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Review Article *Stress Management*

Morphological, Physiological and Biochemical Response to Low Temperature Stress in Tomato (*Solanum lycopersicum* L.): A Review

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Abstract

Growth and productivity are traumatized by the low temperature that triggers a series of physiological, morphological, molecular and biochemical changes in plants that eventually disturb plant life. Most of the cultivable lands of the world are adversely affected by temperature stress conditions which have an adverse impact on global tomato productivity. Plants undergo several water related metabolic activities for their survival during cold stress conditions. Understanding the morphological, physiological and biochemical reactions to low temperature is essential for a comprehensive view of the perception of tomato plant tolerant mechanism. This review reports some aspects of low temperature inflated changes in physiological and biochemical in the tomato plant. Low temperature stress influences the reproductive phases of plants with delayed flowering which enhance pollen sterility resultant drastically affects the harvest yield. It also decreases the capacity and efficiency of photosynthesis through changes in gas exchange, pigment content, chloroplast development and decline in chlorophyll fluorescence photosynthetic attributes. Amassing of osmoprotectant is another adaptive mechanism in plants exposed to low temperatures stress, as essential metabolites directly participate in the osmotic adjustment. Furthermore, low temperature stress enhanced the production of reactive oxygen species (ROS) which may oxidize lipids, proteins and nucleic acids which bring in distortion at the level of the cell. At the point when extreme reactive oxygen species produced, plants synthesize antioxidant enzymes and osmoprotectants that quench the abundance of reactive oxygen species. These reviews focus on the capacity and techniques of the tomato plant to react low temperature stress.

Keywords: Antioxidant enzymes, morphological, osmoprotectan, physiological, ROS, tomato

1. Introduction

Tomato (*Solanum lycopersicum* L.) is a very popular vegetable cultivated and consumed worldwide. Its ranks second in production and consumption in many countries, after potatoes. It is cultivated around the world due to its broader adaptability and flexibility. Tomato, due to its abundance in lycopene, β-carotene, vitamins and minerals, exhibits antioxidant properties. Lycopene is the pigment principally responsible for the characteristic deep-red color of ripe tomato fruits and tomato products (Ghadage et al., 2019). It plays a significant role as an intermediate agent

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in the biosynthesis of xanthophylls and essential carotenoids, such as beta-carotene. Compounds of this type help to combat the harmful effects of substances like free radicalsand various forms of cancers. Low and elevated temperatures are two major challenges seen in tomato development (Opena et al., 1992). To grow tomato plants, the ideal temperature (day/night) is 25-30°/20°C. Low temperature interferes with hormonal imbalance, decreases the content of carbohydrates and irregular pollen, resulting in low production of tomato due to this reason the national productivity of tomato in India is much lesser than that of the world average (Tanvi Raj et al., 2018). The decrease in photosynthetic rate was also observed in wild Lycopersicon species when day temperature was reduced (Fang et al., 2018). The quality of the fruit is often affected by low temperatures; for example, at temperatures below 12°C, the setting of the fruit is completely stopped (Meena et al., 2018).

Plant reaction is a complex physiological and phenotypical mechanism that is strongly influenced by low temperature stress. In order to increase food production, crops are often grown in stressful conditions, resulting in lower yields. Fluctuations in climatic conditions, such as low temperature stress, are the main factors in reducing yield and crop quality. Cold stress adversely damages tomato development during the winter season. In response to low temperature stress, there are several phenotypic symptoms, such as stunted seedling, poor germination, decreased leaf expansion, chlorosis as well as necrosis (Ruelland and Zachowski, 2010). In order to meet global food demand, improved agriculture is very critical and environmentally stress-tolerant crops provide promising solutions. Low and high temperature stresses are becoming the main research problems for agricultural scientists worldwide due to the challenges raised by climate change (Shah et al., 2011). A primary environmental factor that purposely has a direct effect on the growth and production of plants is low temperature stress. It can decrease growth, development, yield and quality, which can lead to significant crop losses in tomato productivity (Zhang et al., 2013; Khan et al., 2015).

