Plants' Physiological Responses to Drought and Water Stress

Subjects: Environmental Sciences

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Drought affects several biochemical and physiological processes of plants, such as translocation, respiration, the uptake of ions, photosynthesis, nutrient and sugar metabolism, and phytohormones. Cell membranes can be destroyed, and leaf water potential can be diminished by drought. Furthermore, heavy drought causes the cessation of photosynthesis and metabolic disorders, and it can lead to the death of plants.

water stress | drought tolerance | sweet potato | abiotic stress | drought

1. Introduction

Drought affects several biochemical and physiological processes of plants, such as translocation, respiration, the uptake of ions, photosynthesis, nutrient and sugar metabolism, and phytohormones. Cell membranes can be destroyed, and leaf water potential can be diminished by drought. Furthermore, heavy drought causes the cessation of photosynthesis and metabolic disorders, and it can lead to the death of plants [1]. However, the drought sensitivity of plants depends on the degree and duration of the stress, the plant variety, and the development stage in which the drought occurs [2].

There are two known mechanisms that reduce the negative effects of drought stress in plants, namely stress avoidance and tolerance mechanisms. Stress avoidance refers to a plant's ability to sustain the high water potential of its tissues under drought stress. Plants reach such levels by increasing their water uptake through deep root systems or by reducing their transpiration losses through thin or meaty leaves [1].

Drought is associated with changes in leaf anatomy and ultrastructure for most plant species [3]. Typical changes include leaf drying, reductions in stomata quantity, stomatal conductance, changes to cell walls, leaf hardening, leaf rolling, and the early induction of senescence. A study found that drought had a detrimental effect on sweet potato growth to the extent that no significant differences were observed among genotypes under severe drought conditions [4].

Different environmental conditions influence the growth, yield, and nutritional quality of sweet potato [5]. Through a water stress simulation experiment, a study found that water deficiency stress did not affect the tubers of sweet potato [5]. It has been emphasized that sweet potato is drought resistant and increases its level of secondary metabolites (for example, amino acids and β-carotene) under drought stress as a form of water stress protection

[6]. These metabolites are useful to humans, as phytochemicals are conducive to a healthy lifestyle [6]. Although sweet potato is a drought-tolerant crop, it is drought-sensitive, especially at its early growth stages [5]. Delazari et al. [7] showed that sweet potato growth is severely stunted under drought conditions, which affects its yield. This corresponds to the conclusions of Martin and Jones [8].

Drought affects sweet potato structure not only at the tissue and cellular levels but also at the subcellular level. A study by Gouveia et al. assessed the physiological responses of sweet potato samples to conditions of water shortage. Sweet potato samples that had an improved WUE were found to be the most drought resistant [9].

In other similar studies, sweet potato samples showed the best physiological and biochemical responses to water stress treatment, showing in particular a higher ratio of above-ground to below-ground plant parts (root/shoot), lower total biomass loss, and lower stress index values [10]. In addition, the studied sweet potato samples showed a good phenotypic response, including water efficiency and nitrogen efficiency for growth and vital functions, as well as higher root mineral content, chlorophyll content index (CCI) values, and shoot nitrogen content [9]. Furthermore, all the samples reduced their biomass by 55.4%, thereby showing drought avoidance behavior under stress conditions. However, all the samples showed differences depending on their water distribution, chlorophyll level, and nutrient utilization. The sweet potato genotypes increased their WUE by +68.1% on average, and the highest water uptake occurred through transpiration. Furthermore, the samples' chlorophyll content index values decreased by −5.3% as a result of a decrease in their photosynthetic rate. Their nitrogen efficiency ratios increased by +38.1%. Additionally, their nitrogen use efficiency increased by +54.4%. Their nitrogen harvest index values also increased, on average, by +2.9%. Overall, drought was shown to reduce the size of sweet potatoes (root/shoot ratio) as a result of investment in shoot development [9].

