to shoot physiology [16]. Anatomical alterations may occur in plants under water deficit to protect and adapt the plants to this stress. In particular, anatomical alterations induced in roots in response to drought result in modification of their soil water extrapolation ability through changes in terms of root branching and rate and direction of growth of individual roots and/or in roots water conductivity [16]. Rooting in deep soil horizons may be an essential component of a plant's strategy to withstand drought at the seedling stage in environments with seasonal drought [6]. Plants native to lower rainfall environments tend to produce roots with longer links [17] and higher specific root length [18].

Plants exposed to drought conditions exhibit inhibition of root growth [19]. A significant reduction in root elongation caused by the application of osmotic stress has been found in maize and bean [19]. A reduction in lateral roots number was also observed in different plants [20]. Furthermore, osmotic stress severely represses the formation of lateral roots immediately after their initiation [21]. On the contrary, there are also several reports indicating an increase in root-to-shoot biomass ratio in drought plants [19]. Under mild water stress conditions, some species were found to promote absolute increases in root elongation rates resulting in a significant increase in total root biomass [19]. This differential behavior of plant root system in response to drought could be related not only to different genotypes examined but also to differences in the rate and the intensity of drought stress applied [20]. Another possible explanation might be based on the indirect effects of drought on root growth. For instance, mechanical impedance may significantly affect root growth and development under field conditions [22]. As soils dry, capillary forces make matric potential more negative, often causing soil strength to increases rapidly [23]. Thus, mechanical impedance could be a major limitation to root growth especially in compacted dry soils with soil water potential less than-100 kPa [22].

Under drought conditions, the rapid adjustment of root hydraulic conductivity to soil water content could be considered as an important mechanism conferring on plants the capability for optimizing soil water uptake. In particular, it was suggested that a transient increase in hydraulic conductivity during the onset of drought might be of great importance facilitating water uptake from the drying soil [24]. Furthermore, drought-induced inhibition of hydraulic conductivity might be beneficial regarding water uptake from soils with non-uniform water distribution. In such conditions, a reduction of hydraulic conductivity in roots exposed to low water availability would lead to a lowering of soil water uptake by these roots while those exposed to other horizons would compensate by increasing their water uptake due to a decrease in xylem water potential [24]. Down regulation of hydraulic conductivity can also serve as a plant protective reaction restricting a possible backflow of water from the plant into the most desiccated zones of the soil, which could especially occur in the absence of any transpirational driving force at night [25].

Water enters into roots through the epidermis, exodermis, cortex, endodermis, the pericycle, stele parenchyma and finally into the xylem vessels. The radial conductance of roots is about two orders of magnitude lower than the axial conductance which is largely determined by the dimensions and the number of xylem

vessels [26, 27]. The composite transport model which comprises apoplastic, symplastic and transcellular flow-paths operating in parallel has been widely used to describe the flow of water through roots [28]. According to this model the apoplastic flow-path consists of water movement outside of the cells' plasma membrane, the symplastic flow-path is through the cytoplasm of cells connected by plasmodesmata and the transcellular flow-path is across cell membranes [27]. Water moves via both the apoplastic and the cell-to-cell pathway driven by hydrostatic gradients, the proportion depending on the relative hydraulic conductance of the two pathways [27]. When transpiration rate is slow, as normally occurred during the night or under drought conditions, the osmotic flow may dominate, because without large hydrostatic-driven water flows ions in the stele are not diluted, creating an osmotic gradient. However, under normal transpiration conditions, the water flow-path taken is mainly influenced by root anatomy. In particular, the apoplastic pathway can be inhibited by the presence of Casparian bands, which are deposits of suberin or lignin in the cell wall. Casparian bands occur in radial and transverse walls of the endodermis and exodermis [27, 29]. Suberin lamellae may also occur on the tangential walls to further inhibit apoplastic flow. Suberin lamellae can also restrict the movement of water along the transcellular pathway.

The formation of these barriers to water movement is often associated with the imposition of stress such as water deficits and aging of the plant. A possible role of this enhanced formation of suberized layers might be correlated to the reduction of excess water losses to the soil which might occur under drought conditions. On the other hand, in certain species, the transcellular path seems to play a major role as it is efficiently facilitated by water channel proteins named aquaporins. These proteins belong to the ubiquitous superfamily of Major Intrinsic Proteins [30]. The structure of several aquaporins [31] enables them to insert as tetramers in the membrane-forming four individual pores which allow the passage of water or small neutral molecules [24, 30]. The Plasma membrane Intrinsic Proteins (PIPs) can control a large part of the root water permeability or hydraulic conductivity [32]. Among them, drought stress usually induces a significant decrease in hydraulic conductivity, whereas abscisic acid can exert either an up- or a down regulating effect, depending on time, dose or species [33].