Low and high temperature stresses are regarded as the two most influential environmental variables. There are two forms of low temperature stress, chilling stress, which ranges to 0°C, and freezing stress, which is below 0°C, causing ice crystallization, which defines the direction and position of freezing injury (Levitt, 1980). Exposure to low temperature stress, summer vegetables such as tomatoes, brinjal, potatoes, cucurbits can display stunted plant growth, increased wilting and necrotic leaf lesions, and susceptibility to diseases and pathogens (Hall-green and Oquest, 1990).In these plants, however, the signs of stress-imposed injuries occur from 48 to 72 hours; this period varies from plant to plant species and often depends on the sensitivity of the plant to low temperature stress. In response to stress from low temperatures, different phenotypic symptoms, *i.e*. increased reduction in leaf expansion, wilting as well as chlorosis (yellowing of the leaves) that may lead to necrosis. It is understood that abiotic stresses are major limiting factors affecting plant growth and development, globally. Thus, there is a growing interest in deciphering the physiological, biochemical, molecular, and cellular mechanisms of abiotic stress responses and tolerance and to introduce potential mitigation techniques that would enhance sustainable agricultural production. (Mirza et al., 2020). Reactive oxygen species (ROS) generation is a usual phenomenon in a plant both under a normal and stressed condition (Mirza et al., 2019). Low temperature stress adversely affects growth, productivity and triggers a series of morphological, physiological and biochemical changes in plants. It is a major environmental cue that limits the vegetable productivity of plants (Yogendra and Nirmaljit, 2017).

2. Morphological Response to Low Temperature Stress

Throughout plant formation, tomato plants are susceptible to chilling temperatures (0-15°C), *i.e*. seed germination, vegetative growth and reproduction. Many seeds do not germinate or germinate irregularly under low temperatures, as plants grow differentially with delayed plant formation, resulting in variability in crop production. At later stages, plant development and growth are extremely retarded, either decreasing or leading to no production of flowers and fruit (Foolad and Lin, 2000). A dynamic syndrome is a physiological condition caused by low temperatures.Different variables affect the degree of injury, which is the temperature, exposure time, organ or tissue of the exposed plant and the physiological stage and temperature at which the plant was grown (Vallejos, 1979). Due to the low viability of the pollen, weak fruit set after a cold period could be (Charles and Harris, 1972). At two separate stages of growth, chilling sensitivity may occur, *i.e*. pollen formation (from meiosis to release of mature pollen) and pollen function (Zamir et al., 1982). The reproductive stages of plants with delayed flowering are affected by low temperature stress, which renders the pollen sterile and severely affects crop yield (Suzuki et al., 2008; Yadav, 2010). In addition, low temperatures limit the production of hilly plants in the agricultural sector and have a direct impact on the survival and geographical distribution of the plants. Plant growth and crop productivity are affected, leading to severe crop failure (Xin and Browse, 2001). Plants show differences in temperature resistance to freezing (<00C) and chilling (0-15°C).Temperate plants are tolerant to chilling, although some of them are also freezing tolerant, they can improve their freezing resistance by being subjected to non-freezing temperatures such as chilling, and this process is called cold acclimation (Levitt, 1980), which involves physiological and biochemical changes (Shinozaki and Yamaguchi-Shinozaki, 1996). During cold acclimatization, cell wall components are also altered. Acclimated cells show an elevation in the thickness and stiffness of phenolic compounds and wall-associated lipids present in the wall and cell wall (Fujikawa et al., 1999). The antioxidant properties of phenolic compounds can reduce the action of reactive oxygen species on lipid peroxidation (Blokhina et al., 2003). Furthermore, the accumulation of osmolytes in acclimated cells (such as sugar, proline and glucose) facilitates the elevation of endogenous solutes that can mitigate cellular dehydration (Xin and Browse, 2000).

Due to its adverse effects on plant growth and production, low temperature stress is an abiotic stress that has been broadly studied in plants, which reduces crop productivity. This is a protective adaptation for growing plants in different climatic areas from colder areas where the temperature is less desirable for crop cultivation (Badea and Basu, 2009). Most commercial tomato varieties, from seed germination to fruit growth, are sensitive to low temperatures (0 to 15°C) at all phages (Foolad and Lin, 2000; Zhang et al., 2010).It delays the onset, lowers the rate, and increases the dispersion of germination events during seed germination, resulting in the poor establishment of stands and crop output.In subsequent stages, low temperature stress results in lowering plant growth and development, poor flower growth and fruit set, and a substantial decrease in tomato fruit yield.By reducing plant growth, low temperature limits crop yield, with negative and erratic impacts on biomass accumulation (Bracale and Coraggio, 2003). Ercoli et al., 2010 have reported that low temperature stress inhibited plant growth, leaf area, root relative growth rate and reduction of dry weight. In contrast to non-stressed tomato control plants, plants grown under temperature stress have a significantly reduced shoot and root length, fresh and dry root, shoot and leaf area mass at 60 DAS (Khan et al., 2015; Meena et al., 2018). In watermelon cultivated under low temperature stress, decreased leaf area, seedling shoot and root fresh and dry weight and chlorophyll content were observed (Korkmaz et al., 2010; Meena et al., 2017, Meena et al., 2018). Growth parameters, including root fresh and dry weight, shoot fresh and dry weight, were decreased under low temperature stress (Sayyari et al., 2013; Meena et al., 2017). Low temperature induced tissue decoloration and increased water loss as a result of suppressed expression of genes usually active at normal temperatures (Saltveit and Morris, 1990). In addition to this, the number of dividing cells decreased rapidly during low temperatures (Lukatkin et al., 2012), while in apices and in the basal piece of young leaves, the mitotic index decreased. The growth of cells was impaired, leading to drastic changes in plant organs (Strauss et al., 2007).

