Physiological Effects of Drought Stress in Plants

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Abstract The most common effect of the drought stress is to reduce the water potential, the turgor pressure in the growing cells, and thus the lack of turgor pressure necessary for their growth. Lack of water accelerates cell differentiation. Under drought stress, root, stem, leaf, and fruit growth decreases. Also, in these conditions, not all plant organs are affected equally. As a rule, due to drought stress, the ratio of leaves to stems decreases. Older leaves and leaves that are exposed to shade usually die sooner, slow down tillering, and increase tiller death in tillering species. Physiologic effects of water stress contain so many cases such as reduction of relative water content (RWC), reduction of intercellular space during wilting, effect of drought stress on photosynthesis, effect of drought stress on respiration, effect of drought stress on photosynthetic derivative distribution, effect of drought stress on metabolism, accumulation of sugars, drought stress and protein breakdown, and the effect of drought stress on ABA hormone, which are among the most important of these cases.

Keywords Water · Stress · Physiology · Plant

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Introduction

Crop susceptibility to drought depends on the economic yield of the plant (Khoshmanzar et al. 2019). Investigation of Firoozabadi et al. (2003) showed that the amount of root yield under normal conditions, mild stress, and severe stress that was applied continuously during the growing season was 6.58, 8.45, and 7.34 tons per acre, respectively. According to Chołuj et al. (2008), drought stress reduced both root yield and glucose yield due to stress time. However, leafy vegetables such as lettuce, which their economic product is fresh leaves, are so sensitive to drought that they will not perform well in seasons and areas where high evaporation is required even if they are irrigated frequently. Crops such as alfalfa, which are cultivated for their dry matter, have a high resistance to drought, so that a balanced lack of water has a little effect on reducing economic yield (Agrawal and Dadlani 1994; Moustafa-Farag et al. 2020). Drought susceptibility in annual plants that are grown for seed or fruit production varies depending on the stage of development in which they are stressed. In these plants, they are generally more drought tolerant in the vegetative state than in the reproductive stages. Plants such as cotton and tomato that have unlimited growth and are able to produce many leaves after flowering are more resistant to drought than plants that have limited growth. In sunflower, the occurrence of a dry period in the vegetative growth stage caused a decrease in grain yield due to lack of leaf growth after re-irrigation, reduced leaf area, and photosynthesis potential (Mao et al. 2020). Most of the annual seed-producing plants are sensitive to drought in the early stage of flowering. If the grains are stressed in the early stages of reproductive growth, their grain yield will be significantly reduced. Corn is highly sensitive to drought during the flowering stage. The main reason for this sensitivity is the delay in the emergence of female organs, which makes the pistil unprepared to accept them when the pollens arrive. Wheat is also sensitive to drought just before pollination. In this case, meiotic division is likely to be impaired, and healthy pollen production is reduced (Levitt 1980). In plants that grow indefinitely, drought has less effect on seed production, because these plants are able to produce more flowers and seeds after drought from rain and irrigation. Drought in the late reproductive period causes the seeds and fruits to shrink. Reduction of grain size due to drought depends on the balance between photosynthetic source and reproductive reservoir and the effect that drought has on these two components (De Micco and Aronne 2012).

In general, the effects of drought at different stages of development on limited and unlimited seed yield can be observed in the model plant. Drought has shrinking effects in grain yield in plants with unlimited growth; in plants with limited growth, drought in the vegetative stage determines the number of seeds in them. As a result, the final grain yield is the number of seeds (which is affected by drought in the vegetative stage and early flowering stage) multiplied by the weight of the seed affected by drought in vegetative stage, which determines the canopy of photosynthetic capacity, and the dryness in the filling stage, which reduces grain size. Seed photosynthesis is the opposite in plants that grow indefinitely because the number of leaves and yield increases cumulatively. The drought of the previous stages will have relatively little effect on the later stages (Agrawal and Dadlani 1994).

