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REVIEW ARTICLE

Revisiting plant stress memory: mechanisms and contribution to stress adaptation

Abu Bakar Siddique[1] · **Sumaya Parveen**[2] · **Md. Zahidur Rahman**[2] · **Jamilur Rahman**[2]

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Abstract

Highly repetitive adverse environmental conditions are encountered by plants multiple times during their lifecycle. These repetitive encounters with stresses provide plants an opportunity to remember and recall the experiences of past stress-associated responses, resulting in better adaptation towards those stresses. In general, this phenomenon is known as plant stress memory. According to our current understanding, epigenetic mechanisms play a major role in plants stress memory through DNA methylation, histone, and chromatin remodeling, and modulating non-coding RNAs. In addition, transcriptional, hormonal, and metabolic-based regulations of stress memory establishment also exist for various biotic and abiotic stresses. Plant memory can also be generated by priming the plants using various stressors that improve plants' tolerance towards unfavorable conditions. Additionally, the application of priming agents has been demonstrated to successfully establish stress memory. However, the interconnection of all aspects of the underlying mechanisms of plant stress memory is not yet fully understood, which limits their proper utilization to improve the stress adaptations in plants. This review summarizes the recent understanding of plant stress memory and its potential applications in improving plant tolerance towards biotic and abiotic stresses.

Keywords Stress memory · Abiotic and biotic stress · Epigenetics · Plant adaptation · Climate change

Abbreviations

AA	Amino acids
ABA	Abscisic acid
APX	Ascorbate peroxidase
BABA	β-Aminobutyric acid
bHLH	Basic helix-loop-helix
CAT	Catalase
CBF	CCAAT motif-binding factor
CDPK	Calcium-dependent protein kinases
DHAR	Dehydroascorbate reductase
DREB	Dehydration responsive element binding
FLC	Flower locus C
GPX	Glutathione peroxidase
GR	Glutathione reductase
GSH	Glutathione
HSF	Heat shock factor
HSP	Heat shock protein
ISM	Intergenerational stress memory
MAPK	Mitogen activated protein kinase
miRNAs	MicroRNAs
ncRNAs	Non-coding RNAs
PEG	Polyethylene glycol
PR	Pathogenesis related protein
PSM	Plant stress memory
SA	Salicylic acid
PP2C	Plant protein phosphatase 2C
siRNAs	Small interfering RNAs
SOD	Superoxide dismutase
SSM	Somatic stress memory

Abu Bakar Siddique and Sumaya Parveen have contributed equally to this work.

✉ Jamilur Rahman
jamilur@sau.edu.bd
https://sau.edu.bd/teacher/157

Abu Bakar Siddique
abubakar.siddique@utas.edu.au

Sumaya Parveen
parveen.sumaya77@gmail.com

Md. Zahidur Rahman
jahidurrahman2013@gmail.com

[1] Tasmanian Institute of Agriculture, University of Tasmania, Prospect, TAS 7250, Australia

[2] Department of Genetics and Plant Breeding, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Sher-e-Bangla Nagar, Dhaka 1207, Bangladesh

TFs	Transcription factors
TSM	Transgenerational stress memory
UV	Ultraviolet

Introduction

Plants are sessile organisms and rooted in their habitats which render them vulnerable to a diverse range of adverse environmental conditions, encompassing biotic and abiotic stresses. Abiotic stresses, such as drought, extreme temperature, salinity, waterlogging, heavy metals, and nutrient deficiency, pose persistent and recurrent challenges to plants (Radha and Sunita 2022). Concurrently, biotic stresses like pathogens and insect pests emerge as prominent threats to plants, mostly acting combinedly (Teshome et al. 2020). These stresses affect plant/crop productivity significantly. Additionally, climate change has further complicated the situation as plants encounter these stresses and a combination of multiple stresses more frequently (Pandey et al. 2017). The majority of the modeling studies exploring the impact of climate change on food production predict that the effect of climate change on crop yields will be negative from 2030, and half of the projections predict that there will be a more than 10% crop loss beyond 2050 (https://ccafs.cgiar.org/bigfacts/#theme=climate-impacts-production; https://www.climatechange-foodsecurity.org/2014_ipcc_ar5). Additionally, a moderate increase (2 °C) of temperature at the local scale is expected to lead to a decrease in the worldwide production of wheat, rice, and maize (Driedonks et al. 2016). Crop-level adaptations increased the simulated yields by an average of 7–15%, with adaptations more effective for wheat and rice than maize (Challinor et al. 2024). Collectively, this information suggests that crop adaptation will be an important tool to combat food security.

