Original Research Article

Effect of LEA Gene on Tomato in response to Drought Stress

Sonam Arya[1*], Aastha[2], Vishakha Burman[2], Khayti Lehri[2], Sandeep Kmar[2], Naresh Pratap Singh[3], Nisha Dhillon[1], Shalu Choudhary[1] and Vaishali[2]

[1]Department of Applied Education and Health Sciences, India
[2]Department of Agricultural Biotechnology, College of Agriculture, S.V.P.U.A.T, Meerut, India
[3]Departmentof Commercial Biotechnology, College of Biotechnology, S.V.P.A.T, Meerut, India
*Corresponding author

A B S T R A C T

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Tomato is one of the most widely grown and popular crop consumed in large scale. Tomato is also known for having high quantity of antioxidant property and beneficial for curing the different types of diseases. Due to the changes in environmental conditions different abiotic stresses like drought causes great harm to our crops. The plant undergoes the morphological, physiological and biochemical changes such as reduction in photosynthesis activity, decrease in CO_2 content, decrease in water content, leaf curling, proline accumulation etc. There are several genes specifically involved in stress response have been identified. The LEA proteins accumulate under stress conditions such as drought, salinity and low temperatures. Numerous transgenic studies revealed a positive effect of LEA gene expression on plant stress tolerance. Most studies report enhanced growth rates and reduced wilting of the aerial parts under stress under laboratory conditions and in some field trials, demonstrating a real potential of LEA proteins in engineering crops more tolerant to stress. Apart from agronomical purposes, LEA proteins could be useful for other biotechnological applications in relation to their capacity to prevent aggregation of proteins. In this review the effect of drought on various plant growth processes will be discussed. This study will be useful in understanding the molecular mechanism of stress tolerance and will enhance the productivity of crop.

Introduction

Tomato (*Lycopersicon esculentum L*) is one of the most universally known, popular, nutritious and widely grown vegetable in the world. The cultivated tomato is the second most consumed vegetable worldwide and a well-studied crop species in terms of genetics, genomics, and breeding. It is an annual herb, belongs to the Solanaceae family and *Lycopersicon* genus (Chaudhury, 1979). The largest tomato-producing country is China (with approximately 34 million tons of production), followed by the United States, Turkey, India, and Italy (Mateljan *et al.,* 2017). Regardless of its name, the tomato is a wonderfully popular and versatile food that comes in over a thousand different varieties that vary in shape, size, and color. Tomatoes are widely known for their outstanding antioxidant content and their oftentimes-rich concentration of lycopene. Lycopene is a carotenoid pigment that has long been associated with the deep red color of many

tomatoes. Researchers have recently found an important connection between lycopene, its antioxidant properties, and bone health. Intake of tomatoes has long been linked to heart health (Mateljan *et al.,* 2017). Fresh tomatoes and tomato extracts have been shown to help lower total cholesterol, LDL cholesterol, and triglycerides. It plays a vital role in providing vitamin C, carotenoids, flavonoids and phenolics for human diet (Horneburg and Myers, 2012).

Responses of drought stress in tomato

Abiotic stresses such as heat, cold, drought, salinity, nutrient deficiency, ozone, heavy metals, UV-B radiation, visible light, chemical toxicity and oxidative stress are serious intimidation to agriculture (Abu *et al.,* 2010). The significant changes in major environmental conditions, like water availability, salt concentration and temperature, limit the growth, development, productivity and reduce potential crop yields by upto 70% (Agarwal *et al.,* 2006). Abiotic stress reactions, especially to water deficiency, high temperature and high level of salts are complex morphological and physiological phenomena in plants. Of all abiotic stresses, drought is regarded as the most damaging. Further, the complex nature of drought tolerance limits its management through conventional breeding methods. Hussain and Syed, (2011) reported that plant growth and productivity are greatly affected by abiotic stresses such as drought, salinity, and temperature.