Another study found that plant signal transduction, phenylpropanoids, an isoquinoline alkaloids, and flavonoid biosynthesis play important roles in the regulation of the tolerance of plants to drought stress. According to the results of a transcriptomic analysis, the tolerance mechanisms of sweet potato varieties are very different, and occasionally some varieties respond oppositely. One drought-sensitive variety resisted drought stress by up-regulating signal production, whereas another drought-sensitive variety avoided drought stress by down-regulating isoquinoline alkaloid biosynthesis and nitrogen/carbohydrate metabolism. Moreover, on the one hand, some drought-tolerant varieties regulated flavonoid and carbohydrate metabolism or isoquinoline alkaloid biosynthesis and nitrogen/carbohydrate metabolism in response to stress; on the other hand, another drought-tolerant variety increased photosynthesis activity and carbon fixation processes. The high drought-tolerant variety was not affected by stress and responded to water deficiency by regulating the cell wall. These pathways are important indicators for selecting the breeding lines of sweet potato [2].

2. Chlorophyll Content Index

A study found that the chlorophyll content index values of sweet potato exposed to drought stress 60 days after planting did not decrease significantly compared to controls under drought conditions, although a decreasing trend was observed [11]. Zhang et al. [12] observed a decrease in CCI values over different periods (40 days, 60 days, 80 days, and 100 days) after planting under drought stress conditions. The Hernandez variety showed a slight increase in its CCI values in the control compared to in the high-stress conditions. Different sweet potato varieties expressed various CCI levels when exposed to the control treatment, including the high-stress treatment group 60 days after planting [11]. This can be explained by genetic differences among the varieties, as well as their photosynthetic activity.

Further, significant and strong decreases in CCI levels were detected 120 days after planting in all the genotypes under drought conditions. Similar data were obtained by Nikolaeva et al. [13], who observed a significant reduction in CCI levels when wheat plants were exposed to drought stress.

Another study found that some varieties of sweet potato (Monate, Resisto, and Bophelo) showed significant decreases in their CCI levels compared to the control. Drought affects the photosynthetic systems of plants and may cause the growth retardation observed in crown and stem development [11].

Chlorophyll breakdown can also affect the intensity of sweet potato’s antioxidant enzyme system, with relatively weak values having been recorded in previous studies. Heider et al. [14] considered the CCI to be a potential marker for selecting for heat tolerance.

3. Reactive Oxygen Species

Certain metabolites play leading roles in the adaptation of plants to a broad range of abiotic stressors [15]. The accumulation of osmolytes or compatible solutes, such as polyamines, free proline, trehalose, glycine betaine, and sugar alcohols, may protect plants against adverse environmental conditions.

A particular feature of sweet potatoes is that they contains sufficient quantities of β-carotene, vitamin C, and antioxidants [16]. These antioxidants provide the basis for the plant’s resistance to stressful conditions. Researchers have studied how the synthesis, activity, and levels of these secondary metabolites vary among sweet potato varieties [17][18][19][20].

In order to reduce the negative impact of abiotic stress, plants use different signaling pathways and react by changing their growth patterns, accumulating compatible solutes, activating antioxidants, and producing chaperones as well as stress proteins. ROS comprise radical and nonradical oxygen species generated by partial oxygen reduction [1]. A common occurrence for plants subjected to several abiotic stressors is ROS overproduction, which ultimately leads to oxidative stress [20]. This stress damages biostructures, such as proteins, lipid membranes, and nucleic acids, leading to plant cell death [1]. To reduce these damaging effects, plants have evolved enzymatic and non-enzymatic mechanisms that can minimize oxidative stress and help to increase their resistance to several abiotic stressors [6]. The activity of a plant’s antioxidant (enzymatic and non-enzymatic) system is an effective indicator of its drought tolerance [11].

4. Betaines

Betaines are non-protein amino acids that possess a quaternary ammonium group and a carboxylic group in their structure. These compounds effectively stabilize the quaternary structures of enzymes, complex proteins, and membrane systems, such as the photosystem 2 complex [21]. The synthesis of betaines is induced under different stress conditions, and their concentration is correlated with tolerance [22]. The accumulation of glycine betaine, the most widely studied betaine, results in the protection of plants against various abiotic stressors and increases their yields under non-stress conditions [23].

A study subjected embryogenic suspensions of sweet potato to an *Agrobacterium tumefaciens*-mediated transformation with a gene from spinach (*Spinacia oleracea*) called betaine aldehyde dehydrogenase (BADH). Transgenic sweet potato plants overexpressing this transgene were shown to have increased glycine betaine synthesis and an improved tolerance to multiple abiotic stress conditions, including oxidative, salt, and low-temperature conditions [24]. It has also been shown that transgenic sweet potato plants overexpressing the BADH gene from *Spinacia oleracea* chloroplasts have enhanced tolerance to osmotic, low temperature, and oxidative stressors [25].

