



Genetic and Microbial Insights into Drought Stress Alleviation in Tomato (*Solanum lycopersicum* L.)[†]

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Abstract: Drought is a significant environmental stress that severely affects the development, productivity, and overall quality of various key crops. Tomato production is globally significant due to its economic importance and is considered the second horticultural crop produced in terms of yield and consumption worldwide, and yet, it is facing challenges posed by drought in agriculture. Drought stress negatively affects various characteristics of tomato plants, including physiological, genetic, biochemical, and morphological traits, leading to reduced seed production and fruit quality, and it also poses threat towards significant yield loss. In response to the need to mitigate the impacts of drought stress on tomato plants, the focus is on the assessment of the delicate interplay between genetic variables and microbial interactions. Some key genes, such as ABA-responsive genes, transcription factor genes, aquaporin genes, ROS-related genes, etc., and their function in drought tolerance in tomato plants have been discovered and analyzed to understand their role in stress adaptation. Additionally, microbial interactions, notably with plant growth-promoting rhizobacteria (PGPR), mycorrhizal fungi, and *Pseudomonas*, have emerged as key components in the context of drought stress alleviation. Mycorrhizal fungi form symbiotic relationships with plant roots, expanding the root system's reach and improving water and nutrient availability. On the other hand, certain microorganisms, like *Bacillus subtilis*, produce antioxidants such as catalase and superoxide dismutase, which scavenge reactive oxygen species (ROS), protect plant cells, and enhance resistance to oxidative damage during drought. Overall, this study emphasizes existing information on molecular principles underpinning stress tolerance and underscores the relevance of microbial-assisted stress amelioration and the interplay between genetic variables and microbial populations in relieving drought in tomato.

Keywords: drought; resistance; sustainability; drought tolerance; genetic variables; microbial insights



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1. Introduction

Drought stress poses a significant challenge to global tomato (*Solanum lycopersicum* L.) production, potentially resulting in up to 50% yield losses due to factors such as inadequate rainfall, elevated temperatures, and low soil moisture. Genetic and microbial factors collectively influence drought tolerance in tomatoes. Genetic determinants include the expression of drought-responsive genes, accumulation of compatible solutes, and water transport regulation. Key genes enhancing drought tolerance include DREB1A, a transcription factor activating drought-responsive genes, PAD4, which produces protective proline, LEA genes for protein stabilization, and P5CS for proline synthesis.

Additionally, genes like MdEPF2, cwInv, AtGAMT1, SIADL1, ATHB-7, SIPIP2;1, SIPIP2;7, SIPIP2;5, osmotin, TAS14, SIMAPK3, and SIJUB1 contribute to drought resistance

in tomatoes. Plant growth-promoting bacteria (PGPB) stimulate growth and aid drought tolerance by hormone production, inhibition of harmful microbes, nutrient enhancement, and improved water relations. Biofertilizers, housing beneficial microorganisms, enrich soil quality and nutrient availability, further enhancing drought resistance.

Understanding the interplay of these genetic and microbial elements is crucial for developing drought-resistant tomato cultivars, ultimately promoting sustainable agriculture by mitigating drought's adverse effects on crop yields.