Drought stress is closely associated with high temperature stress and, together they can affect 64% of the global land area (Cramer *et al.,* 2011). Water is a major factor influencing plant productivity, so when water is insufficient in the soil, and atmospheric condition cause a continuous loss of water, drought stress occurs. In plants, water is

essential for the photosynthesis reaction- a reaction process that is mainly affected by physiological pathways and environmental factors (Shao *et al.,* 2007).

Plants adapt to survive and to maintain their growth and development. Many mechanisms may be involved and these mechanisms may include drought avoidance and drought tolerance (Mishra *et al.,* 2011). Drought avoidance is the ability of plants to retain a high tissue water potential either through increased water absorption from roots or reduced evapo-transpiration from their aerial parts, while drought tolerance refers to the plants ability to sustain normal function even at a low water potential (Mishra *et al.,* 2011). Drought can affect the plants morphology, physiology and biochemistry, leading to a reduction in plant growth and productivity (Thapa *et al.,* 2001). Different plant species have different family-specific responses to cope with drought. However, there are some common responses such as slowed cell division and gene expression leading to altered physiological reactions, for example, a reduction in photosynthesis (Thapa *et al.,* 2011).

When water stress was introduce, photosynthesis and transpiration might be inhibited but will gradually recover during on-going stress even under low leaf water potential (Shinohara *et al.,* 1995). Drought stress may induce morphological, physiological, and biochemical changes in plant (Mishra *et al.,* 2011) through reduction in tissue water content and water potential (Garcia *et al.,* 2007).The effect on shoot and root growth and development, limit photosynthetic activity by decreasing CO_2 influx, decrease in carboxylation, and electron transport chain activities of the chloroplasts in the mesophyll cells (Akinci, 1997). It also affects many other metabolic pathways, mineral uptake, membrane

structure, stomatal structural changes, conductance, and CO_2 uptake (Akinci, 1997). Water deficit in plants causes the closure of stomata that decreases both transpiration and photosynthesis in many plant species (Fatemy *et al.,* 1985). Water stress results in stomatal closure, reduction in transpiration rates, decrease in the water potential of plant tissues, decrease in photosynthesis and growth inhibition, accumulation of ABA, proline, mannitol, sorbitol, formation of radical scavenging compounds (ascorbate, glutathione, a-tocopherol, etc.), and synthesis of new proteins and mRNAs. Besides these physiological responses, plants also undergo morphological changes (Lichtenthaler *et al.,* 1981).

Morphological responses

Generally under stress, plant growth is reduced and this reduction is manifested as a reduction in stem elongation, leaf expansion and numbers of leaves (Sanchez-Rodrriguez *et al.,* 2010). Drought may cause a significant reduction in leaf area but root growth may be maintained in order to extract more water from deeper soil layers (Mishra *et al.,* 2011). When plants are waterlogged, root biomass is greatly decreased (Horchani *et al.,* 2008). After a period of exposure to severe stress, observers note wilting, leaf curling and rapid senescence in the old leaves, leading to plant death (Sairam *et al.,* 2008).

Physiological responses

It was reported that there is a significant reduction in leaf relative water content (LRWC) in tomatoes under water stress(Yuan *et al.,* 2010). This restriction in plant water supply is probably caused by an oxygen deficiency in the root zone, which then disturbs the metabolic activity of the roots. Some plants have the ability to adopt coping mechanisms for water stress. Reducing water loss, which will help maintain water potential, is a means of overcoming water stress (Sanchez-Rodriguez *et al.,* 2010). This mechanism is termed osmotic adjustment. This metabolic process involves the accumulation of compatible osmolytes or osmo-protectants such as organic solutes, amino acids, polyamines and quaternary ammonium compounds (QAC), and incurs energy costs (Sanchez-Rodriguez *et al.,* 2010).

Features of photosynthesis such as photosynthetic rate, stomatal conductance and intercellular CO_2 concentration are reported to be significantly lowered under drought conditions (Mishra *et al.,* 2011). When there is a water deficit, the photosynthetic rate is lowered directly via a reduction in internal CO_2 supply or lowered indirectly through the inhibition of photosynthetic enzymes (Haupt-Herting & Fock, 2000).

