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Plants Abiotic Stress Memory: Molecular Insights

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As sessile species and without the possibility of escape, plants constantly face numerous environmental stresses. Certain environmental stresses rarely occur during plant life, while others, such as heat, drought, salinity and cold are repetitive. Subsequently, plant's physiological, metabolic and genetic adjustments to the stress occurrence provide necessary competencies to adapt, survive and nurture a condition known as "memory." Priming is a process through which a transient environmental cue causes adaptive responses (usually rapid or stronger) when exposed to repeated stresses. Priming makes the plant self-prepare for better inducible stress responses (Galviz *et al.*, 2020). Moreover, plants that are pre-exposed to an eliciting factor become more tolerant against subsequent stress events. To date, several molecular mechanisms of stress memory response have been identified. The hormonal/antioxidative cross-talk associated with stress memory generation, assimilation of several key proteins or signaling metabolites as the sustained alteration in various transcription factors, explains how plant metabolism is altered and maintained in response to various stresses. Another possible molecular mechanism of stress memory formation entails chromatin remodeling, which involves histone modifications like methylation and results in a change in the gene expression pattern that underpins memory response.

Keywords: Stress memory, Stress memory mechanism

Introduction

In the 19th century, the father of evolution, Charles Darwin along with his son Francis Darwin hypothesized that plant root cells have something like the brain *i.e.*, the 'root brain hypothesis'. One of the path-breaking experiments in the plant memory field carried out by Gagliano *et al.* (2014), with the touch-sensitive plant, *Mimosa pudica*, concluded that plants are able to learn, interpret, and memorize. Recently, it was discovered that seeds of *Arabidopsis thaliana* contain a group of cells at the radicle portion which functions as a decision-making centre for the future development of the plant, as stated in the root-brain hypothesis of Darwin.

Short-term changes causes adaptive responses (usually rapid or stronger) when exposed to repeated stresses which makes the plant self-prepare for better inducible stress responses. The priming events are consequently pursued by stress memory. Plant stress priming involves three distinct phases: Pre-challenge priming phase (characterized by the stimulus perception), post-challenge stress response phase (strong modulation of gene expression and genome reprogramming), inter- /trans generational priming phase (ensures that the offspring inherit a degree of resilience and contributes to long term evolution). Stress priming refers to stress conditioning, hardening, or training, where any stress event with mild intensity/short-term exposure allows the plants to become more resilient to additional stress(es). Priming induces stress memory thereby enabling the plants to retain the imprints of a stress incident for future reference.

Stress memory

It is defined as a phenomenon in which information from a previous stress stimulus is retained and used to adjust resilience to future stress. Plant that experiences a period of drought wilts under the dehydration stress and then recovers after rehydration. During a second drought stress, the plant 'remembers' the past drought experience, allowing it to achieve better resistance to dehydration and improve its survival prospects. (Fig. 1)

