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PLANT PHYSIOLOGY

Physiological Responses of Drought stress in Tomato: A Review

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Abstract

Tomato has important role in food and commercial utilization in the whole world. It is an undetached part of food due to its taste and nutritional value. It is full of minerals, vitamin and antibiotic characteristics. Climate change produces so many natural hazards such as abiotic and biotic stress in the plant. Drought is an important natural phenomenon which affects morphological, physiological, biochemical and yield attributes of plants leading to death. During water stress many physiological and molecular processes are disturbed such as root-shoot growth, water relation, mineral absorption, leaf expansion and orientation, stometal behavior, transpiration rate, photosynthesis and respiration rate, solute translocation, etc. Toxic elements such as reactive oxygen species (ROS) produced during stress period create oxidative damage to the cellular organization. Plants have its antioxidant system to scavenge such harmful element and accumulate osmoprotectants such as proline, glycien betaine, etc to maintain osmotic adjustment. All these and many more aspects have been discussed in case of tomato plants in this review.

Highlights

- Drought stress exerts physiological impact on various growth and developmental stages in tomato plants.
- Drought resistance mechanism, signal transduction and oxidative adjustment in tomato plants under drought stress are discussed.

Keywords: Antioxidant system, climate change, drought, tomato, reactive oxygen species

India is the second largest producer of tomato accounting for 10.58% of the world's production (Source: FAO Database 2011). The production of tomato in India is about 168.26 lakh tonnes in 2011 (Source: NHB Database 2011). According to the fifth assessment report of IPCC (2014), drought is the significant impact of current climate related extremes. In India, drought is a regular problem which affects agriculture production and life of animals and humans frequently. Of the total geographical area of India, two third parts receive rainfall less than 1000 mm which is not distributed equally. According to statistical review, India has only 40% water use efficiency of total existing irrigation projects. Around 68% of net sown area (140 million hectare) is affected by drought conditions and 50% of this area is known as severe region where drought regularly shows its affect (http://www.dsc.nrsc.gov.in). Tomato is sensitive to water scarcity and requires abundance of water for vegetative and reproductive growth, especially flowering and fruit enlargement stage (Rao *et al*. 2000). Stress is an adverse condition in which plant is influenced by external factors such as low and abundant water, high and low temperature, light which exert a disadvantageous effect. In water stress condition tomato crop is affected in various ways such as reduced growth and leaf surface area, flower shedding, mineral deficiency due to lack of absorption, reduction in fruit size, fruit splitting, puffiness and many physiological disorders related to calcium deficiency such as blossom end rot (BER), poor seed viability etc. (Kumar *et al*. 2012). There are many factors which affect the impact of drought on plants such as environmental and genotypic interaction, timing, severity and duration of water stress condition. Plants have an ability to cope the unfavorable environment, known as stress tolerance.

Effects of drought stress on tomato plant

Germination

Seed germination is very sensitive to environmental factors such as soil moisture, oxygen and light. According to Hsiao (1973), entire stages from seed germination to harvesting are very susceptible to drought stress in tomato. In seed germination of tomato water absorption is most important process, in which three phases occur. First phase is imbibition in which seed surface absorbs water, in second phase, hydration of cotyledons takes place, in third phase, radical emergence takes place followed by subsequent growth of seedling. Lower water potential reduces the water uptake and moisture content in first phase, increases the length of second phase and seed cannot enter in third phase (Bradford 1986). Low availability of soil moisture decreases seed germination and seedling growth (Gamze *et al*. 2005). According to Dodd and Donavan (1999), lower water potential during drought stress decreases germination percentage. Related research shows reduction or delay in germination of seed during low water availability at germination stage (Turk *et al*. 2004). In tomato seeds, most favorable germination is found at 50-57% of field capacity. Drought stress is also associated with increased salinity level which reduces seed germination in tomato. Foolad and Lin (1997) experimented with tomato seed germination and found reduction in seed germination due to the osmotic stress.