Biochemical responses

Proline is an amino acid that contributes to osmotic adjustment. Proline has several major functions including mediating osmotic adjustment, protecting protein structures from denaturation, stabilising cell membranes by interacting with phospholipids, scavenging ROS and serving as energy and nitrogen sources (Sanchez-Rodriguez *et al.,* 2010). Some authors have reported that high drought stress tolerant plants often have high proline concentrations. Under drought stress, proline biosynthesis and accumulation may be associated with the detoxification of ROS, a reduction in water potential and a reduction in photosynthesis rates (Thapa *et al.,* 2011). Proline accumulation in plants may be caused by either the activation of enzymes of proline biosynthesis (P5C synthase) or the inactivation of proline degradation (Reddy *et al.,* 2004). Reddy *et al.,* (2004) suggested that

proline can protect membranes and proteins even when LRWC was decreased during drought stress.

Phenolic compounds significantly increased under severe stress conditions. Phenol compounds particularly flavonoids and anthocyanins, because of their strong antioxidant nature, trap free antioxidants and reduce oxidative stress. They also reduce the damage by controlling oxidation macromolecules and damaged DNA (Sunka *et al.,* 2003).

Secondary metabolic products are ubiquitous in the plant kingdom; particularly, their intensity often presents in stress situations. Phenolic compounds, widely distributed in higher plants, belong to one of the major classes of secondary metabolites including lignins, flavonols, iso flavonoids and anthocyanins (Vogt *et al.,* 2010). These compounds contribute many important functional aspects of plant life such as UV sunscreens, pigments signaling. Additionally, accumulation of phenolic compounds is stimulated by biotic and abiotic responses. Tomato consumption has recently been demonstrated to be beneficial to human health, because of its content of bioactive compounds such as carotenoids, β-carotene (precursor of vitamin A), ascorbic acid (vitamin C), phenolic compounds namely flavonoids and phenolic acids, tocopherols (vitamin E) and many essential nutrients (Soto-Zamora, *et al.,* 2005).

The drought tolerance mechanism controlled by endogenous phenolic compounds is observed in many plants, but it differs among species (Akula *et al.,* 2011). In rice, some compounds, mainly phenolic acids and anthocyanins, have been detected and examined for their bioactivities in germinated stages and under normal growth status (Walter *et al.,* 2013).

Genetic responses

Many of the genes that are known to respond to drought stress have been identified, and the products of these genes can be classified into two groups (Yamaguch-Shinozaki and Shinozaki, 2006). The first group includes proteins that probably directly protect against stress such as enzymes for osmolyte biosynthesis, LEA proteins, and detoxification enzymes. The second group consists of proteins involved in the regulation of gene expression and signal transduction of stress responses, such as transcription factors (TF), protein kinases, protein phosphatases, and enzymes involved in biosynthesis of signaling molecules.

In many plants that adapt to water stress, a set of genes are transcriptionally activated, leading to accumulation of new proteins in seeds, vegetative organs and provide greater tolerance to drought. Proteins termed LEA (Late Embryonic Abundant), which were first characterized in cotton (*Gossypium hirsutum*), are a set of proteins that accumulate in embryos late in seed development (Xu *et al.,* 1996) where they are associated with acquisition of desiccation tolerance in maturing seeds. These proteins are also found in vegetative tissues in response to exogenous ABA, as well as osmotic and dehydration stress at any stage of plant development (Baker *et al.,* 1988). At least six groups of LEA proteins have been categorized by virtue of the similarity in their deduced amino acid sequences (Wang *et al.,* 2006).

Their hydrophilic nature and high solubility indicate that the proteins are maintained in the cytosol, where they are assumed to function as chaperone-like protective molecules to combat cellular damage (Umezewa *et al.,* 2006) and to act as hydrophilins, retaining water (Reys *et al.,*

2008) during dehydration. An association between tolerance to drought stress and these groups of proteins has been observed in some crop plants.