Leaves are complex structures mainly consisting of two dissimilar layers (spongy and palisade mesophyll) of photosynthesizing cells, with different packing and cell orientation, interspersed by vascular tissues, all between two epidermises, which is perforated by stomatal pores. This structure results in an appreciable volume so that the photosynthesizing cells and chloroplasts are located at some distance from the points of entry of CO_2. Once CO_2 reaches the leaf surface, diffusion into the leaf depends on the stomatal resistance as the cuticle is usually regarded as effectively CO_2 impermeable [34]. During photosynthesis, the CO_2 entering the leaves through stomata has to diffuse from sub-stomatal internal cavities to the sites of carboxylation inside the stoma through the leaf mesophyll. Therefore, understanding CO_2 diffusion in leaves is considered very important because the characteristics of the overall diffusion pathway are one of the determinants of the photosynthetic rate [35]. The width/length ratio of stoma cells decreased in stressed plants. Differences in terms of the stomata index were also observed. While the stomata index varies from species to species, it is also well known that this trait is among the environmentally influenced anatomical characters [36]. Similarly, Güvenç and Duman [37] reported that environmental factors affect some anatomical characters such as pubescence, organization of the mesophyll and distribution of the supporting tissue elements.

The anatomical structure varies greatly and is of significant value in many plants [38]. The distribution of sclerenchyma cells on the phloem and diameter of parenchymatous cells of stem and leaf were variable in unstressed and stressed plants. Parenchymatous cells of the stem and leaves of unstressed plants are smaller than those of the stressed ones. It is thought that the parenchymatous cells with thin walls are affected by drought conditions. The distribution of sclerenchyma tissue in the stem cortex and phloem is of considerable taxonomic value [39]. While the fibers spread as a continuous layer between cortex and phloem in stressed plants, they occur as grouped layers in unstressed plants. Yentür [40] indicated that sclerenchyma tissue provides an advantage against the loss of water. Vessel diameters in stressed root, stem and leaf were smaller than those in the unstressed plants. Ristic and Cass [41] reported that the vascular tissue area was decreased by low soil moisture. Similar results were also presented [42]. Width of cortex/width of vascular bundle rate belonging to the root and stem varies between the stress and unstressed soybean [43]. Özörgücü *et al.* [36] showed that the anatomical characters are influenced by environmental conditions. Abrams [44] and Karabourniotis and Bornman [45] also reported that leaf

pubescence increased under drought stress. The varying pubescence can provide an advantage in some plants growing in xeric environments but it was seen that pubescence is not a valuable character for the plant used in this study.

Morphological Response of Plants to Drought Stress:
Roots are essential for plant functions and productivity, such as water and nutrient uptake, forming symbioses with other microorganisms in the rhizosphere. Root characteristics, especially root length, root density and the number of thick roots, are important for a plant to have comparatively well-established aboveground parts by exploiting the available water [46]. Drought avoidance due to a profound root system that enhances the ability of a plant to capture water is a fundamental adaptation mechanism to drought [47]. A prolific root system can confer the advantage to support accelerated plant growth during the early crop growth stage and extract water from shallow soil layers that are otherwise easily lost by evaporation [48]. More severe drought stress suggests that the dynamics of root growth under drought conditions might be a key factor in the understanding of the contribution of roots to drought avoidance [49]. Drought stress decreased the seedlings' root length in different plants [50]. Moreover, in alfalfa (*Medicago sativa*), germination potential, hypocotyl length and shoot and root fresh and dry weights were reduced by polyethylene glycol-induced water deficit, while the root length was increased [51]. Water stress reduces the biomass of fibrous roots in Avocado cultivars [52] and pearl millet [46, 47]. The root-to-shoot ratio increases under water-stress conditions to facilitate water absorption [52] and that it is related to the abscisic acid content of roots and shoots [53]. The growth rate of wheat and maize roots was found decreasing under moderate and high water-deficit stress [53]. The root dry weight decreased under mild and severe water stress in sugar beet [54]. A significant decrease in root length was reported in water-stressed Populus species [55]. On the other hand, the root growth was not significantly reduced underwater deficits in maize and wheat [56]. However, water availability is preliminary sensed by roots affects roots growth and root system architecture [57].