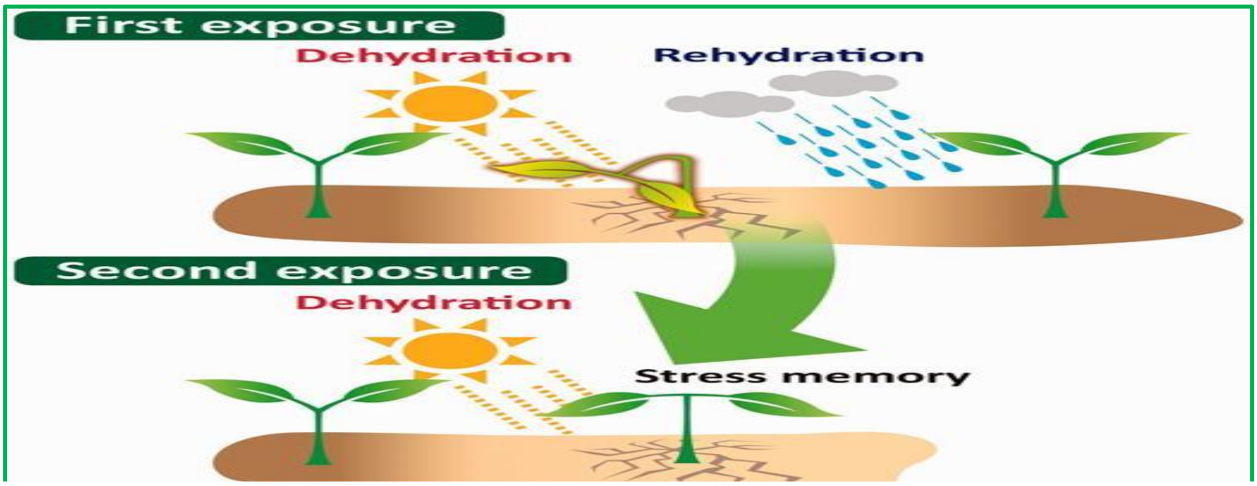

Fig. 1: Diagrammatic representation of stress memory (Kinoshita and Seki, 2014)

For better understanding, memory can be subdivided into somatic, intergenerational, and transgenerational memory (Liu *et al.*, 2022), where memory that affects the present generation is called somatic memory, memory that is transmitted from parent to offspring is called intergenerational memory and the memory that can be transmitted to multiple generations is termed transgenerational memory. Stress memory based on abiotic stressors can be categorized into drought (water scarcity), cold (low temperature), heat (high temperature) and salinity (excess salt).

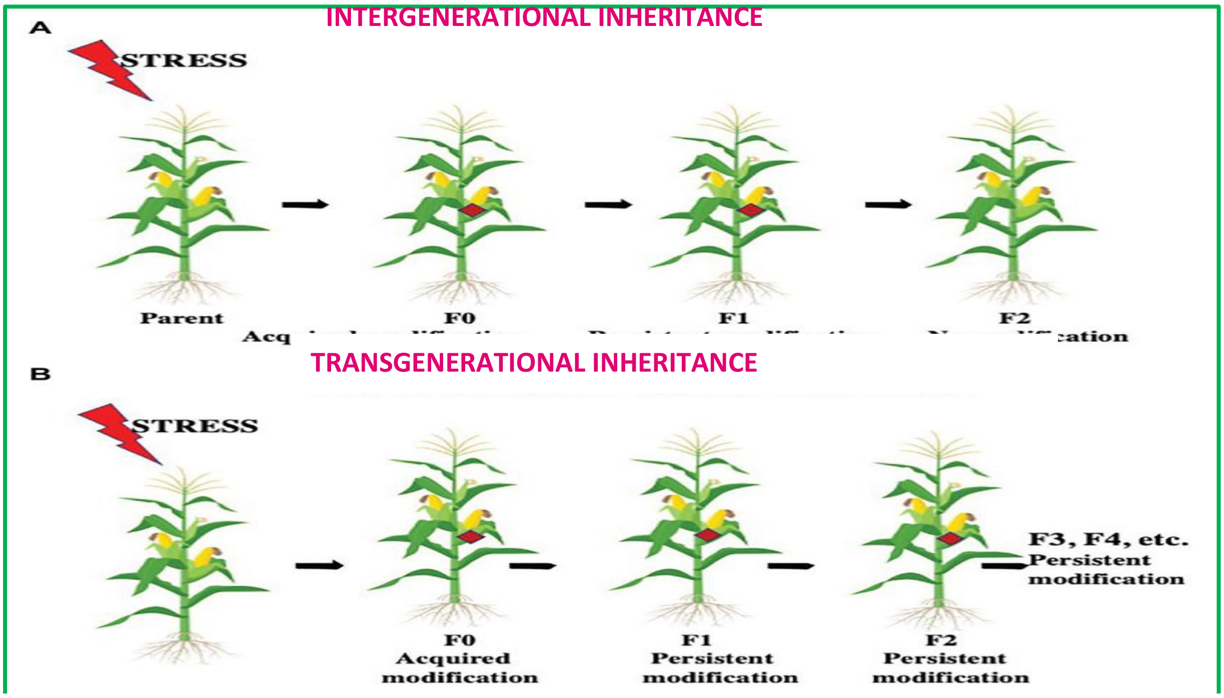

Fig. 2: Difference between intergenerational and transgenerational memory inheritance (Bhadouriya *et al.*, 2021)