Effects of Drought Stress on the Plant

General Effects of Drought Stress

The most common effect of drought stress is to reduce the water potential, the turgor in the growing cells, and thus the lack of expansions necessary for their growth (Ghassemi et al. 2018; Khoshru et al. 2020). The effects of drought stress can be divided into anatomical and physiological changes. Physiological changes include the opening and closing of stomata, different movements of plant organs, structure of proteins and enzymes, amount and action of hormones, carbohydrate metabolism, pattern of accumulation of substances in the cell membrane, photosynthesis, respiration, and rate of action of photosynthesis. Anatomic changes can be seen in reducing the size of cells and the distances between them, thickening of the cell wall, more development of mechanical tissues, and reducing the number of stomata per unit area and changes in organ growth (Levitt 1980; Heshmat et al. 2020).

Drought Effect on Cell and Tissue Growth

Because plant growth is the result of cell growth, it is necessary to consider cell growth in three stages of division, development, and differentiation in relation to drought stress. It is often concluded that cell division is less sensitive to drought stress than its enlargement (leaf development). In support of this result, corn leaf development and early germination were limited to 0.75 MPa, but cell division continued (Vyas et al. 1985).

Similarly, soybean tissue culture showed a decrease in cell size (Sinclair 1985). The growth of sugarcane sprouts (possibly by cell division) was reduced to a potential of 5 atmospheres and stopped completely at 20–30 atmospheres. This difference can be explained by the fact that developing and enlarging cells need several times more water than cell division (Kumar et al. 1994). A 1996 study by Gzik on sugar beet found that drought stress increased proline content, which reduced plant growth and net leaf weight. When the lack of water is present in the plant, cell growth ends earlier than when there is plenty of water, and the structural differentiation of cells begins earlier. In general, a lack of water accelerates cell differentiation. It is found that the final effect on growth will depend on the frequency and duration of stress periods. Drought stress does not affect all plant organs in the same way. As a rule, leaf-to-stem ratio decreases due to drought stress, and older and shaded leaves die sooner (Doorenbos and Kassam 1979; Hayat et al. 2020). Also water scarcity decreases speed of tillering stage and increases tiller death in tillering species. In maize, the ability of the cell wall to expand decreases due to lack of water, while the ability of the root cell to expand increases (Westage and Boyer 1985). With the onset of drought stress, the root growth rate decreases. However, root growth is less affected than the aerial parts of the plant, and in general, the root-to-stem ratio increases. Roots are reduced and grow toward the water in the soil as long as they are close to the water. When the rainfall is light and frequent, only a small part of the potential root area is moistened, and root penetration is limited to the shallow layer. In this case, the plant will be sensitive to dry periods, especially in the later stages of the growth (Black and Ong 2000).

During the drought stress, the growth stops and continues after stress relief. The amount of damage to plants depends on physiologic age, amount of water stress, length of stress period, and species of plants. In general, organs of the plant that grow rapidly during stress are damaged more than other organs (Mao et al. 2020).

Vyas et al. (1985) showed that sesame in drought stress strongly affects the internode length, capsule length, and biomass, but the traits of first capsule height to ground, number of capsules, average capsule thickness and 1000 seed weight, root length, and number of branches whether with capsules or not were less affected by stress.

Physiological Effects of Drought Stress

Reduction of Relative Water Content (RWC)