Water and mineral uptake

Solubilization and translocation of minerals are reduced in soil solution due to drought stress. According to Subramanian *et al.* (2006), nitrogen and phosphorous content decreases in root and shoot of tomato during water stress. Root nutrient uptake reduces due to less transpiration rate, stomatal closer and lower energy input (Baligar *et al.* 2001). Plant has many anatomical and physiological changes to reduce the effect of stress. Increase in root length and biomass are the good characteristics of drought tolerance. According to Wu and Cosgrove (2000), root: shoot ratio increases during water deficit condition. It facilitates increased capacity of plant to absorb more water and mineral. There are many changes in plant anatomy during drought stress such as lignifications, suberization and development of casparian bands (North and Nobel 2000, Aroca 2012).

Abscisic acid and stomatal behavior

Water stress stimulates biosynthesis and metabolism of abscisic acid (ABA) in root and shoot of plant. During drought stress, ABA concentration can increase up to 50 times in plant leaves (Taiz and Zeiger 2002). It is the responsible hormone for stomatal closer under water stress condition. Several researchers have shown that root system of plant sense soil water status (Davies and Zhang 1991). In water stress condition, root system increases ABA biosynthesis in tomato (Cornish and Radin 1990). Zeaxanthin epoxidase (ZEP) is an important component of ABA synthesis which catalyzes the synthesis of violaxanthin. According to Thompsom *et al.* (2000), root increases ZEP transcript level but not in leaves in tomato plants during drought stress. ABA has a significant role in signal transduction under water stress condition, it regulates stomatal behavior and reduces transpiration rate by closing stomata. Decrease in soil water status stimulates root growth of plant as compared to shoot. Root-shoot ratio of tomato plant is also regulated by ABA under water stress condition. According to Sharp *et al.* (1988), root growth is accelerated under low water potential while shoot length decreases.

Proline accumulation

Proline accumulation is a significant response of plant under drought stress. According to Shtereva *et al.* (2008), PEG induced drought stress increases endogenous proline concentration in tomato calli. According to Anjum *et al.* (2000), proline is a scavenger of OH^- radical and plays an important role in osmotic adjustment during oxidative stress. It reduces the damaging effect of ROS to the membrane lipid and protein, enzymes and DNA. Proline has an important role to sustain root growth under water stress condition. It accumulates in root growing zone and increases the activity of enzyme such as xyloglucan endotransglycosylase (XET) and the expansions which accelerate cell elongation by loosening of cell wall (Hartung *et al*. 1999).

Plant Growth and development

Drought stress is the combination of various types of stress so it shows very complex effect on plant growth and development process (Zlatev and Lidon, 2012). Due to drought stress, there is inhibition of cell division and enlargement leading to reduction in vegetative and reproductive growth. Leaf area and stem length get reduced due to decrease in cell size. Low level of soil water disturbs water relation in plant, which is directly related to uptake of water and mineral. It influences biochemical and metabolic changes in cellular organization, such as turgor pressure, membrane stability, reduction in cell size (Yordanov *et al*. 2003). Plant growth under stress condition depends on water availability, its use efficiency and the severity of stress level. Along with dehydration, influences of other related stress such as temperature, salt, oxidative stress and transpiration rate are also the main components which affect plant growth. Water use efficiency is affected by Leaf area ratio (LAR) and net assimilation rate (NAR), which are the main components of relative growth rate (RGR) (Van den Boogaard *et al*. 1997). Water loss by transpiration per unit time is also the main factor which influences water use efficiency and growth rate. Decreased leaf area ratio reduces the photosynthesizing area and finally growth rate. In the initial stages of water stress, root growth is accelerated. According to Hamblin *et al.* (1991) and Gorai *et al*. (2010), the relative biomass allocation to root system increases as compared to shoot. Reproductive stages in tomato such as flower and fruit setting are most sensitive to drought stress (Salter 1954). Water deficit condition decreases tomato growth cycle by accelerating different growth and development stages. According to Desclaux and Roumet (1996), plant developmental phase is stimulated to turn from vegetative to reproductive phase by the indication of drought stress.