5. Trehalose

Trehalose, a sugar consisting of two glucose molecules, functions as an osmoprotectant and plays a protective role against different adverse environmental conditions in both plants and animals [26]. It has also been implicated in the regulation of stomatal movement and water use efficiency in higher plants. Significant levels of trehalose in plant cells are vital for supporting growth under stressful conditions [27]. In plants, trehalose is synthesized in two stages by the enzymes trehalose-6-phosphate synthase (TPS) and trehalose-6-phosphate phosphatase (TPP). First, TPS synthesizes trehalose-6-phosphate, and then TPP catalyzes the dephosphorylation of trehalose-6-phosphate to trehalose [27]. A study isolated the TPS gene from *I. batatas* (*IbTPS*) and found that the overexpression of this gene in transgenic plants improved their resistance to salinity compared to control plants [28].

6. Polyamines

Polyamines are small polycations that play various important roles in all organisms. Polyamines, which are positively charged at physiological pH, interact with various negatively charged molecules, such as membrane phospholipids, nucleic acids, and certain proteins, which activate and stabilize them under abiotic stress [29]. Putrescine (a diamine), spermidine (a triamine), and spermine (a tetramine) are the most common polyamines in plant cells. They can be synthesized from positively charged amino acids, such as L-ornithine, L-lysine, and L-arginine [30]. A study found that transgenic sweet potato plants expressing the spermidine synthetase gene *FSPD1* from *Cucurbita ficifolia* showed higher levels of spermidine in their tissues and an increased tolerance to heat-mediated damage, chilling, and oxidative stress compared to wild-type plants [31].

7. Sugar Alcohols

Inositol is a well-known osmolyte, and its phosphorylated derivatives function as secondary messengers in signal transduction pathways under various stressors. A key limiting stage of myo-inositol biosynthesis is catalyzed by the enzyme l-myo-inositol-1-phosphate synthase (MIPS). A study isolated the *IbMIPS1* gene from *I. batatas* and found that its overexpression greatly impacted the salinity and water stress tolerance of transgenic sweet potato plants in field conditions [32].

8. Free Proline Content

Proline (Pro) accumulation is associated with abiotic stress tolerance mechanisms in plants. It helps to stabilize proteins and membranes as well as neutralize free radicals. Proline plays a role in supporting plants affected by stress conditions [33]. As an osmotic agent, proline helps to maintain the osmotic pressure between a plant's extracellular and intracellular regions and protects plant cells from damage under osmotic stress conditions. The amount of free proline in plant cells increases significantly in response to various environmental stressors. Several studies have shown that the exogenous application of this amino acid may enhance plant resistance to drought [11][34]. The accumulation of free proline in transgenic plants can be achieved by enhancing its de novo biosynthesis [35] or by preventing the degradation of proline [36].

The key enzyme involved in proline biosynthesis is pyrroline-5-carboxylate reductase (P5CR). A study found that the overexpression of the *IbP5CR* gene isolated from *I. batatas* enhanced salt tolerance in transgenic sweet potato plants [37]. In a number of other studies, it has been shown that transgenic sweet potato plants with an enhanced tolerance to abiotic stress have a higher accumulation of free proline than wild-type plants exposed to the same stressors [15][38][39].

Laurie et al. [11] identified significant differences in free proline content among various genotypes. Proline accumulation increased from 2 µmol/g to 22 µmol/g under drought stress conditions compared to the control. An overall increase of up to five times that of the control group in plants exposed to the treatment conditions was observed 120 days after planting. This indicates that the plants were grown under drought conditions, which resulted in increased proline production either through free proline from the root system [40], an increase in enzyme production [41], or protein breakdown. The drought stress treatment conducted 60 days after planting found that the Bophelo sweet potato variety accumulated a higher level of proline compared to other varieties [11].