One of the most important changes due to drought stress is reduction of leaf relative water content (Heshmat et al. 2020). This index can show the ability of plants to tolerate drought stress. Kaiser et al. (1985) categorized the potential effects of increased defoliation as follows: By reducing the relative moisture content of the leaf (RWC) between 70% and 100%, photosynthesis is reduced due to the closure of the stomata, which is rapidly reversible. Upon reaching the relative moisture content between 35% and 70%, photosynthetic capacity is only slowly improved with rehydration. Light inhibition is the main cause of decreased photosynthesis under stress condition. Electron transfer is also one of the restrictive actions, and if the relative water content of the leaf is reduced to less than 30%, photosynthetic capacity is reduced due to membrane damage that it is in chloroplasts leads to death. To calculate the relative water content, the leaves are separated from the plant and weighted. They are then submerged in water to reach the maximum turgor pressure for re-weighing, calculating indicators such as relative water content, water saturation deficit, and relative saturation deficit. Because relative water content and water saturation reduction require accurate determination of leaf dry weight, it is often preferable to use relative saturation reduction. The proposed method for selecting cereal seedlings for drought resistance is based on a relative turgidity index (Kumar et al. 1994). The index of relative water content of leaves to determine the water status is proper than the parameter of water relation, because the relative moisture content of the leaf is related to the cell volume and may better express the balance between leaf water supply and evapotranspiration (Sinclair 1985). In sucrose-transmitting species, sucrose and hexose levels increase as the target level decreases with water stress (Vyas et al. 1985). The increase in sucrose and hexose levels appears to be due to increased starch hydrolysis and sucrose synthesis. Accumulation of sucrose and hexose is performed to play the role of osmotic regulation in these species (Vyas et al. 1985). In drought conditions, stomatal conductance and leaf photosynthesis also decreased (Saghafi et al. 2020). Water stress does not affect all aspects of plant development equally. Some processes are very sensitive to increasing drought stress, while other processes are less affected by water stress (Nayyar and Gupta 2006). Decrease in relative humidity in plants causes morphologic changes in them, such as reducing the number and size of leaves and finally stopping leaf growth and falling of them, reducing the number of nodes.

Reduction of Intercellular Space during Wilting

If the cells are in a state of wilting (in some organs), due to reabsorption of water and increase of cell water content, it increases the intercellular space, and the contact between the cells decreases. Conversely, if the intercellular water content decreases, the released cell walls collapse and exit. Water flows from the intercellular space. Therefore, reducing the amount of tissue water by about 30% in tobacco reduces the gas flow to the tissues (Kirda 2002).

In corn leaves, the decrease in gas volume is more than the decrease in total leaf volume, which coincided with a decrease in tissue water in the scale of 0.6–0.65 of the maximum amount of water (Sharp et al. 1994). Intercellular space in sunflower leaves decreased from 0% to 50% water reduction interval (Sharp et al. 1994). Citrus leaves have strong surfaces that prevent it from shrinking and reducing the intercellular space. Reducing the intercellular space reduces or eliminates the gas flow path in the leaf and also reduces the diffusion flow in the intercellular liquid phase. It is comparable to aperture resistance (Kirda 2002). As the leaf water potential decreases until it reaches a critical or threshold of water potential, the changes in stomatal resistance are small, and at a value below the threshold, the stomatal resistance decreases significantly (Black and Ong 2000). Sharp et al. (1994) showed that the potential of the water critical point for stomatal closure varies in genotypes of plant species and cultivars, but there are less differences between cultivars. Also, the amount of potential of leaf water in which the stomata closes varies according to the position, leaf, shoot, age, and the rate of stress progression (Kaiser et al. 1985).

The Effect of Drought Stress on Photosynthesis

The most important physiologic effect of water stress is to limit photosynthesis. When plants are exposed to water stress, often photosynthesis is not the first reaction to be affected. As drought stress increases, photosynthesis decreases significantly and usually reaches zero at higher stress levels. Water scarcity reduces photosynthesis by reducing leaf area, closing stomata, and reducing carbon fixation efficiency. Decreased leaf area due to drought stress is an important cause of reduced crop yield. The decrease in photosynthesis in stress-affected plants is primarily attributed to the closure of stomata, which simultaneously prevents the fixation of CO_2 due to damage to the photosynthetic system (De Swaef and Steppe 2010). It has also been suggested that carbohydrate accumulation may reduce photosynthesis when growth is confined by drought stress (Gzik 1996). Water deficiency also affects the activity of enzymes that mediate photosynthesis in the dark. A number of researchers have reported that the activity of enzymes that mediate the photosynthesis in the dark is effective.