Genetic responses

During drought stress several genes are activated in plants, leading to physiological and metabolic changes against the stress condition. According to Zhu *et al*. (1997), many plant genes and physiological mechanisms are concerned with response to water stress in plant system. Plant has specific quality to reduce the effect of drought stress by adaptation and escaping mechanism. Many scientists have observed that drought tolerance is complex mechanism in which several genes are involved; it is a polygenic trait. Stress induced genes regulate synthesis of plant hormone (ABA, ethelene), amino acids (proline) and accumulation of different types of protein (LEA, HSPs), osmolytes (mannitol, sorbitol, quercitol, pinitol, proline, glycine betaine, etc.) (Cushman and Bohnert, 2000). Drought induced genes are regulated by a specific signal transduction pathway which activates transcription factors. Activated genes during drought stress are involved in protection with creation of efficient antioxidant system by synthesis of enzyme i.e. superoxide dismutase, catalase, ascorbate reductase, glutathione reductase, etc. Drought stress alters gene expression and, therefore, the production of new proteins i.e., late embryogenesis abundant (LEA) and mRNAs. LEA proteins are strongly hydrophilic in nature and have a specific quality to retain water in tissue during water stress. These proteins also protect cell membrane.

Table1: Characteristics of six sequenced genes potentially involved in stress response in tomato

Name	Gene length (bp)	Functions	Descriptions	Reference
*erd*15	974	Defense protein	dehydratation induced protein	Kariola *et al*. (2006), Kiyosue *et al.* (1994)
*asr*2	811	Transcription factor	abscicic acid stress ripening 2	Finkelstein *et al*. (2002), Giombini *et al*. (2009)
*mkp*1	3605	Signal transduction	MAP kinase phosphatase	Jonak *et al.* (1999), Ulm *et al.* (2001)

*tas*14	746	Protein response and damage repair	abscisic acid and environmental stress-inducible protein	Parra *et al.* (1996), Godoy *et al.* (1994)
*tsw*12	891	Protein response and damage repair	non-specific lipid-transfer protein 1 precursor	Torres-Schumann *et al.* (1992), Treviño and O'Connell (1998)
*cip*1	3344	DNA synthesis, cell growth and division	zinc-finger protein CONSTANS interacting protein 1	Ben-Naim *et al.* (2006)

Source: Sacco *et al.* (2013)

Table 2: Photosynthetic parameters affected by water limitation in tomato plants

S.No.	Photosynthetic Parameter	Effects	Reference
1.	Net CO_2 assimilation rate	Decreased	Mäkelä *et al.* (1999), Srinivasa *et al.* (2000)
2.	Internal CO_2	Increased	Srinivasa *et al.* (2000)
3.	Stomatal conductance	Decreased	Mäkelä *et al.* (1999), Srinivasa *et al.* (2000)
4.	Transpiration	Decreased	Mäkelä *et al.* (1999),
5.	Rubisco activity	Decreased	Mäkelä *et al.* (2000)
6.	Electron transport rate	Decreased	Haupt *et al.* (2000)

Source: Ather and Ashraf (2005)

Senescence

Senescence program is accelerated by biotic and abiotic stresses. Oxidative degradation in lipid, protein and DNA content by ROS stimulates ageing and reduces the life duration of plant. In tomato, water stress increases the production of proteases which induce senescence by degradation of protein into amino acid. According to Zhu (2001), protein content of plant decreases during drought stress because of damaging effect of reactive oxygen species (ROS) to the amino acids. Growth retardants such as abscisic acid (ABA) and ethylene production increases during drought stress in tomato plants which lead to senescence, abscission and program cell death in response to biotic and abiotic stress.