3. Physiological responses to Low Temperature Stress

This section emphasizes various aspects of the effect of low temperatures on plant physiology and biochemical metabolism. Through changes in gas exchange, pigment content, chloroplast development and decrease in chlorophyll fluorescence, low temperature stress decreases photosynthesis capacity and efficiency (Farooq et al., 2008). Low temperature stress causes the total leaf chlorophyll content of the tomato plant to drop slightly (Iseri et al., 2013; Meena et al., 2018). Many studies have shown that cell membrane is the primary site of tomato chilling injury (Khan et al., 2015). In tomatoes with decreasing temperature, low temperature stress significantly decreases the content of chlorophyll (Esra et al., 2010; Meena et al., 2018) and photosynthetic characteristics (internal CO_2 concentration, net photosynthetic rate, stomatal conductance and transpiration rate) (Khan et al., 2015). Cold stress damages cell membranes in two ways: disruption of the structure of protein lipids, denaturation of proteins, and leakage of solutes, indicating the variability of the membrane. Because of this, the fatty acids become unsaturated and the membrane's lipid/protein ratio changes under low temperature stress, which eventually affects the fluidity and structure of the membrane. The stability of the membrane also leads to free electron leakage and the production of reactive oxygen species (Khan et al., 2015). Cold stress leads to a significant increase in ion leakage through membranes compared to tomato control plants (Khan et al., 2015). The response of the plant to the low temperature varies from species to species and varies within the same family of plants. However, irrespective of the complexity of plant species, the common mechanism used by plants to cope with low temperature stress changes in membrane lipid composition to protect the stability and integrity of the membrane. In response to cold stress, a considerable accumulation of soluble sugars has also been seen. The increased level of unsaturation of membrane lipid fatty acids was a common effect of low temperature stress (Zhu et al., 2007; Badea and Basu, 2009). In plants exposed to low temperatures, chilling stress often causes inhibition of water absorption and water loss, leading to symptoms of water stress in plants.Water loss is associated with membrane loss or membrane transition from a normal fluid state to a small, less fluid, semi-crystalline state (Wright, 1974). A quantitative indicator of the water status of the plant is the relative water content (RWC). Wilting during and after exposure to low temperatures is the most visible symptom. Leaf wilting and curling tend to be less pronounced in the acclimatized community, associated with lower RWC (observational interpretation). Low temperatures cause a major decrease in RWC in tomato plants (Iseri et al., 2013; Meena et al., 2018).