Plants memorize the water scarcity conditions and respond differently than the first time they encountered it to survive the recurrence of drought stress, which is known as drought stress memory. Drought tolerance in plants has been related with osmoprotective proteins such as dehydrins, soluble sugars, phytohormones e.g. ABA and jasmonic acid, ferulic acid, and decrement in the photosynthetic system along with the mechanism that protects this system from reactive oxygen species. Various epigenetic mechanisms such as sRNAs, histone modifications, and DNA methylation also regulates gene expression during stress transmit the signal to subsequent generations through mitotic cell divisions. Thermopriming mediates the higher expression of HS transcription factors (HSFs) which modulate the expression of heat-shock proteins (HSPs) and many antioxidant genes, allowing quick and robust heat stress recovery (Lin *et al*., 2018). In plants, Heat-shock factor-A2 (HSFA2) is necessary for heat stress memory response. Similarly, plants have evolved a strategy to anticipate low temperatures and prepare themselves for upcoming freezing temperatures, known as cold acclimation which includes the cryoprotectants accumulations i.e. soluble sugar, prolines, and flavonoids, etc.

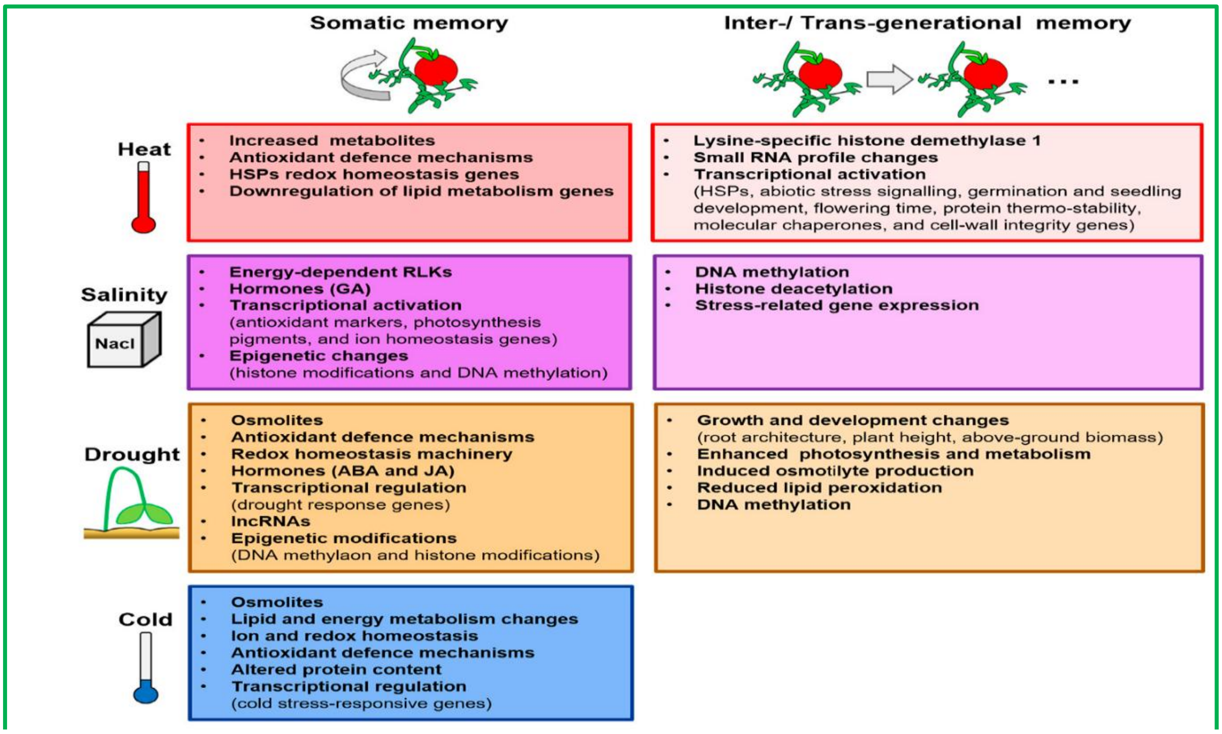

Fig. 3: Graphical outline of the known biological mechanisms involved in abiotic stress-specific memory (somatic and inter-/transgenerational) in crop plants (Lagiotis *et al*., 2023)

Mechanism of stress memory

1. Epigenetic memory
2. Hormonal/antioxidative cross-talk
3. Regulatory networks of protein

