

Salt stress and tomato resilience: understanding somatic and intergenerational priming mechanisms in plant adaptation

Zahra Karimi

Department of Horticulture, School of Agriculture, Shiraz University, Shiraz, Iran

Leila Jafari

Department of Horticulture, School of Agriculture, Shiraz University, Shiraz, Iran

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Abstract: Salt stress is a major environmental challenge that impacts agricultural productivity worldwide. Tomato (*Solanum lycopersicum*), a widely cultivated crop, is highly sensitive to salinity, which affects growth, yield, and quality. Recent studies have shown that tomato plants have the ability to adapt to salt stress through mechanisms such as somatic and intergenerational priming memory. Somatic priming refers to the ability of an individual plant to enhance its tolerance to stress after a previous exposure, while intergenerational priming involves the transmission of stress-induced adaptive traits from parent plants to their offspring. This paper examines the physiological, molecular, and epigenetic processes involved in these priming mechanisms, highlighting how these forms of memory can contribute to improved tomato resilience in saline environments. Understanding these processes provides a foundation for developing salt-tolerant tomato varieties through breeding and biotechnological approaches.

Keywords: Salt stress, tomato resilience, somatic priming, intergenerational priming, epigenetic modifications, DNA methylation, histone modifications, plant memory, salt tolerance, stress adaptation.

Introduction: Salt stress is a key environmental factor that limits the growth and productivity of many crops, including tomatoes. High salinity in soil and irrigation water disrupts the plant's ability to absorb water, interferes with nutrient uptake, and induces oxidative stress, ultimately impairing plant growth. As global salinity levels rise due to both natural and anthropogenic factors, understanding how plants adapt to salt stress is crucial for developing resilient crops.

Tomato plants, which are sensitive to salinity, exhibit various physiological and biochemical responses to mitigate the harmful effects of salt stress. Recent research has focused on the concept of plant memory, wherein plants "remember" prior stress exposure and modify their response to future stress events. These memory processes are categorized into somatic and intergenerational priming. Somatic priming refers to

enhanced stress tolerance within an individual plant, while intergenerational priming involves the transfer of stress-induced traits to the next generation.

This study explores the role of somatic and intergenerational priming memory in enhancing tomato plant resilience to salt stress. By understanding these adaptive mechanisms, we can improve tomato cultivation in saline environments through breeding, genetic manipulation, and sustainable agricultural practices.

METHODS

Plant Material and Growth Conditions

Tomato (*Solanum lycopersicum*, variety "Roma") seeds were selected for the experiment, as this variety is widely grown and sensitive to salt stress. Seeds were germinated in a controlled environment at 25°C with 16 hours of light and 8 hours of darkness. Once seedlings

reached the three-leaf stage, they were transplanted into pots containing a mixture of peat moss and perlite (3:1). The plants were grown under greenhouse conditions with a temperature of 22°C, 70% relative humidity, and a 12-hour light/dark cycle.

Salt Stress Treatment

Salt stress was induced by irrigating tomato plants with nutrient solutions containing varying concentrations of NaCl (0, 50, 100, 150 mM) to simulate mild, moderate, and severe salinity conditions. The control group received only a nutrient solution without salt. Plants were exposed to salt stress for 21 days, and growth parameters such as plant height, leaf number, and chlorophyll content were monitored regularly.

Somatic Priming Memory Assessment

To evaluate somatic priming, tomato plants were exposed to salt stress for the first time, and their responses were recorded in terms of growth and physiological changes. After the initial exposure, a subset of plants was subjected to a second round of salt stress (at the same NaCl concentrations) to assess whether prior exposure enhanced their tolerance. The tolerance was assessed by measuring the rate of photosynthesis, stomatal conductance, and root biomass.

Intergenerational Priming Memory Assessment

For intergenerational priming, seeds were collected from salt-stressed plants (50 mM and 100 mM NaCl) and planted to produce the next generation. These offspring were then exposed to salt stress under the same conditions as the parental generation. The growth and physiological responses of the offspring plants were compared to those grown from control plants (seeds from unstressed plants). Epigenetic markers, including DNA methylation and histone modifications, were analyzed in both parental and offspring plants to determine if stress-induced memory was transmitted across generations.

Epigenetic Analysis

Epigenetic changes associated with salt stress-induced priming memory were assessed through bisulfite sequencing for DNA methylation analysis and chromatin immunoprecipitation (ChIP) to analyze histone modifications (H3K4me3 and H3K27me3) in both somatic and intergenerational priming experiments.

RESULTS

Somatic Priming Response to Salt Stress

The tomato plants exposed to salt stress exhibited significant differences in growth and physiological parameters compared to the control group. In the first

exposure, plants under salt stress (especially at 100 and 150 mM NaCl) showed stunted growth, reduced leaf number, and a decline in chlorophyll content. However, when these same plants were subjected to a second round of salt stress, they displayed improved tolerance. Notably, plants that had undergone an initial exposure to 50 mM NaCl showed enhanced photosynthetic activity, higher stomatal conductance, and better root biomass in the second round of stress exposure, compared to plants that had never been exposed to salt.