4. Biochemical Responses to Low Temperature stress

4.1. Osmoprotectant response to low temperature stress

This section emphasizes various aspects of the impact of low temperatures on plant physiology and biochemical metabolism. Via changes in gas exchange, pigment content, chloroplast production and decrease in chlorophyll fluorescence, low temperature stress decreases photosynthesis ability and performance (Farooq et al., 2008). Low temperature stress causes the total leaf chlorophyll content of the tomato plant to drop slightly (Iseri et al., 2013; Meena et al., 2018). Many studies have shown that the cell membrane is the primary site of tomato chilling injury (Khan et al., 2015). Low temperature stress significantly decreases the content of chlorophyll (Esra et al., 2010; Meena et al., 2018) and photosynthetic attributes in tomatoes with decreasing temperature (internal CO_2 concentration, net photosynthetic rate, stomatal conductance and transpiration rate) (Khan et al., 2015). Cold stress damages cell membranes in two ways: disruption of the structure of protein lipids, denaturation of proteins, and leakage of solutes reflecting the variability of the membrane. Because of this, the fatty acids become unsaturated and the membrane's lipid/protein ratio changes under low temperature stress, which ultimately affects the fluidity and structure of the membrane. The stability of the membrane also contributes to free electron leakage and the formation of reactive oxygen species (Khan et al., 2015). Cold stress contributes to a large increase in ion leakage across membranes relative to tomato control plants (Khan et al., 2015). The response of the plant to the low temperature varies from species to species and varies within the same family of plants. However, irrespective of the variety of plant organisms, the typical mechanism used by plants to cope with low temperature stress changes in membrane lipid composition to maintain the stability and integrity of the membrane. In response to cold stress, a significant accumulation of soluble sugars has also been seen. The increased level of unsaturation of membrane lipid fatty acids was a common effect of low temperature stress (Zhu et al., 2007). In plants exposed to low temperatures, chilling stress often causes inhibition of water absorption and water loss, leading to symptoms of water stress in plants. Water loss is associated with membrane loss or membrane transition from a normal fluid state to a small, less fluid, semi-crystalline state (Wright, 1974). A quantitative indicator of the water status of the plant is the relative water content (RWC). Wilting during and after exposure to low temperatures is the most visible symptom. Leaf wilting and curling tend to be less pronounced in the acclimatized community, associated with lower RWC (observational interpretation). Low temperatures cause a major decrease in RWC in tomato plants (Iseri et al., 2013; Meena et al., 2018).

Another adaptive mechanism in plants subjected to extreme temperatures is osmoprotectant accumulation, as primary metabolites are directly involved in osmotic change. The accumulation of Proline has been shown by the stress faced by plants (Manivannam et al., 2007). It has been suggested that by functioning as a cellular osmotic regulator between cytoplasm and vacuole, proline protects plants and also detoxifies reactive oxygen species (ROS), thus maintaining membrane integrity and stabilizing antioxidant enzymes (Claussen, 2005). Positive associations between endogenous proline accumulation and enhanced cold tolerance in chilling sensitive plants have been identified (Korkmaz et al., 2010; Zhao et al., 2009). By functioning as a free radical scavenger (Mansour, 1998), cytosolic proline helps to preserve osmotic modification, membrane stability and decreases the destructive effects of ROS because proline builds up in plants at cold temperatures (Yadegari et al., 2007; Koc et al., 2010). The potential role of proline accumulation and acclimation of H_2O_2 has been investigated (Iseri et al., 2013). Proline accumulates in tomato roots of cold stressed acclimatized plants. In plants that were given low temperature stress, higher leaf proline content was seen. With a decrease in tomato temperature (Khan et al., 2015) and pepper temperature, the amount increased (Esra et al., 2010)

4.2. Reactive oxygen species response to stress

It is safe to assume that there are two ways for reactive oxygen species (ROS) to be dangerous when formed in excess and useful at lower concentrations. ROS plays an important role at beneficial levels in managing plant growth and development as well as in acclimatizing the environment (Quan et al., 2008). One significant effect of cold and other abiotic stress is the induction of lipid peroxidation in plants due to excessive ROS production (Miller et al., 2008; Gill and Tuteja, 2010; Ahmad et al., 2010; Mutlu et al., 2013). Species of cold responsive plants, including major vegetable crops such as cucumber, tomato, eggplant and potato, suffer from chilling injury at temperatures below 10-12°C (Duan et al., 2012). Under cold stress, imbalances in metabolic processes, such as hydrogen peroxide, hydroxyl radical, superoxide and singlet oxygen, can result in increased ROS accumulation (Hung et al., 2005; Goud and Kchole, 2011). By over-production of ROS which causes protein oxidation, membrane lipid peroxidation, and damage to various macromolecules, cell structures, cell membrane, photosynthetic apparatus, DNA and RNA damage. Cold stress reduced plant growth, leading to cell damage and ultimately cell death (Liu et al., 2013; Goud and Kachole, 2011). Many plants species have developed various mechanisms to deal with low temperature stress in this regard (environment stress). Therefore, plants have developed enzymatic and non-enzymatic antioxidant defense mechanisms to scavenge ROS. To protect plant cells, antioxidant enzymes including catalase, superoxide dismutase and ascorbate peroxidase quench ROS. In addition, many non-enzymatic antioxidants such as tocopherols, carotenoids, ascorbic acid and osmoprotectants have a significant role to play in this regard (Ahmad et al., 2013) and (Farooq et al., 2008, Gautam and Singh, 2009; Ahmad et al., 2013). It is thought that differential activation of the antioxidant system confers cold sensitivity and crop plant improvement. Many tropical or subtropical origin species are injured at temperatures below 10°C and frequently exhibit different symptoms of chilling injury as a result of failure to adapt to non-freezing low tomato temperatures (Sanghera et al., 2011; Khan et al., 2015). Abiotic stresses lead to the accumulation of ROS, which can be a source of oxidative injury in plants. Initially, ROS were considered as toxic molecules and products of aerobic metabolism, found in several subcellular compartments. The metabolism of ROS is crucial in crop growth, development, adaptation, and existence under stressful environments (Mirza et al., 2020). Plants are subjected to various environmental stresses throughout their life cycle. Reactive oxygen species (ROS) play important roles in maintaining normal plant growth, and improving their tolerance to stress (Honglin et al., 2019).