2. Genetic Basis of Drought Tolerance in Tomatoes

2.1. ABA-Responsive Genes

ABA is an important plant hormone that plays a significant role in drought tolerance and stress response. When plants experience drought stress, ABA levels increase, which activates a signaling cascade that leads to physiological changes and the expression of drought-responsive genes [1–3]. The effects of ABA are complex and multifaceted. It regulates stomatal closure to reduce water loss, enables intercellular signaling of plant water stress status, stimulates antioxidant production to protect against drought damage, and activates transcription factors that activate drought-responsive genes [1–5]. ABA regulates two types of drought-responsive genes: those directly related to drought tolerance, such as aquaporins and antioxidants, and genes related to stress signaling, such as DREB and RD29 [6–8]. DREB genes activate other drought-responsive genes in response to ABA and stress signals [6]. RD29 genes produce proteins that are important for ABA synthesis [6]. LEA genes encode proteins that protect cells against dehydration damage [6]. ABA activity is mediated by ABA-responsive transcription factors that bind to ABREs, cis-acting DNA sequences in the promoters of ABA-responsive genes [1–4,8]. When ABA levels increase due to drought stress, ABA-responsive transcription factors are activated and bind to ABREs, which activates ABA-responsive genes [1–4]. In summary, ABA is essential for drought tolerance and activation of drought-responsive genes. It stimulates physiological changes, antioxidant production and transcription factors that bind to ABREs and activate genes involved in drought tolerance and stress signaling. ABA-responsive genes produce proteins that reduce water loss, protect cells and facilitate the transmission of stress signals.

2.2. Aquaporin Genes

Aquaporins are water channel proteins that facilitate the passage of water through cell membranes and are important in drought tolerance of plants [9]. Reuscher and his team identified 47 aquaporin genes in the tomato genome and found that they are expressed in a tissue-specific manner. Some aquaporin genes are upregulated in response to drought, suggesting a role in drought tolerance [10]. Wang (2017) found that overexpression of the apple aquaporin gene MdPIP1;3 in tomato increased fruit size, improved drought tolerance and reduced water loss. Transgenic tomatoes had slower water loss, more drought-sensitive stomatal feathers, larger fruit cells and larger fruits [11]. This indicates that MdPIP1;3 increases drought tolerance by increasing water transport and regulating stomata. Ouziad found that colonization of tomato roots with arbuscular mycorrhizal fungi (AMF) resulted in silencing of two aquaporin genes and increased drought-induced downregulation of three aquaporin genes. This suggests that AMF regulates aquaporin expression and water flow in tomato during drought [12]. This indicates that AMFs directly ameliorate plant drought through aquaporins. Gong identified many drought-responsive genes in drought-tolerant tomato, including aquaporins, transcription factors, signaling proteins, and genes related to growth, development, energy production, and oxidative stress. Drought-tolerant lines had a unique expression of ~400 drought-responsive genes, suggesting that these genes, especially aquaporins and transcription factors, likely contain drought-tolerant QTLs [13]. Transgenic plants showed improved chlorophyll fluorescence parameters during drought, indicating that chlorophyll fluorescence can inform drought tolerance and can be used for high-throughput screening [14]. Zupin found that two varieties of beans with different drought tolerance had different expression of four aquaporin genes in response to

drought and liquefaction. The more drought-tolerant variety had a greater downregulation of the two aquaporins during drought and a higher relative water content, suggesting that aquaporin regulation is important for drought tolerance [15]. In summary, aquaporins and their regulation are important genetic components in drought tolerance in tomatoes and other plants. Overexpression of certain aquaporins or transcription factors can improve drought tolerance. AMF also directly improves drought tolerance by regulating aquaporin expression. Chlorophyll fluorescence parameters can be used as a proxy for drought tolerance screening. The genetic basis of drought tolerance is complex, but understanding aquaporins and their regulators is key.

