**Comprehensive Review on the Physiological Adaptations of Tomato (Solanum lycopersicum) to Drought Stress**

**Abstract**

Tomato (*Solanum lycopersicum*) is greatly impacted by drought. Under drought stress, tomatoes produce an excessive amount of reactive oxidative species (ROS), which has a disastrous effect on tomato productivity and growth. One of the major risks to crop productivity and world food security is drought stress. This review aims to examine the physiological mechanisms of drought tolerance in tomatoes. ROS produced by drought-induced oxidative stress harms chloroplasts and other cellular components, further reducing photosynthetic efficiency. Many adaptation techniques have been developed by plants to mitigate these consequences. Tolerance is also strengthened by structural modifications like rearranged leaves and changed root architecture. Developing crop types resistant to drought and guaranteeing sustainability requires an understanding of these intricate relationships and adaptive techniques.

**Keywords:** Tomato, drought, productivity, adaptation, enzymes

**Introduction**

Abiotic stressors include factors like oxidative stress, metal toxicity, excessive soil salinity, temperature swings, and drought. These stressors have the potential to permanently harm a plant by causing stunted growth, impaired metabolism decreased yield, and genetic behaviour changes that result in mutations in the offspring. Climate change and soil aridification are expected to lower soil moisture content and have a considerable impact on crop growth, making drought one of the main abiotic factors that restrict plant growth, development, and yield globally (Good *et al.,* 2015; Ekinci et al., 2015). Numerous physiological and biochemical processes in crops are negatively impacted by drought. A great disaster will be done to society, the environment, and the economy by drought. It is estimated that 16% of the world's geographical area, or around 21–22 million km2, is comprised of dry and semi-arid regions. Lack of precipitation, erratic precipitation patterns and resource scarcity are some of the primary issues facing agriculture in these areas (Falkenmark et al. 1989).

Abiotic stresses are a menace to plant productivity affecting their growth and development potential. Engineering plants with proline synthesizing genes could be one strategy to develop heat-resistant plants. Phytohormones are also involved in inducing plants’ abiotic stress tolerance. Among them, salicylic acid has gained importance in recent years due to its effect on various stresses and its interesting relation with stress hormones like abscisic acid (ABA) and ethylene (Iqbal et al,.2019; Salvi et al. 2021). In the last decade, the interest in understanding the spatiotemporal changes of ABA to modulate plant responses has grown (Müller, 2021; 36. Muhammad et al. 2022). ABA is critical for plant development and can redesign various physiological and biochemical signal transduction cascades in plants to cope with environmental stresses particularly drought (Wani & Kumar, 2015; Chaves et al. 2003). Major agro-systems around the world, particularly rain-fed ecosystems, experience drought stress due to climate change, which also decreases water availability and efficiency (FAO, 2020). The productivity of vegetable crops is particularly impacted by water constraints. Root growth, root length, photosynthetic activity, water nutrient uptake and transport, seed germination, seedling emergence, carbon assimilation, dry matter buildup, flowering, pollen generation, fertilization, and, eventually, vegetable crop output are all negatively impacted by drought (Nephali *et al.,* 2020; Gedeon *et al.,* 2022). Crops such as corn, soybeans, beans, and peas are said to be somewhat vulnerable to water stress, while tomatoes are highly sensitive to drought (Nemeskeri & Helyes, 2019).

Globally, tomato (Solanum lycopersicum) is a highly valued and lucrative vegetable crop, native to South and Central America, and widely cultivated for its nutritional and economic benefits. The Solanaceae family, which includes the tomato, also includes many other well-known crops, including the potato, eggplant, and pepper. One of the most heat-sensitive vegetable crops with significant economic and commercial value is the tomato (John and Stephen, 2024; Kousalya et al. 2022). After China, Turkey is the world's biggest producer of tomatoes. However, due to a number of biotic and abiotic challenges during the past ten years, tomato production is not meeting demand (Ali *et al.,* 2021). Reduced leaf surface area, decreased mineral absorption, flower shedding, smaller fruits, puffiness, fruit splitting, and disorders linked to calcium deficiency, including blossom-end rot and poor seed viability, are all consequences of climate change, particularly water stress (Jangid and Dwivedi, 2016). Reduced pistil and pollen development, proline toxicity, hormonal imbalance, reduced photosynthesis, root branching, and root growth, cellular dehydration, decrease in water potential leading to reduced cell growth, shoot growth, hampered cell expansion and cell wall synthesis, salt deposition around stomatal openings causing their malfunction, and the accumulation of reactive oxygen species are all common outcomes of drought stress in tomato (Turan *et al.,* 2021).