Some researchers have reported that activity of imported enzymes such as ribulose 1, carboxylase 5 bisphosphate, ribulose 5 phosphate kinase, and phosphopyruvate carboxylase was reduced due to drought stress. Also water potential less than 0.5 MPa reduces chlorophyll production and chlorophyll a to b ratio. Degradation of chlorophyll molecules is accelerated by drought stress. In maize, which is a C4, chlorophyll molecule degradation is much greater in mesophilic cells than in cells or vascular sheaths (Westage and Boyer 1985). Degradation of chlorophyll a and b molecules in chloroplasts and loss of light-receiving lamellae are affected by drought stress. Another study on sugar beets showed an increase in chlorophyll content. This researcher attributed this to the shrinkage of plant cells under drought stress conditions and greater accumulation of chlorophyll in these conditions (Mohammadian et al. 2003). Khafagi and El-Lawendy (1997) also reported an increase in chlorophyll content under drought stress in sugar beet. Due to the high differences between and within plant species, it is difficult to generalize the impact of drought stress on photosynthesis (Khafagi and El-Lawendy 1997).

The Effect of Drought Stress on Respiration

Lack of water, which is enough to close the stomata and reduce photosynthesis, usually reduces dark (true) breathing. But the decrease in dark breathing rate will be less than its amount in photosynthesis. By reducing the leaf water potential of sunflower from −0.4 to −1.8 MPa, the rate of leaf photosynthesis decreased by 70% while the reduction in respiration rate reached 33% (Gray 1984). Drought stress in sugar beet increased dark respiration and breakdown of starch into sucrose, and in general drought stress increased the sugar content in this plant (Ober 2001). In sunflower stalks of maize and soybeans, dark respiration decreased as much as photosynthesis meaning that the lack of water in dark respiration for stems decreases more than its amount in leaves. With the decrease of water potential in soybean, the amount of respiration also decreased, but in the range of −1.6 to −0.4 MPa, no decrease was assumed in respiration. This context demonstrates that enzyme complexes are relatively associated with wilting. Sometimes with reduction of plant's water content, an increase in respiration occurs; therefore it is possible that drought stress causes hydrolysis of starch and its conversion to sugars and provides more substrate for respiration (Ferus and Arkosiova 2001).

Drought stress in sunflower and beans has small effect on respiration, and photorespiration has less effect than gross photosynthesis. Therefore, the ratio of photorespiration to gross photosynthesis increases with drop of leaf water potential. Decreased activity of RuBp carboxylase shows up in parallel with pure photosynthesis, so it can be concluded that the relative increase in photorespiration is associated with the inhibition of the activity of enzymes in the Calvin cycle and reduces the photosynthetic efficiency due to drought stress (Ferus and Arkosiova 2001).

The Effect of Drought Stress on the Distribution of Photosynthetic Derivatives

In some cases, drought stress can change the pattern of photosynthetic material allocation. If drought stress occurs in the filling stage of soybean, by reducing grain formation in the final stages of grain growth and by transferring derivatives, reduction of grain size happens. Also, reducing leaf size and change in root-to-system ratio indicates a change in derivative distribution pattern (Sinclair 1985). The effect of water deficiency on the distribution of photosynthetic materials in different plant organs depends on plants' age, stress intensity, occurrence or non-occurrence of stress in earlier stages of growth, and degree of stress sensitivity in different organs, for example, the dwarf species of lolium temulentum is more sensitive to water deficiency and the pathway of photosynthetic derivatives to young leaves, pods, and roots. While under favorable conditions, the pathway of photosynthetic derivatives is intended to meet the reproductive growth needs of the plant, but in conditions of water scarcity, the current photosynthetic material decreases and the proportion of stored material that is transferred to the seeds increases (Black and Ong 2000).