Drought stress is an important environmental limiting factor at the juvenile stage of plant growth and establishment. The first and foremost effect of drought is impaired germination and poor stand establishment [58]. Drought stress has been reported to severely reduce germination and seedling stand [59]. In a study on field pea, drought stress impaired the germination and early seedling growth of the tested five cultivars [60]. Visible syndromes of plant subject to water deficit in the vegetative phase are leaf wilting, a decrease in plant height, number and area of leaves and delay information of buds and flowers [61]. During water stress, depending on the intensity and duration of the drought, plants tend to minimize transpirational water loss by reducing their number of leaves [63]. Water deficits reduce the number of leaves per plant and individual leaf size, leaf longevity and leaf reduced by decreasing the soil's water potential. Water-deficit stress mostly reduced leaf growth and in turns the leaf area in many species of plants [64]. Limitation of leaf growth is among the earliest visible impacts of water stress because leaves determine radiation interception and are the main photosynthetic organs [65]. Water deficit stress mostly reduced leaf water potential and growth and in turn, the leaf areas in many species and leaf senescence could be observed under severe water stress [66]. Reduction in leaf area by water stress is an important cause of reduced crop yield through a reduction in photosynthesis [67]. Leaf extension can be reduced under drought environment to get a balance between the water status of plant tissues and the water absorbed by plant roots [68]. Besides, Blum [69] suggested that a small leaf area is beneficial under drought stress to avoid hydration.

During water stress, the total leaf area and leaf number per plant generally diminished significantly in different plant species [70]. The loss of leaf area is an important stress avoidance strategy and is considered a plant's first defensive mechanism against drought stress [71]. This reduction arisen before stomatal conductance declined in the remaining viable leaf area [72]. Leaf area and leaf number were affected adversely in both the main shoot and tillers of five almond species [73]. The reduction in plant height and leaf area under water stress may be associated with the decline in the cell enlargement and more leaf senescence. Leaf water potential, osmotic potential and relative water content decreased in stressed plants at all the growth stages. The decrease in osmotic potential in response to water deficit was more compared to the leaf water potential at all the growth stages, indicating the ability of the leaves to maintain turgor through osmotic adjustment in sorghum [74]. Leaf area expansion depends on leaf turgor, temperature and assimilating supply for growth, which are all affected by drought in *Arachis hypogeae* [75]. The leaf growth was more sensitive to water stress in wheat, but it was not so in the case of maize [76]. The report indicated that stem length was significantly affected by water stress in potato [77].

Specific leaf weight indicates leaf dry mass per area. It has been broadly exploited as a reliable morpho-physiological marker contributing to drought tolerance for various plants [78]. Drought stress was found to have caused an increase in specific leaf weight in most plant species. Continuous water deficit results in fewer and smaller sizes and several leaves, which have smaller and more compact cells and greater specific leaf weight in peanut [77]. Increases in specific leaf weight under drought conditions have also been reported in some fruit trees such as peaches [79] and kiwifruits [80]. Variations in specific leaf weight under drought conditions may be caused by variations in the concentration of carbohydrates such as starch [81]. Specific leaf weight increased by drought stress in peach trees is due to the decrease in the fruit's competition [82]. As competition between fruits and leaves decreases, the accumulation of dry masses in leaves and subsequently leaf weight per area increases. Kramer [83] found that mild drought increased specific leaf weight by increasing leaf and cuticle thickness and the number of surface waxes. Krause *et al*. [84] suggested that because cell division is more sensitive to low water availability than photosynthesis, assimilates are used for differentiation products. It has been also reported that drought stress causes an increase in sclerenchyma cells and cell wall thickness and thereby increases specific leaf weight [84].

Physiological Response of Plants to Drought Stress: The naturally occurring gradient in water potential between the environment of plant roots and the environment of the shoots drives the uptake of water [85]. Hydraulic resistances both in the root and shoot can limit the flow of water through the plant. The main hydraulic barrier to water uptake by roots is the radial transport pathway between root epidermis and xylem, rather than the axial path along xylem conduits [29]. Restrictions on the leaf surface could be the first action of defense for water deficit [86]. The process of shedding leaves during water stress, largely the result of increased synthesis and sensitivity to various hormones in plants [87]. Although components of plant water relations are affected by reduced availability of water, stomatal opening and closing are more strongly affected. Under drought stress, sensitive field pea genotypes were more affected by a decline in relative water content than tolerant ones [88]. Plants have developed many mechanisms to survive water deficit, including escape, tolerance and avoidance of tissue and cell dehydration [89]. Avoidance of stress includes rapid phonological development, increased

stomatal and cuticular resistance, changes in leaf area, orientation and anatomy, among others [63]. The relative water content of wheat leaves was higher initially during leaf development and decreased as the dry matter accumulated and leaf matured [90]. Under limited supply, the water-use efficiency of wheat was greater than in well-watered conditions [91]. The study on clover (*Trifolium alexandrinum*) also showed that water-use efficiency was increased due to lowered water loss under drought stress, primarily by decreased transpiration rate and leaf area and relatively lesser reduction in yield [92]. Similarly, lucerne (*Medicago sativa*) grown under drought had greater water-use efficiency than that under irrigated conditions [93].