Photosynthesis

Water is the important component in cellular structure and has very significant role in all metabolic processes. Photosynthesis, pigments and plastids are affected by less water condition; it damages cell membrane structure (Levitt 1980). Drought stress causes reduction in photosynthetic process; it leads to deterioration of thylakoid membranes and substantial damage to photosynthetic pigments (Huseynova *et al*. 2009, Anjum *et al*. 2011). Chlorophyll content also decreases under drought stress, it may be because of reduction in activity of the enzymes involved in chlorophyll synthesis (Ashraf and Karim 1991), or may be due to increase in chlorophyll break down (Kaewsuksaeng, 2011). Drought stress leads to dehydration of mesophyll cell and reduction in water use efficiency, which decreases photosynthetic rate.

Dry matter production

Water availability is the key factor for dry matter production in plant. Low water availability decreases water and nutrient uptake, photosynthetic rate and translocation of photo assimilates. An experiment done by Nahar *et al.* (2011) with four tomato genotype showed reduction in dry matter production under water deficit condition, similar to those reported by Aragon (1988).

Lycopene content

Lycopene is a key quality parameter in tomato which plays an important role in biosynthesis of carotenoids. It is responsible for red color in tomato fruit and processing product. Lycopene acts as an antioxidant. It has a specific role in defense mechanism against environmental stress by scavenging peroxyl radicals and quenching singlet oxygen. An experiment done by Giannakoula *et al.* (2013) estimated quality parameter in tomato genotypes under drought stress condition and there was a significant increase in lycopene content during water and salinity stress.

Yield

Drought stress is a serious environmental stress which affects agriculture productivity and yield. It is an important factor, which harms more than 50% of crop yield worldwide (Bray *et al*. 2000; Wang *et al*. 2003). According to Kramer (1969), drought stress affects physiological process of plant at different stages and reduces the quality and quantity of yield. Uptake of mineral nutrition also reduces under low soil water condition i.e., nitrogen, sodium, sulphur, potassium, magnesium and calcium (Nahar and Gretzmacher, 2002). According to Giardini *et al.* (1988), under low water condition, tomato plant has reduced yield and fruit size. Many scientific studies have revealed that low water availability decreases number of leaves, branches, flowers and fruits in tomato cultivars. Fruit quality, shape, diameter and weight decreases under drought stress as compared to the normal condition. Experimental studies show significant reduction in number of seeds per tomato fruit under water stress condition. According to Simiciklas *et al.* (1989) drought stress during seed formation or seed filling reduces seedling vigour and germination in next generation.

Drought resistance mechanisms

Plant has a special quality to survive in adverse condition. Tomato plants also produce physiological and biochemical changes at different levels to adapt tolerance against stress environment. Drought escape, avoidance, tolerance are the main mechanisms of drought resistance (Levitt, 1972). In tomato, various factors involved in drought tolerance process are root system, water relation, turgor maintenance, cuticle thickness, osmotic adjustment, antioxidant defense system, etc. Drought escape is the process of drought tolerance in which plant completes it life cycle before the beginning of drought. Drought avoidance is the drought tolerance mechanism in which plant has ability to maintain high plant water status in tissue (Blum 2005). Reduced leaf area, increased stomatal and cuticular resistance, less and small stomata, vertical leaf orientation are the important physiological characters of drought resistance which are involved to minimize the water loss by plant. More active and deeper root system, higher root–shoot ratios increases water uptake from soil solution during low water availability. These characters are well associated with drought stress resistance (Farooq *et al*. 2012).

Signal Transduction during drought stress

Plant cell membrane perceives signal from water stress environment leading to signal transduction cascade to express various types of genes and molecules in tomato. ABA has important role in signal transduction pathway, it is known as stress hormone. In signal transduction pathways number of transcription factors and secondary molecules are involved such as calmodulins, G-proteins, Mitogen activated protein kinases (MAPK), calcium dependent protein kinases (CDPK) in response to water stress (Shinozaki and Yamaguchi-Shinozaki 2007). In plant cell, Ca^{2+} level increases in response to water stress which functions as a second messenger during stomata closer. ABA accumulation is the main feature of drought stress, osmotic stress gene may be ABA dependent or independent (Joshi and Karan, 2013). According to Trouverie *et al.* (2003), the *RD29A* gene is the best example of excellent paradigm of ABA-dependent and independent gene regulation. ABA dependent factors are involved in the activation of DRE by DREB2A in response to drought stress (Xiong *et al.* 2001). Ethylene production is also involved in drought stress induced signal transduction pathway. During drought stress an increased level of ethylene is found in tomato leaves leading to reduction in leaf growth (Sobeih *et al.* 2004).