LEA gene family

LEA stands for late embryogenesis abundant, as coined by Galau *et al.,* (1986). Their name reflects the fact that the proteins originally described are expressed at high levels during the later stages of embryo development (post-abscission) in plant seeds. In plants, most of LEA proteins and their mRNAs accumulate to high concentrations in embryo tissues during the last stages of seed development when desiccation occurs (Hand, 2011). Members of the LEA family seem to be ubiquitous in the plant kingdom. Since their first description, hundreds of LEA proteins from vascular to nonvascular plants have been isolated. Their presence has been confirmed not only in angiosperms and gymnosperms (Bartels, 2005) but also in seedless vascular plants (e.g. *Selaginella*) (Alpert, 2005), bryophytes (e.g. *Tortula, Physcomitrella*) (Oliver, 2004), pteridophytes (e.g. ferns) (Reynolds, 1993) and algae (Honjoh, 1995).In blueberry (*Vacinium spp.*), the dehydrins were found to accumulate in response to changes in ABA levels during drought stress (Panta *et al.,* 2001). LEA genes, when over-expressed in rice (Xiao *et al.,* 2007), tobacco (*Nicotiana tabacum*) (Wang *et al.,* 2006), and *Arabidopsis thaliana* (Figueras *et al.,* 2004) led to drought tolerance in transgenic plants. Although the specific roles of the LEA proteins are not known, it is clear that they are regulated by ABA and cellular water loss.

LEA protein groups 1, 2 and 3 were identified, and members of each group were categorised by the presence of particular sequence motifs (Dure *et al.,* 1989): Group 1 LEA proteins (Pfam 00477) are mostly present in plants and they contain at least one copy of a 20 amino acid motif and confers tolerance to osmotic stress in yeast (Swire-Clark *et al.,* 1999). Group 2 LEA proteins or dehydrins (Pfam 00257) are also found in algae and share a common K-segment present in one or several copies; many dehydrins also contain an S-segment (polyserine stretch) that can undergo extensive phosphorylation and a Y-domain (DEYGNP), similar to the nucleotide-binding site of plant and bacterial chaperones. Group 3 LEA proteins (Pfam 02987), also found in nematodes and prokaryotes, contain at least one copy of a 11 amino acid motif. Also, the group 3 LEA protein of rice has been found to induce resistance to drought when over-expressed transgenically (Xiao *et al.,* 2007).

Studies have shown the great potential of LEA in controlling stress as reported by several authors. Transgenic wheat and oat expressing HVA1, an LEA protein, showed increased desiccation tolerance, biomass productivity, and water use efficiency under high salt, osmotic, or drought conditions via membrane protection (Babu *et al.,* 2004). Accumulation of Arabidopsis AtRAB28 (LEA V) protein through transgenic approach improved the germination rate under standard conditions or salt and osmotic stress (Borell *et al.,* 2005). Rapeseed (*Brassica napus*) LEA III gene MEleaN4 introduced into Chinese cabbage (*Brassica campestris*) or lettuce (*Lactuca sativa L.*) resulted in improved drought tolerance (Park *et al.,* 2005). The constitutive expression of maize dehydrin rab17 gene in transgenic Arabidopsis increased the sugar and proline contents; in addition, these plants showed more tolerance to drought conditions and recovered faster from drought stress than non-transformed control plants (Figueras *et al.,* 2004).

Transgenic approaches have shown that over-expression of LEA proteins from different

species in Arabidopsis, tobacco, rice, wheat, maize, lettuce or cabbage produces improve abiotic stress resistant phenotypes (Guo, 2013). However, the precise molecular function of LEA proteins is still unclear and so far LEA proteins have been suggested to act as stabilizers, hydration buffers, membrane protectants, antioxidants, organic glass formers and/or ion chelators (Tunnacliffe, 2007). LEA proteins have the capacity to protect target proteins from inactivation and aggregation during water stress. A role in protein stabilization is supported by the fact that some LEA proteins preserve enzyme activity in vitro after partial dehydration, desiccation or freezing (Grelet, 2005). Apart from agronomical purposes, LEA proteins could be useful for other biotechnological applications in relation to their capacity to prevent aggregation of proteins. (Boudet *et al.,* 2006).

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