4.3. Antioxidant enzymes response to low temperature stress

The quenching of ROS requires several antioxidant enzymes. Superoxide dismutase (SOD) reacts with radical superoxide and creates peroxide of hydrogen (H_2O_2) scavenged by peroxidases (POD) and catalase (CAT). To generate oxygen and water, CAT reacts with H_2O_2. Among the peroxidases, ascorbate peroxidases (APX) and glutathione peroxidase (GPX) are those that use ascorbate and glutathione as electron donors and contribute to the detoxification of H_2O_2 in plants (Orabi et al., 2015). Exposure of plants to cold stress results in excessive ROS production due to the restricted fixation of carbon dioxide in chloroplasts and the transport chain of mitochondrial electrons (Davidson and Schiestl, 2001; Suzuki and Mittler, 2006). Therefore, plants have developed complex defense mechanisms to cope with ROS-induced oxidative damage, including enzymatic antioxidants such as APX, SOD, CAT, GPX, GR, and non-enzymatic antioxidants such as glutathione and ascorbic acid (Kang and Saltveit, 2002; Erdal 2012; Erdal et al., 2015). As the temperature drops, the activity of antioxidant enzymes, *i.e.,* SOD, POX and Pet, increases dramatically. In addition, in the plants exposed to the lowest temperature (10/3°C), the highest values of SOD, POX and CAT were found. With the decrease in temperature levels, antioxidant enzyme values have increased (Khan et al., 2015). The typical effect of almost all stresses at any point of stress exposure is that they result in increased development of ROS, which can oxidize lipids, proteins and nucleic acids, resulting in cell-level deformity (Sanita and Gabbrielli, 1999). Plants synthesize antioxidant enzymes (SOD, CAT and POX) and osmoprotectant (proline) that quench excess ROS when excessive ROS is generated. Low temperature tension, on the other hand, shows increased development of ROS and malondialdehyde (MDA), used as a lipid peroxidation indicator (Liu et al., 2010). In order to protect against the injurious effects of ROS and maintain cellular redox homeostasis, plants have evolved many enzymatic and non-enzymatic mechanisms (Ahmad et al., 2012; Sabir et al., 2012; Mishra et al., 2014). Malondialdehyde (MDA) levels demonstrated oxidative damage caused by low temperature regulation and non-acclimatized plants. MDA persists in acclimatized plants around unstressed conditions, which indicates that acclimatization of hydrogen peroxide (H_2O_2) protects tissues against cold-induced lipid peroxidation (Apel and Hirt, 2004).The roots of acclimatized plants, the APX and CAT levels were found to be increased, while levels in unstressed plants remained unchanged (Iseri et al., 2013). Whereas, under low temperature stress, the H_2O_2 content in the roots of acclimatized plants was significantly lower than that of regulated and non-acclimatized plants in tomatoes. Under unfavorable or adverse conditions, ROS production exceeds the capacity of the antioxidant defense system. Both non-enzymatic and enzymatic components of the antioxidant defense system either detoxify or scavenge ROS and mitigate their deleterious effects.

5. Conclusion

Low temperature stress induces profound changes in morphology, physiology and biochemistry that adversely affect plant development, growth and ultimately yield. Tomato is very susceptible to cold stress and shows a decrease in overall growth, yield and parameters that contribute to quality. The reproductive process leading to enhanced flower abortion and fruit set is adversely affected by low temperature stress. Low temperature stress greatly decreases the quality of chlorophyll, photosynthetic characteristics and metabolic dysfunction.

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