Oxidative stress and scavenging system

Oxidative stress is the common feature of water deficit stress. According to Larson (1988), plants have specific antioxidant and scavenging system to protect under stress condition. It is well known by scientific research that drought stress enhances the production of ROS and redox imbalance in plant cell. Drought stress produces excess amount of ROS including singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($OH^{\bullet}$), this process is known as oxidative burst. It causes damaging effect on cell structure and metabolism; and creates a different type of stress known as oxidative stress. ROS are produced in chloroplast, mitochondria and peroxisoms, and its production enhances during drought stress which causes oxidative damage of cell membrane, lipid peroxidation, disrupt electron transport system (Asada, 1999). Excess amount of ROS has a consequence on oxidative damage to cellular molecule such as protein, lipids and DNA. ROS also has a specific role in responses to abiotic stress and plant developmental process by functioning as signaling molecules (Foyer and Noctor, 2005). According to Miller *et al.* (2010), ROS plays dual role in plant metabolism during abiotic stress, in high concentration it functions as toxic byproduct which has damaging effect to the cell, and in low concentration, it has an important role as signal transduction molecule. Plant has specific antioxidant mechanism and scavenging system for adaptation to drought stress. It has two types of mechanism: enzymatic and non enzymatic. Enzymatic antioxidants include superoxide dismutase, catalase, ascorbate reductase, glutathione reductase, monohydroascorbate reductase, dehydroascorbate reductase, guaiacole peroxides, while non enzymatic antioxidants include carotenoides, ascorbate, glutathione etc. Sánchez-Rodríguez *et al.* (2010) in their experiment with five tomato genotypes under drought stress found that genotypes showed higher tolerance capacity by strong antioxidant defense system. Some cultivars had increased H_2O_2 and MDA content during low water condition.

Osmotic Adjustment

According to Boyer *et al.* (2008), plant accumulates osmotically active solutes inside the cell during drought stress which causes reduction in cell water potential. Plants maintain water absorption and cellular turgor pressure during water stress by osmotic adjustment. According to Cattivelli *et al.* (2008), this process keeps up higher photosynthetic rate and increased growth during water scarcity. An experiment done by Nahar *et al.* (2011) with five tomato genotypes to evaluate osmotic adjustment and fruit quality under drought stress showed that concentration of proline, glucose, fructose, sucrose, malic acid, ascorbic acid and citric acid increased significantly. Compatible solutes such as fructose, sucrose, glucose, glycerol, mannitol, sorbitol, quercitol, pinitol, proline and glycine betaine are synthesized and accumulated by plants and these organic solutes play an important role in osmotic adjustment. Proline reduces proteolytic damage of folded protein organization by reducing the denaturation and increases cell membrane stability. Acording to Claussen (2005), proline has a specific role in osmotic adjustment and scavenging of hydroxyl radical during stress environment. These intracellular solutes maintain turgor pressure and decrease water potential as compared to surrounding environment thereby increasing water uptake.

Conclusion

Frequent drought is the major consequence of global climate change. Tomato is sensitive to water deficit condition during each stage of life cycle. Physiological, biochemical, molecular changes occur in plant during stress condition. Low water availability reduces metabolic process such as water and mineral absorption, rate of photosynthesis, dry matter production and yield. Oxidative damage of cellular organization occurs during drought stress by the production reactive oxygen species. Plant has specific innate anti oxidant mechanism to mitigate the effect of water stress. Physiological and molecular changes make plants resistant to drought stress. Screening of various drought resistant genotypes can be useful in breeding program for release of drought resistant varieties of tomato. Some chemicals with antioxidant property are also involved in mitigation of drought stress by changing physiological paradigms.

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