9. Ascorbate Peroxidase

Water stress has been found to cause a significant increase in APX activity, especially when treated with high drought stress. For instance, Zhang et al. [42] recorded an increase in APX activity and a defense reaction during the growth of sweet potato impacted by water deficiency stress. The APX activity increased by nine times under the drought treatment compared to the control. In addition, there was no difference in APX activity among sweet potato varieties. These findings are in accordance with the results of a study conducted by Dalton et al. [43], wherein a slight increase in APX activity was observed under drought stress conditions in wheat plants. Lu et al. [17]

demonstrated that APX expression in sweet potato chloroplasts increases their drought tolerance and ability to recover from drought stress. Although most sweet potato varieties and breeding lines express moderate levels of APX activity under water stress, peroxidase enzymes are not the only antioxidant pathway used by sweet potato to reduce its ROS scavenger levels under water stress [11][12].

10. Superoxide Dismutase

A study observed an increase in the superoxide dismutase activity of different sweet potato varieties subjected to water stress. This ranged from 0.350 units/mg protein under the control conditions, to 0.85 units/mg protein under the drought treatment. These findings were similar to those made by Zhang et al. [12] and Masoumi et al. [44], who demonstrated increased SOD activity in soybean varieties under drought stress conditions. Differences among the varieties were observed at 60 and 120 days after planting in the severe-stress treatment group. The SOD activity values of the plants exposed to severe stress at 120 days after planting were also generally higher, which may have been related to the greater drought conditions experienced by the varieties, and also to an increase in diatomic oxygen recorded in the plant leaves [11].

11. Glutathione Reductase

A study found that glutathione reductase (GR) levels were increased in varieties subjected to drought stress at both 60 and 120 days after planting compared to the control group. Although the increase in GR was similar in the control and heavy stress treatment groups for each variety, the simultaneous increase in SOD activity confirmed the possibility of drought tolerance [45]. GR activity differed significantly among breeding clones because of drought stress. The GR activity ranged from 2 nmol NADPH min-1 mg protein-1 under the control conditions to 73 nmol NADPH min-1 mg protein-1 under the stress conditions. Among the varieties, significant differences in the activity of this enzyme were also found in the control treatment group at 60 days after planting. This may indicate the genotypic diversity of the varieties in terms of their GR activity under control conditions [11]. At 120 days after planting, the sweet potato variety Bophelo under drought conditions showed a significant increase in the activity of this enzyme. Furthermore, Masoumi et al. [44] observed a decrease in GR activity during drought experiments, indicating that tissue degradation may lead to decreased GR levels.

12. Nitrate Reductase

Xia et al. [46] investigated the activity of nitrate reductase (NR) under highly stressful drought conditions, finding that NR plays various roles in the regulation of NO_3 assimilation and N-fixation, which are associated with the modulation of photosynthesis. The impact of drought was severe, meaning that no significant differences were observed among different genotypes. The rapid decrease in the enzyme’s activity in these trials was theorized to have a negative effect on plant growth. Reduced photosynthesis also has negative effects on nitrate reductase, which is consistent with the authors of [47]’s reasoning that stomatal conductance affects photosynthetic speed and therefore causes a decrease in the NR level of plants. A study found that the concentration of nitrate reductase ranged from 2.4 µmol NO_2 $g^{-1}h^{-1}$ under control conditions to 0.0016 µmol NO_2 $g^{-1}h^{-1}$ under drought conditions. No considerable differences in NR activity were found among varieties under conditions of severe stress at 60 or 120 days after planting when the activity was already at an extremely low level as a result of protein degradation [48]. Such a decrease in NR affects plant growth because nitrogen is an important precursor of the synthesis of secondary metabolites [11].

During breeding, the study of plant protection mechanisms under stress is important for the development of plant resistance and tolerance. This, in turn, is important for improving the productivity and yield quality of sweet potato and other crops [2]. Researchers have recommended field experiments using more sweet potato genotypes and in greater areas so that adaptation on a larger scale can be investigated [2][49]. Further, the determination of various physiological and biochemical parameters, such as sugar content and contents of secondary substances, such as phenols, which are related to water stress, is recommended for future sweet potato studies involving monitoring under drought conditions [1]. When selecting parents to cross for drought resistance, varieties with high antioxidant contents should be used to improve drought tolerance and avoid yield loss due to stress. Antioxidant levels should guide researchers in selecting and suggesting varieties for use in drought-prone regions in order to ensure sustainable agriculture and food availability.

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