The first response of virtually all plants to acute water deficit is the closure of their stomata to prevent the transpirational water loss [94]. This may result in a response to either a decrease in leaf turgor and/or water potential [95]. The drought tolerance species control stomatal function to allow some carbon fixation at stress, thus improving water use efficiency or open stomata rapidly when water deficit is relieved [96]. Stomatal conductance is more closely linked to soil moisture content than to leaf water status [97]. Because of their role in transpiration and photosynthesis, stomata can influence water loss, water use efficiency and plant yield [98]. As light intensity or water status of the plant changes, larger stomata tend to open faster and to close later than smaller ones; therefore, they are more sensitive to drought deficit [99]. Leaves that developed during drought usually have smaller stomata than leaves under well-watered conditions [100]. The number of stomata per leaf area may be a good criterion for identifying and selecting drought-resistant genotypes. Giorio *et al*. [101] reported that good positive relationships were found between stomatal conductance and both leaf water potential and soil moisture. This is commonly found in many species and may indicate control of stomatal conductance through a hydraulic feedback mechanism [102]. A study by Blum and Sullivan [103] on millet indicated that there is a direct correlation between low stomatal density and resistance to drought stress. Moreover, a positive correlation between sensitivity to drought and the stomatal length was reported in temperate deciduous trees [104]. It was also reported that lower stomatal size might be related to drought resistance in cultivated almonds [105]. During the last decade, stomatal closure was generally accepted to be the main determinant for decreased photosynthesis under mild to moderate drought [106].

Osmotic adjustment is generally thought to be the major mechanism to maintain cell turgor in many species as the water potential decreases, enabling water uptake and the maintenance of plant metabolic activity and therefore growth and productivity [107]. It helps to maintain the cell water balance with the active accumulation of solutes in the cytoplasm, thereby minimizing the harmful effects of drought [108]. It is an important trait in delaying dehydrative damage in water-limited environments by continued maintenance of cell turgor and physiological processes [109]. It is recognized as an effective component of drought resistance in several plants [110]. It involves the net accumulation of solutes in a cell in response to a fall in the water potential of the cell's environment. As a consequence of this net accumulation, the osmotic potential of the cell is lowered, which in turn attracts water into the cell and tends to maintain turgor pressure. Underwater deficit conditions, concentrations of soluble sugars (sucrose, glucose and fructose) are generally increased [111], although the concentration may decrease under severe dehydration [112]. Using osmotic adjustment, the organelles and cytoplasmic activities take place at about a normal pace and help plants to perform better in terms of growth, photosynthesis and assimilate partitioning to grain filling [113]. This is essential for maintaining physiological activity for extended periods of drought [110]. The osmotic adjustment also facilitates a better translocation of pre-anthesis carbohydrate partitioning during grain filling [113], while high turgor maintenance leads to higher photosynthetic rate and growth [95, 113]. Several reports suggest that plant metabolic processes are more sensitive to turgor and cell volume than to absolute water potential [63].

A major effect of drought is a reduction in photosynthesis, which arises by a decrease in leaf expansion, impaired photosynthetic machinery, premature leaf senescence and an associated reduction in crop yield [114]. At a whole-plant level, soil drought and leaf water deficit lead to a progressive suppression of photosynthesis and is associated with alterations in carbon and nitrogen assimilation [115]. Drought is limiting photosynthesis through stomatal closure which limits CO_2 uptake by leaves and prevents the transpirational water loss as result to the reduction in leaf turgor and/or water potential [106]. The decrease in net photosynthetic rate under drought stress observed in many studies is often explained by a lowered internal CO_2 concentration that results in a limitation of photosynthesis at the acceptor site of ribulose-1, 5- bisphosphate carboxylase/ oxygenase (Rubisco) [116] or by the direct inhibition of photosynthetic enzymes like Rubisco or ATP synthase [117]. Similarly, Chaves *et al*. [107] reported that the main cause of reduced photosynthetic rate under mild to moderate water deficits is a reduction in the diffusion of atmospheric CO_2 to the site of carboxylation. This is as a result of both stomatal closure and a reduction in mesophyll conductance, although the extent of the influence of mesophyll conductance is still debated [118]. Water stress also directly impacts internal transport of CO_2 and enzyme activity and hence photosynthetic capacity [119] and these metabolic and diffusive limitations become predominant relative to stomatal limitation as water stress becomes more severe [120]. Moreover, drought stress not only limits the size of the source and sink tissues but the phloem loading, assimilate translocation and dry matter partitioning are also impaired. However, the extent of effects varies with the plant species, stage, duration and severity of the drought.

CONCLUSION

Drought affects the development, growth and yield in plant crop, but the tolerance crops to this stress vary remarkably. Water deficit reduces plant growth and development, leading to the production of smaller organs and hampered flower production and grain filling. Timing, duration, severity and speed of development undoubtedly have pivotal roles in determining how a plant responds to water stress. Therefore, changes in anatomical, morphological and physiological aspects are generally noted in response to drought stress. Understanding these responses to drought is important for screening tolerance of genotypes to water stress conditions.

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