1. **Epigenetic memory:** Epigenetics refers to the study of heritable changes in chromatin function that do not involve changes in DNA sequence.

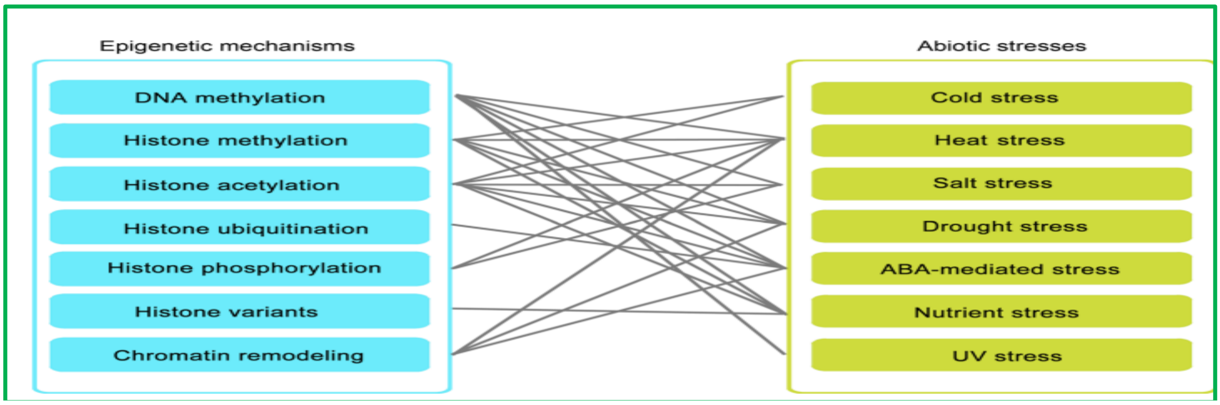

Fig. 4: The cross-talks between epigenetic mechanisms and abiotic stress responses (Chang *et. al*., 2020)

2. **Hormonal/antioxidative cross-talk:** Alterations in hormonal and antioxidative activities due to stress priming generated stress memory and plant can thus cope with any upcoming abnormalities.

3. **Regulatory networks of protein:** Various post-transcriptional changes leads to modulation in protein concentration and play a crucial role in mitigating the negative effect of environmental stressors. Example: HSP during the recovery phase of heat stress, Ribosomal/translation associated proteins, Prion-like proteins (PrLPs), transcription factors (TFs).
4. **Calcium Signaling:** Calcium ions (Ca^{2+}) act as secondary messengers in response to abiotic stress. Stress-induced changes in the cytosolic concentration of Ca^{2+} ($[Ca^{2+}]_{cyt}$) occur as a result of influx of Ca^{2+} from outside the cell, or release of Ca^{2+} from intracellular stores. These alterations in $[Ca^{2+}]_{cyt}$ results in a signal that is transduced via calmodulin, calcium-dependent protein kinases, and other Ca^{2+}-controlled proteins to effect a wide array of downstream responses involved in the protection of the plant and adjustment to the new environmental conditions.
5. **Reactive Oxygen Species (ROS):** ROS are involved in plant memory by acting as signaling molecules that activate stress-related genes and proteins. After an initial stress event, ROS signaling pathways can remain primed, enabling faster and more efficient responses when stress occurs again.