Mohammadian et al. (2003) announced that in plants under drought stress conditions, the transfer of photosynthetic substances is affected and causes leaf saturation by these substances, which may lead to confinement of photosynthesis.

Drought Stress Effects on Metabolism and Accumulation of Sugars

Drought stress increases respiration and decreases photosynthesis, thereby reducing vegetative growth and reducing the utilization of carbohydrates. Dehydration and high temperatures during the growing season increase sugar in the roots and increase the impurities of sugar beet roots, especially nitrogenous compounds (Kumar et al. 1994). Increased amylase activity in stressed leaves as a result of starch hydrolysis is intensified, and the concentration of soluble sugars is increased. The conversion of starch to sugar is often correlated, but there have been reports of no close association between decreased polysaccharides and increased simple sugars (Hussein et al. 2008). If the plants are exposed to drought stress frequently, the plant will suffer from hunger related to lack of carbohydrates in parallel with stomatal closure. The conversion of structural sugars and polysaccharides to soluble sugars regulates the osmotic pressure and thus counteracts cell water and loss of turgor continuation (Ferus and Arkosiova 2001). Carbohydrates and starch levels in cotton plants during the wilting point were one-half and one-third of plants in optimal conditions. Decreasing the leaf water potential in soybeans increases soluble sugars and decreases insoluble sugars, including soluble sugars which showed an increase in glucose and fructose in leaf water potential of -2.5 MPa; the amount of soluble sugars was doubled compared to the control (Ferus and Arkosiova 2001). Ferus and Arkosiova (2001) experimented the effect of drought stress on sesame and measured various factors and concluded that the amount of soluble sugars in stressed plants increased compared to the control sample.

Drought Stress and Protein Breakdown

The effect of wilting on changes in protein structure has been studied by scientists. In tobacco and sunflower, due to drought stress, in the lower leaves, proteins were converted to asparagine and glutamine and then transferred to younger leaves, in which the synthesis of new proteins was used again. The leaves also accelerate the aging of the leaves. Under the drought stress effects, the plant copes with the stress at cellular level, which results in the consumption of materials and high energy, which is spent on cell construction under optimal conditions. On the other hand, a decrease in intercellular energy, which is mostly used as ATP in the vital activities of the plant, and decreased synthesis of essential proteins are also two of the cases that are affected by environmental stresses. Barlow et al. (1977) reported that a delay for 3 hours caused a 40% reduction in intercellular ATP and increased free amino acids by about 20%. Perhaps this phenomenon could be interpreted as stress causing free amino acid synthesis. Proline is one of the amino acids that accumulate in a number of laboratory and field products in response to drought stress in plant leaves. Under stress, the amount of proline may reach 40 to 100 times the initial level (Aspinall and