**Drought stress and mechanisms of drought resistance**

Adequate water supply is essential for maintaining the maximum output of horticulture crops since water is a fundamental component for maintaining crop physiological activity and metabolism. The ability of agricultural plants to finish their life cycle before soil water deficiencies arise through early flowering and maturity, as well as plant remobilization and assimilation into the grain, is known as drought escape. However, drought avoidance refers to crop plants' capacity to maintain high tissue water potential in the face of a shortage of soil water by maintaining turgor through increased rooting depth and efficiency, hydraulic conductance, stomatal conductance, reduction of radiation absorption through leaf folding, and reduction of leaf surface evaporation (Srinivasa Rao *et al.,* 2016).

The ability of agricultural plants to produce with the least amount of loss in their economic production and the ability to tolerate water scarcity with a low potential for tissue water are characteristics of drought tolerance. There are a number of drought tolerance strategies that cause solvent buildup in plant cells and maintain turgor by osmotic adjustment (Srinivasa Rao *et al.,* 2016). The physiological reactions and stress tolerance of the species have a significant influence on the chlorophyll content determined by Zhou *et al.* (2017). One of the most crucial indicators for determining a tomato's drought resistance is its chlorophyll level.

**Physiological responses of tomato to drought**

Crop plants react physiologically to drought stress in a number of ways. The most crucial factors for assessing crop plant physiological processes under drought stress are leaf chlorophyll content, stomatal conductance and behaviours and canopy temperatures. Physiological measures that can be employed as screening methods for determining agricultural plant water stress resistance include the crop water index, leaf water potential, relative water quantity, turgor potential, osmotic change, and the difference between canopy and air temperature (Chatterjee and Solankey, 2015).

**Impact of drought on leaf chlorophyll content, stomatal conductance and canopy temperature**

In order to measure the change in canopy temperature and identify the temperature differential between the crop plant canopy and air during drought stress, the crop water index is computed using an infrared thermometry technique. The size, density, and behaviour of stomata are directly correlated with canopy temperature. A canopy's temperature difference from the air temperature is considered good if the crop is experiencing water stress ( Nemeskeri & Helyes, 2019). Based on the air temperature, it can be concluded that transpiration reduces as the amount of water available for crop plants in the soil decreases causing the canopy's temperature to increase.

Therefore, a decrease in transpiration brought on by stomata closing raises the temperature of the crop plants' canopy. Because there is less water available during drought stress, the tomato has a lower relative water content (Khan *et al.,* 2015; Agurla *et al.,* 2018). When there is insufficient soil water content for healthy growth or water delivery, drought stress results. First, a drop in the relative water content (RWC) of leaves causes stomatal closure, which lowers the amount of carbon dioxide (CO2) that mesophyll cells receive and, consequently, lowers the rate at which leaves photosynthesize.

Depending on the environmental factors and crop plant categories, stomatal conductance in tomatoes cultivated without irrigation can range from 14% to 73% when compared to well-watered crop plant varieties (Nemeskeri *et al.,* 2019) (Helyes *et al.,* 2013). It can be inferred that stomatal resistance increased during water deficit situations, such as drought stress, because stomatal conductivity for both water and CO2 flow decreased by closing the stomata (Sing & Reddy, 2011).

An osmotic movement of water from plant cells results from drought stress, which raises the solute concentration in the soil solution (Ghosh *et al.,* 2021). As a result, the solute content in plant cells rises, lowering the water's potential and interfering with membranes and biological functions like photosynthesis. Additionally, a decline in the relative water content of leaves results in stomatal closure, which lowers the carbon dioxide supply and ultimately lowers photosynthesis (Prasil *et al.*, 1996).

Due to metabolic disruption, drought stress alters the amount of chlorophyll in the leaf, which results in a decrease in light absorption. The total quantity of photosynthetic pigments in leaves affects how much light the leaves absorb. The photochemical photo-systems (PSI, PSII) of leaves use photosynthetic pigments to collect light and transform it into chemical energy during the photosynthesis process. Under drought stress, a final decline in photosynthesis and chlorophyll concentration is anticipated.

**Impact of drought on channels for solute transport**

The phloem and xylem's normal function is disrupted by drought stress, which has a significant effect on the movement of water and nutrients in plant tissues. The maintenance of physiological balance and the control of plant hydration and nutrient distribution depend on these vascular networks. Drought affects the phloem and xylem's efficiency, which has a number of negative consequences on plant development and output. The upward transpiration stream of water and dissolved minerals from a plant's root to its aerial portions is caused by the xylem. A cohesive tension mechanism that necessitates a continuous water column facilitates the movement of water in the xylem (Fahad *et al.,* 2017). Due to soil water deficits brought on by drought, there is less water available for roots to absorb, which lowers the water potential gradient between the soil and the roots. As a result, drought stress inhibits the flow of water into a plant. Cavitation and embolism may result from the breakdown of water column cohesiveness brought on by increasing drought stress (Qiao *et al.,* 2024).