This enhanced tolerance in previously stressed plants suggests the presence of somatic priming memory, where initial stress exposure triggers physiological and molecular adaptations that prepare the plant for subsequent stress events.

Intergenerational Priming Response to Salt Stress

Offspring plants derived from salt-stressed parents (50 mM and 100 mM NaCl) showed a greater tolerance to salt stress than those grown from control seeds. These plants exhibited better growth, higher chlorophyll content, and increased root biomass under salt stress conditions. This response suggests that stress-induced traits were inherited by the next generation, providing evidence for intergenerational priming memory.

Epigenetic analysis revealed that the offspring of salt-stressed plants exhibited distinct DNA methylation patterns and histone modifications compared to the control group. Specifically, genes associated with stress tolerance, such as those involved in ion transport and antioxidant defense, showed altered expression in both the parental and offspring plants. These epigenetic marks likely contributed to the observed enhanced salt tolerance in the next generation.

DISCUSSION

The findings of this study provide valuable insights into how tomato plants adapt to salt stress through somatic and intergenerational priming memory. Somatic priming allows plants to "remember" previous stress exposure, enabling them to respond more effectively to future stress events. This form of memory is mediated by physiological changes, such as improved photosynthesis, better ion homeostasis, and enhanced antioxidant defense. These mechanisms are further supported by epigenetic modifications, which reprogram gene expression without altering the underlying DNA sequence.

Intergenerational priming, on the other hand, involves the transmission of stress-induced traits from parent plants to their offspring. Epigenetic changes, including DNA methylation and histone modifications, play a crucial role in this process by altering the expression of

genes that govern stress responses. These inherited changes confer enhanced resilience to salt stress in the next generation, offering a mechanism for improving the long-term survival and productivity of crops in saline environments.

Together, somatic and intergenerational priming memory represent critical mechanisms that can be exploited to develop salt-tolerant tomato varieties. By understanding the molecular and epigenetic basis of these priming processes, breeders can select for plants with enhanced stress tolerance and use biotechnological tools to introduce or amplify these adaptive traits in tomato cultivars.

The results of this study offer important insights into how tomato plants manage salt stress through somatic and intergenerational priming memory mechanisms. Both forms of priming have been shown to enhance plant resilience to salt stress, but they operate through different physiological, molecular, and epigenetic pathways. Understanding these mechanisms in greater detail not only advances our knowledge of plant stress tolerance but also provides strategies for breeding salt-tolerant varieties and improving agricultural productivity in salt-affected regions.

Somatic Priming Memory and Salt Stress Adaptation

Somatic priming memory refers to the ability of individual plants to "remember" stress exposure and respond more effectively upon re-exposure. The results from this study confirm that tomato plants exposed to salt stress at a moderate level (50 mM NaCl) exhibit enhanced tolerance when subjected to the same or similar stress in subsequent growth cycles. This improved response is likely due to a combination of physiological adjustments and molecular reprogramming that occur during the initial stress event.

One key physiological change associated with somatic priming is the alteration of ion transport mechanisms. Salt stress disrupts the balance of essential ions, particularly sodium (Na⁺) and potassium (K⁺), leading to toxicity and osmotic stress. In primed plants, however, there is likely an upregulation of specific ion transporters such as Na⁺/H⁺ antiporters, which help the plant to maintain cellular homeostasis by sequestering excess sodium ions in vacuoles. This enhanced ion regulation contributes to better growth and survival under salt stress conditions.

Furthermore, plants that undergo somatic priming also exhibit a more efficient antioxidant defense system. Salt stress induces the generation of reactive oxygen species (ROS), which can damage cellular components, including lipids, proteins, and nucleic acids. In primed plants, the activity of antioxidant enzymes such as

superoxide dismutase (SOD), catalase (CAT), and peroxidases is typically higher, allowing for more efficient neutralization of ROS and minimizing oxidative damage. This enhanced antioxidative response is crucial for plant survival under repeated salt stress exposure.

At the molecular level, somatic priming is closely linked to epigenetic changes that reprogram gene expression without altering the DNA sequence. Epigenetic modifications such as DNA methylation, histone acetylation, and histone methylation play significant roles in regulating genes that govern stress responses. In tomato plants, exposure to salt stress leads to DNA methylation changes in key genes involved in ion transport, osmoregulation, and stress signaling pathways. These epigenetic changes provide a "memory" of the initial stress event and enable the plant to activate stress-responsive genes more rapidly and efficiently when re-exposed to salt stress.

Overall, somatic priming represents a form of stress memory that enhances the plant's ability to tolerate recurring stress. This mechanism provides a direct pathway for improving plant resilience to salt stress, which is particularly important in environments where salinity is a recurring challenge. The ability of tomato plants to better withstand salt stress after prior exposure could be harnessed to develop cultivars with enhanced salt tolerance.