2.3. ROS Genes Are Related

Drought stress induces an influx of reactive oxygen species (ROS) in tomato plants, which triggers a series of reactions to neutralize their harmful effects while exploiting their signaling potential [16]. Dehydration accelerates ROS generation due to increased respiration and oxygenation in dehydrated cells [17]. Because antioxidants are limited during drought, ROS accumulate rapidly [17]. However, ROS have a dual role, as they mediate defense genes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) to produce antioxidants, as well as promote the synthesis of osmolytes (e.g., proline, glycine, betaine) for defense [18]. Stress response genes such as heat shock proteins (HSP) and transcription factors also help plants adapt [19]. The ROS signaling pathway activates various target genes involved in antioxidant defense, stress signaling and cell death, removing damaged cells and preventing further damage [20]. In fact, drought-tolerant tomatoes use a complex ROS-related network in which ROS simultaneously trigger defense responses that reduce damage and increase resistance to adversity [21]. ROS are key players in stress signaling involved in growth, development and biotic/abiotic responses [22]. Recent findings indicate that stress responses depend on ROS signals that interact with other signals using stress-specific chemicals, compounds and hormones [22]. In summary, drought stress in tomatoes increases ROS production through different cellular mechanisms [16,17]. Although ROS accumulate and cause damage without sufficient antioxidants [17], they also signal defense genes and osmolytes for protection [18,19]. Stress response genes further aid adaptation [19]. The ROS signaling pathway activates target genes of antioxidant defense, stress signaling and cell death, mitigating damage and increasing tolerance [20,21]. ROS are crucial in stress signaling and response [22]. Stress responses depend on ROS signaling, which interacts with other signals [22]. Other genes that play crucial role against drought stress in tomato could be found in Table 1 below.

Table 1. List of other genes that plays crucial role against drought stress in tomato.

Gene/Origin	Function	Expression/Regulation	Results
BEL1-like genes	Transcription factors, part of the TALE superfamily, regulate various plant biological processes	Exhibit tissue-specific expressions and respond to heat, cold, and drought stress	Plant growth and abiotic stress response [23]
AtCDF3, AtDREB1a, AtJUB1, CcHRD	Increases abiotic stress tolerance of tomatoes, including cold, salt, and drought stress	Overexpression	Stress tolerance [23]
SlHB2, SlAGO4A, SlMBP8	Tolerance to salt, drought stress	Overexpression, Gene silencing	Tolerance to salt, drought stress [23]
SlbZIP1	Salt and drought stress tolerance	Expression	Salt and drought stress Tolerance [23]

3. Metabolic Pathways

Drought tolerance in tomato plants is orchestrated through a sophisticated network of metabolic pathways, strategically designed to uphold essential physiological processes and safeguard cellular integrity in the face of water scarcity. The photosynthetic path-

way, challenged by drought-induced stomatal closure limiting carbon dioxide availability, employs adaptive strategies to elevate leaf carbon dioxide levels and transition to a less water-sensitive form of photosynthesis, thus ensuring sustained energy production. Concurrently, increased respiratory rates, a response to drought, furnish the requisite energy for growth, reproduction, and defense, albeit accompanied by the generation of reactive oxygen species (ROS). To counteract ROS-induced cellular damage, the plant activates defense mechanisms, including the production of antioxidants. Moreover, drought-induced stress leads to the augmented production of specific amino acids, like proline, serving as osmolytes for cellular protection, although amino acids may be catabolized to meet energy demands. Complementary metabolic pathways, encompassing carbohydrate synthesis and degradation, lipid metabolism for membrane stability, and a sophisticated stress signaling pathway, collectively underpin the plant's adaptation to water deficit, thereby enhancing its drought resilience.

4. Microbial Interactions and Drought Tolerance in Tomatoes

Drought significantly impacts tomato plant growth, development, and productivity, but microbial interactions offer a versatile strategy to enhance drought tolerance.

4.1. Beneficial Microbes

Microbes like plant growth-promoting rhizobacteria (PGPR) stimulate drought tolerance by producing plant growth hormones (e.g., auxins, gibberellins) that foster root growth and water absorption. Additionally, mycorrhizal fungi form symbiotic relationships, expanding the root surface area for improved water absorption and nutrient provision [24].

4.2. Antioxidant Production

Microbes like *Bacillus subtilis* produce antioxidants that shield plants from reactive oxygen species (ROS) generated during drought stress, mitigating damage [25].

4.3. Genetic Modulation

Microbes can influence drought tolerance-related gene expression, aiding tomato plants in adapting more efficiently to dry conditions [26].

Examples of microbial effects on tomato drought tolerance encompass PGPR promoting root growth, enhancing water absorption, and ROS protection. Mycorrhizal fungi improve both water absorption and nutrient supply. *Pseudomonas* bacteria produce antimicrobial compounds to fend off pathogens. These diverse microbial mechanisms collectively empower tomato plants to better withstand drought stress.