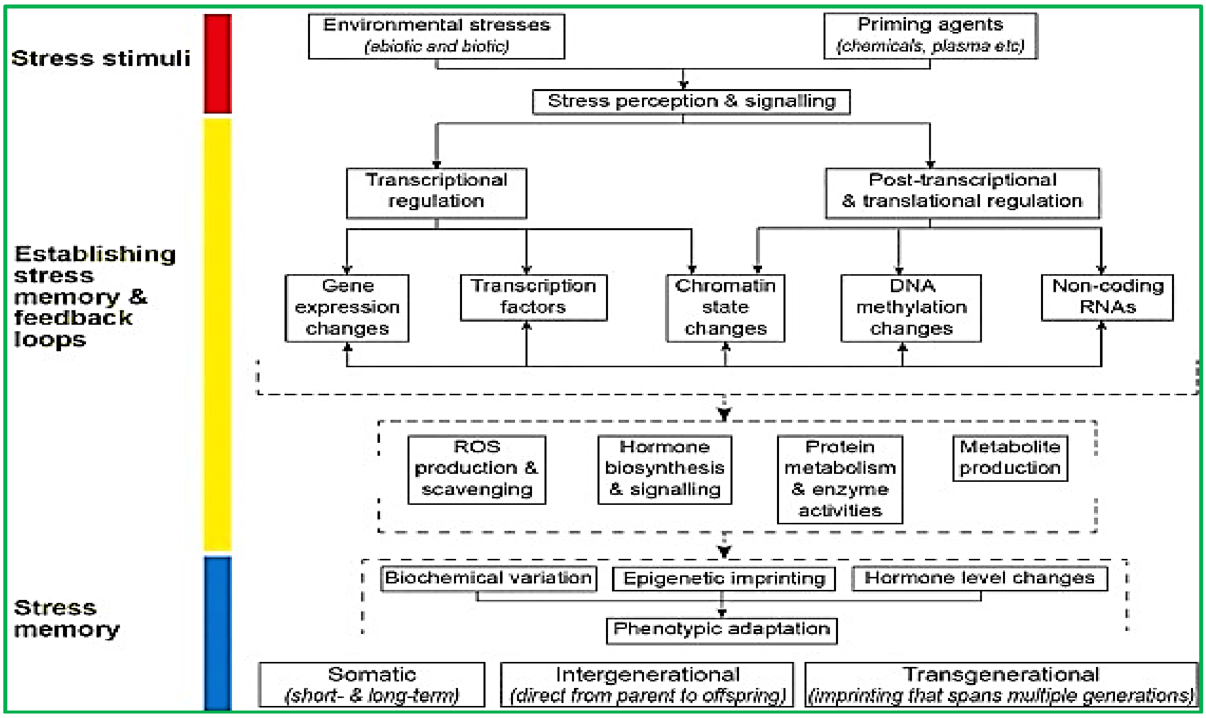

Fig. 5: Plant stress memory overview (Kashyap *et al.*, 2024)

Conclusion

With the global scenario of environmental shift, the depletion of crops due to abiotic stresses *i.e.* heat, drought, salinity and cold is the biggest constraint to agricultural crop productivity.

Abiotic stresses adversely affect plant growth and development causing plants to rapidly adapt their structural organization, photosynthetic process, metabolism (primary and secondary) and function (lipid/hormonal signaling, *etc*.) to withstand it. Drought, heat, cold and salt stress memory possibly positively impact plant endurance wellness in natural ecosystems. Unravelling the regulatory networks involving genes, non-coding RNAs, TFs, DNA and protein modification in response to stress condition elucidated the exact mechanism of stress memory response in plants. The consensus view is that abiotic stress memory is regulated at different levels, such as histone modifications, hormonal and proteins cross-talk which enable plants to cope with these stresses.

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