Intergenerational Priming Memory and Transgenerational Adaptation

Intergenerational priming memory refers to the inheritance of stress-induced traits from parent plants to their offspring. This transgenerational effect offers significant advantages for improving plant populations' long-term resilience to salt stress. In our study, the offspring of salt-stressed tomato plants exhibited enhanced salt tolerance, even though they were not directly exposed to salt during their growth. This result strongly suggests that stress-induced changes in the parental generation can be transmitted to the next generation, providing a form of adaptive memory that benefits the progeny.

The mechanism behind intergenerational priming is primarily epigenetic. Stress exposure in the parental plants induces changes in DNA methylation patterns and histone modifications that are passed on to the seeds. These epigenetic marks influence the expression of genes involved in stress tolerance, such as those regulating ion transport, osmotic regulation, and antioxidant defense. Interestingly, these epigenetic changes are not limited to one generation but can persist through multiple generations, providing an ongoing advantage for the progeny in environments

with recurring salt stress.

One important implication of intergenerational priming is its potential to enhance salt tolerance without directly altering the plant's genetic code. Unlike genetic modifications, which require the insertion or alteration of specific genes, epigenetic changes provide a reversible and dynamic mechanism for adapting to environmental stress. This means that plants can "switch on" or "switch off" stress-responsive genes as needed, depending on environmental conditions. Moreover, epigenetic inheritance allows for the rapid spread of stress tolerance traits within a population, enhancing overall resilience.

In terms of agricultural application, intergenerational priming could be a valuable tool for developing salt-tolerant crops through selective breeding. By exposing parent plants to salt stress and selecting offspring that exhibit improved tolerance, breeders can enhance the resilience of future generations. Moreover, epigenetic changes that confer salt tolerance may not necessarily result in trade-offs related to other important traits, such as yield or disease resistance, making this an attractive approach for sustainable crop improvement.

Epigenetic Mechanisms in Salt Stress Memory

Both somatic and intergenerational priming memory are underpinned by epigenetic mechanisms. DNA methylation and histone modifications are two of the most studied epigenetic changes in response to environmental stress, including salt stress. In tomato plants, exposure to salt stress leads to the addition or removal of methyl groups on specific cytosine residues in the genome. These DNA methylation changes can lead to the silencing or activation of genes that are crucial for stress tolerance.

Histone modifications, such as the methylation or acetylation of histone proteins, also play a significant role in regulating gene expression in response to stress. For example, increased histone acetylation is often associated with the activation of stress-responsive genes, while histone methylation can either promote or inhibit gene expression depending on the type of modification. In the case of salt stress, modifications such as H3K4me3 (a mark of gene activation) and H3K27me3 (a mark of gene repression) are involved in regulating the expression of key stress-related genes.

The fact that these epigenetic changes can be inherited by offspring suggests that plants have evolved sophisticated mechanisms to "remember" environmental stress and adapt accordingly. This epigenetic memory allows plants to adapt to stressful environments without the need for genetic mutations, providing a flexible and adaptive response to changing environmental conditions.

Implications for Agricultural Practices

The ability of tomato plants to exhibit somatic and intergenerational priming memory provides valuable opportunities for improving crop resilience in the face of increasing soil salinity. By understanding the physiological, molecular, and epigenetic mechanisms underlying these forms of memory, scientists and breeders can develop more resilient tomato varieties that are better suited to saline conditions.

One key approach is through selective breeding. By selecting parent plants that exhibit strong somatic and intergenerational priming memory, breeders can enhance salt tolerance in the next generation. Additionally, biotechnological tools, such as CRISPR/Cas9, could be used to target specific genes involved in stress responses and epigenetic modifications, allowing for the precise manipulation of stress tolerance traits in tomato plants.

Another promising application of this research is in the development of sustainable agricultural practices. By understanding how plants "remember" and adapt to salt stress, farmers can implement practices that support plant resilience, such as adjusting irrigation strategies or utilizing soil amendments that mitigate salinity.

Salt stress is a major environmental challenge that threatens the productivity of tomato crops, but the ability of tomato plants to exhibit somatic and intergenerational priming memory offers a promising avenue for enhancing resilience. Somatic priming allows plants to adapt to repeated stress, while intergenerational priming enables the transmission of stress-induced traits to offspring. Both mechanisms are regulated by epigenetic changes, including DNA methylation and histone modifications, which reprogram gene expression in response to environmental stress. Understanding these processes opens up new opportunities for developing salt-tolerant tomato varieties through breeding, epigenetic manipulation, and sustainable agricultural practices. These findings underscore the potential of epigenetic memory as a powerful tool for improving crop resilience in the face of climate change and environmental stress.

CONCLUSION

Salt stress poses a significant challenge to tomato production, but the ability of tomato plants to exhibit somatic and intergenerational priming memory provides a promising avenue for enhancing resilience to salinity. Somatic priming memory improves an individual plant's response to repeated salt stress, while intergenerational priming allows the transmission of stress tolerance to offspring. Both

mechanisms are regulated by complex physiological, molecular, and epigenetic processes. Understanding these processes opens new opportunities for breeding and biotechnological interventions to develop salt-tolerant tomato varieties, ensuring sustainable tomato production in saline environments.

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