Paleg 1981). Aspinall and Paleg (1981) believe that the process of proline accumulation in drought-sensitive cultivars is faster than drought-resistant cultivars, and this can be attributed to the difference in the amount of reduced leaf water potential. Accordingly, Moustafa-Farag et al. (2020) suggested that proline accumulation may be a sign of a stress adaptation mechanism, but there is insufficient evidence to support this theory. Proline accumulation in cells has been discussed to regulate osmotic pressure, reduce cell water loss, maintain turgidity and also solubility of different proteins, conserve albumin, and prevent their breakdown. On the other hand, water stress causes the accumulation of toxins such as ammonium ions and proline and prevents the destructive effects of this toxic substance on metabolism. Most reported cases of proline accumulation are as follows: (1) through its synthesis from other amino acids such as glutamic acid and arginine, (2) reduction of oxidation, and (3) participation of these amino acids in the process of protein synthesis in dry conditions and vice versa. Proline is oxidized to other amino acids such as glutamic acid. Gzik (1996) reported an increase in proline and free amino acid composition in sugar beet. Moustafa-Farag et al. (2020) showed that in rye under drought stress, total amino acids are released to a lesser extent than proteins. With the exception of proline, which is more likely to be synthetized from other amino acids, some amino acids were initially increased in sunflower under drought stress, but proline accumulated only under severe stress. Sharp et al. (1994) showed that in low water potential conditions, in the end of the maize root and in the elongation zone, the amount of proline reaches ten times per unit length compared to their non-growth stress conditions; the increase in proline plays an essential role in osmotic regulation. And it continues to have elongated roots. Vyas et al. (1985) experimented with drought in sesame and reported that stress increased proline. Aspinall and Paleg (1981) stated that a positive correlation between proline accumulation and drought resistance could not be used as an indicator of drought resistance in grain screening in breeding programs. The differences in the results are not only due to the plant species but also due to the amount of wilting, leaf age to be measured, and other conditions. Betaine accumulation, like proline, has been reported in association with drought stress. According to the research done by Hanson et al. (1977), the accumulation of betaine resulting from its new synthesis is from two organic precursors during drought stress. Under drought stress, barley leaves accumulate betaine at a rate of 200 nmol per square decimeter of leaf area per day. Another important effect of drought stress is photic inhibition due to the destruction of photosystem 2 in chloroplasts (Nayyar and Gupta 2006). The photic inhibition obtained by drought stress or other stresses is detected by chlorophyll fluorescence, which we will discuss in detail in the next section.

Drought Stress Effects on Abscisic Acid Hormone

One of the first effects of wilting in mesophytic plants is a decrease in growth inhibitors. Therefore, under the influence of drought stress, the synthesis and accumulation of ABA in the leaves and roots of stressed plants occur (Sharp et al. 1994). Abscisic acid is a growth inhibitor whose wilting conditions increase its concentration and accelerate its synthesis rate when the isolated leaves of cotton, chickpea, and bean are exposed to air, and up to 9% heavier, water is lost and withered (for 4 years at 22 °C). ABA was synthesized and accumulated in the dark (Agrawal and Dadlani 1994). The ability of ABA synthesis in the response of plant organs to wilting in leaves and young organs is higher than old organs. ABA enables the recovery of cell turgor by controlling the opening and closure of stomata, and thus the application of ABA in wheat and barley under stress has increased water consumption efficiency (Peña-Valdivia et al. 2010). De Swaef and Steppe (2010) reported an increase in abscisic acid concentration under drought stress conditions in sugar beet. Some of the effects of drought on plant growth are explained by the effects of abscisic acid concentrations. The general response of plants to high concentrations of abscisic acid is to reduce stem growth, which is more sensitive to increasing concentrations of abscisic acid than to decrease the turgor. The effects of abscisic acid on root responses to water stress are not well understood.

Conclusion

Crop susceptibility to drought depends on the conditions and type of the plant. For instance, most annual plants that produce seeds are sensitive to drought in the early stages of flowering. Also, in plants with unlimited growth, drought has less effect on seed production. With the onset of drought stress, root growth rate decreases; however, root growth is less affected than the growth of the aerial parts of the plant. The amount of damage to plants depends on physiologic age, amount of water stress, length of stress period, and plant species. In general, organs of the plant that grow rapidly in the event of stress are damaged more than other organs. In drought conditions, stomatal conductance and leaf photosynthesis are also reduced. Water stress does not affect all aspects of plant growth equally, and some processes are very sensitive to increased water stress, while other processes are less affected by water stress. The most critical effect of water stress is the limitation of photosynthesis, and drought stress sometimes changes the pattern of photosynthetic material allocation. Drought stress increases respiration and decreases photosynthesis, thereby reducing vegetative growth and reducing the utilization of carbohydrates. Decreased synthesis of essential proteins and accumulation of ABA in the leaves and roots of plants are also some of the cases that are affected by environmental stresses.

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