Cavitation occurs when air bubbles form in xylem vessels, disrupting the water column's continuity and rendering water transfer ineffective. The moisture content of plants is greatly impacted by this process, which lowers their capacity to sustain turgor pressure. Plants that are unable to sustain their turgor may wilt, which is accompanied by a decrease in photosynthesis. Drought causes callose to deposit in the xylem vessels in addition to cavitation (Qiao *et al.,* 2024). Water circulation is restricted by callose, a carbohydrate that obstructs the xylem channels. Although this reaction increases water restriction, it is protective because it reduces harm and the propagation of air embolism. This illustrates the intricacy of plant reactions to water restriction and the harmony between activity limitation and protective function (Qiao *et al.,* 2024; Lynch, 2018).

The distribution of assimilates, such as photosynthates and other organic compounds, from source to sink tissues is carried out by phloem transport, which may also be hampered. Because solutes have osmotic potential, phloem movement relies on turgor pressure to promote assimilation (Braun *et al.,* 2014; Sato *et al.,* 2024). Reduced water supply during drought also lowers phloem turgor pressure, which impairs the movement of signalling chemicals and nutrients. Callose buildup in the sieve plates impairs the delivery of vital nutrients, such as carbohydrates and amino acids, and restricts the assimilation of substances into the sink tissues (Sevanto, 2019).

**Impact of drought on WUE**

Improved water use efficiency (WUE) is another essential strategy used by plants to survive and thrive in water-deficient environments. In order to maintain increased RWC under drought, plants use a variety of tactics to increase WUE. WUE is a measure of a plant's capacity to effectively use water to provide the energy and nutrients required for growth and development. It is calculated as the ratio of the total biomass generated by the plant to the amount of water it uses. In order to sustain increased RWC during drought, plants employ a variety of strategies to boost WUE, such as regulating stomata and altering leaf shape. Also, a crucial component of plant survival under drought stress is water uptake maintenance through root system modifications, which include changes in root architecture with deep root system development, decreased lateral root branching density, and an increase in the root-to-shoot ratio (Lucob-Agustin *et al.,* 2021)

**Impact of drought on ROS production**

Plants under drought stress produce more reactive oxygen species (ROS), which damages cells and damages photosystems. As previously mentioned, the photosynthetic machinery, including PSII and the electron transport chain, is one of the main targets of ROS (Apel and Hirt, 2004; Mittler *et al.,* 2004). Furthermore, lipid peroxidation caused by ROS can harm the lipids in thylakoid membranes, impairing photosynthetic efficiency and destabilizing the membrane. The efficient functioning of the photosynthetic machinery depends on the integrity of the chloroplast membranes, and any disruption can have a significant impact on the photosynthesis of the plant (Lee and Park, 2012).

Drought-induced oxidative stress impacts nucleic acids in addition to photosystems, resulting in strand breakage, mutations, and adduct formation. The entire cellular metabolism and stress response mechanisms may be impacted by these damages, which may disrupt the transcription and replication processes (Noctor *et al.,* 2014). Furthermore, the buildup of ROS during drought can trigger the pathways leading to programmed cell death (PCD), which can cause the death of cells and tissues that are essential for the growth and development of plants. The degree of damage and the plant's capacity to recover from drought-induced oxidative stress are determined by the interaction of ROS generation, antioxidant defences, and cellular repair processes (Miller *et al.,* 2010).

**Impact of drought on antioxidant enzymes**

The effects of drought stress on RWC are mostly modulated by antioxidant enzymes, which prevent oxidative damage and preserve cellular homeostasis. Superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) are examples of enzymatic antioxidants that are essential for scavenging reactive oxygen species (ROS) and safeguarding cellular structures and functions. Superoxide radicals, for example, are dismutated by SOD into hydrogen peroxide, which is then detoxified into oxygen and water by CAT and POD. By preventing the loss of cellular water content, this detoxification procedure aids in preserving the integrity of cell membranes (Bijanzadeh and Emam, 2010; Martinez-Vilalta *et al.,* 2019; Ahmad *et al.,* 2022). According to studies, these antioxidant enzymes are more active in drought-resistant plant species than in susceptible ones, which may indicate that they help increase drought resistance.

**Conclusion**

The productivity of tomatoes is greatly impacted by drought stress because it alters a number of plant physiological and reproductive functions. Reduced nutrient intake, poor photosynthesis, and compromised reproductive development are frequently the causes of yield decline during drought. Under drought stress, plants use a variety of tactics to sustain yield, which can be viewed as adaptive processes to improve drought resilience. The extensive impacts of drought on photosynthesis in important food crops highlight how crucial it is to comprehend and address this environmental stress. Both the light-dependent and light-independent processes of photosynthesis are negatively impacted by drought stress, which results in notable drops in crop quality and output. A comprehensive grasp of the influence of this stressor will be crucial in assessing how climate variability affects tomato growth. Numerous processes are impacted by drought stress, including tomato crop physiology, growth, development, yield, and quality. Hence, a multidisciplinary strategy combining genetic, physiological, and agronomic techniques is necessary to address drought stress.

**Conference details**

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