5. Molecular Mechanisms of Microbial-Mediated Drought Tolerance in Tomatoes

The molecular mechanisms underlying microbe-mediated drought tolerance in tomato plants are complex and multifaceted, involving several important processes. Together, these processes allow tomato plants better withstanding of the challenges of water scarcity.

First, hormonal regulation plays a central role in this microbial interaction. Beneficial microorganisms produce plant hormones, including auxins and gibberellins. Hormones introduced by microbes stimulate root growth and increase water absorption. In addition, these microorganisms can modulate the expression of genes related to stress signaling pathways. This modulation improves the adaptation of the plant to dry conditions and contributes to drought tolerance [24].

Second, stomatal regulation is another critical aspect of microbe-mediated drought tolerance. Microbes can affect stomatal conductance, gatekeepers control water loss through evaporation. Some microorganisms have the ability to fine-tune stomata, which reduces water loss during drought. This reduction in evaporation helps the plant conserve water and maintain optimal hydration [27].

Third, osmotic regulation is another mechanism by which microbial partners improve drought tolerance in tomato plants. Drought-tolerant microorganisms contribute to osmotic

adaptation, a process that involves the accumulation of solutes such as proline and sugars in plant cells. This accumulation reduces the water potential of the cells, allowing them retention of water and maintenance of turgor pressure even in the absence of water [28].

Fourth, antioxidant defense mechanisms play an important role in protecting tomato plants against the harmful effects of reactive oxygen species (ROS) generated during drought stress. Certain microorganisms such as *Bacillus subtilis* produce antioxidants such as catalase and superoxide dismutase. These antioxidants scavenge ROS, protect plant cells from oxidative damage and strengthen overall resistance [25].

Fifth, nutrient uptake and homeostasis are also influenced by microbial interactions, particularly those associated with mycorrhizal fungi. These fungi form symbiotic relationships with plant roots, effectively expanding the reach of the root system. This extension improves both water and nutrient availability, which critically contributes to plant survival during periods of water scarcity. In addition, mycorrhizal fungi increase the assimilation of essential elements such as phosphorus, which are often limited during drought stress [26].

Finally, cell wall modification is another layer of protection provided by certain microorganisms. These microbes can change the composition and structure of a plant's cell wall, strengthening it against drought challenges. These changes improve the plant's ability to retain water, maintain cell turgidity and resist cell damage, increasing overall dryness.

Taken together, the complex molecular mechanisms of microbial-mediated drought tolerance in tomato plants include hormonal regulation, stomatal control, osmotic regulation, antioxidant defense, nutrient uptake, induced systemic resistance, gene expression regulation and cell wall modification. These processes work together to allow tomato plants thriving under water-scarce conditions. Understanding these mechanisms offers enormous potential for developing innovative strategies to improve drought tolerance not only in tomatoes but also in other crops, thus promoting more sustainable and sustainable agricultural practices in a changing climate.

6. Conclusions

Using microorganisms to enhance drought tolerance in tomato plants is a promising area of research. Understanding how microorganisms mediate drought tolerance can help devise new strategies for tomato plant adaptation. The study of microbial mediated drought tolerance in tomatoes is a rapidly developing field. Understanding how microorganisms help plants manage arid conditions can lead to effective strategies for increasing yields and food security in the face of climate change. Prospects for the molecular mechanisms of microbial mediated drought tolerance in tomatoes are promising. Advancements in technology and research have improved scientists' comprehension of microorganism-plant interactions, allowing for the development of new strategies to increase drought tolerance in tomato plants. Gene editing techniques, such as CRISPR-Cas9, can be used to introduce drought-resistant plant genes into tomato plants, enhancing their ability to cope with adversity. Sustained research can further develop strategies to increase the arid tolerance of tomato plants and ensure food security in the face of climate change.

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