The adaptation process in plants encompass the alterations at morphological, physiological, and molecular levels (Breusegeum and Remacle 2023). Plants recognize the stress stimuli, transduce the signal, and activate the defense mechanisms resulting in tolerance to the stresses. Additionally, the repetitive nature of abiotic and biotic stresses enables plants to remember and recall the previous exposures, resulting in eliciting a quick defense response against that stress (Charng et al. 2023). The phenomenon that enables plants to remember past experiences and recall the responsive mechanisms is known as plant stress memory (PSM) (Kambona et al. 2023; Trewavas 2003). The establishment of PSM prepares the plants for future stressful events and improves tolerance with a minimum and/or no reduction in growth (Liu et al. 2021a). The quicker and more precise responses towards the secondary stress and/or stress at the later phase has been observed in other organisms and have been reported in plants (Trewavas 2003; Berry and Dean 2015), animals, and microorganisms (Wolf et al. 2008). However, stress memory in plants has been overlooked compared to other organisms. In recent times, PSM has become a fascinating phenomenon after the discovery of vernalization-mediated flowering (Berry and Dean 2015). The concept of immunogenic memory in plants was first postulated and described by Chester in 1933 (Chester 1933). Later this idea was combined with immunogenic reactions during the end of the 1990s and the beginning of 2000 (Reimer-Michalski and Conrath 2016).

Currently, the most popular method to develop stress-resilient plants is the direct genetic intervention of transcriptional regulators or translation products. However, in recent years, the adaptation phenomenon led by PSM has drawn the attention of researchers, resulting in an increasing number of studies (Fig. 1). Studies on PSM have revealed epigenetic mechanisms, encompassing DNA methylation, histone modifications, chromatin remodeling, non-coding RNAs (including small interfering RNAs and Micro RNA-miRNA), and RNA-mediated gene silencing as the most important factors in establishing stress memory and adaptation (Lämke and Bäurle 2017; He and Li 2018; Gao et al. 2022). During the primary stress condition, these mechanisms govern the activation of stress-responsive genes and remain quiescent during the favorable conditions leaving behind a memory signature. These regulatory mechanisms are reactivated quickly upon exposure to subsequent stress and impart tolerance to the plants (Kambona et al. 2023). In addition to epigenetic mechanisms, several other factors, including transcription factors (TFs), metabolites, enzymes, and phytohormones are integral parts of PSM establishment, storing, and reactivation (Mladenov et al. 2021; Zhang et al. 2022). Several studies have reported that epigenetic and other regulatory mechanisms collaborate to regulate the PSM (Crisp et al. 2016).

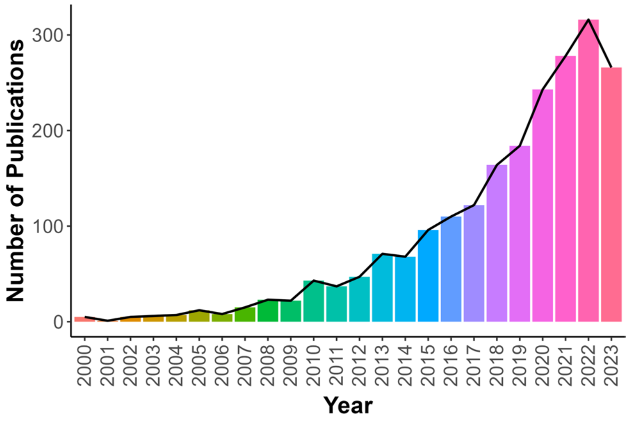

Fig. 1 Number of publications found in the Web of Science database in a query of "Plant stress Memory" for the period of 2000–2023. The number of publications related to PSM increased more than twice in recent years in comparison to previous years

Depending on the mechanisms involved, the duration of the PSM can either be short-term (limited to one generation only) or long-term (transmissible to the next generation) (Kambona et al. 2023). Plants having the ability to store stress experiences for a short period and the ability to react towards the subsequent stresses are known as somatic stress memory (SSM) which can last for a few days to a few weeks (Bäurle and Trindade 2020). This type of stress memory, is stored at the somatic level, does not pass to the next generation, and fails to respond quickly at the later stages or next generation. Plants having the ability to store and transfer the stress memory at a later phase and/or to the next generation are known as long-term stress memory including transgenerational and intergenerational stress memory (ISM and TSM respectively) (Lukić et al. 2023). The underlying regulatory mechanism controlling the duration and transfer of stress memory from one stage to another stage, or the next generation is yet to be understood. However, the activation of stress memory through priming of plants using initial mild stresses and priming agents has revealed the potential roles of both short-term and long-term stress memory for a diverse range of stresses which has provided a better tolerance at the later stage (Zhou et al. 2020; Liu et al. 2021a).

Extensive research has revealed that treating the seedlings and/or seeds with mild primary stresses and priming agents improve the plant tolerance against biotic and abiotic stresses including drought (Jacques et al. 2021), salinity, high temperature (Nishad and Nandi 2021), low temperature (Sharma et al. 2019), waterlogging (Lukić et al. 2023), heavy metal (Cong et al. 2019), pathogens, insects, and pests (Bhar et al. 2022). These studies hint towards the potential prospect of PSM for the improvement of stress-tolerant varieties. However, the detailed mechanisms involved in establishing, storing, reactivating, and transferring PSM are not fully understood which is a prerequisite for utilizing this concept in large-scale applications, as an example, in plant breeding programs. Being PSM a new branch of plant science, there are a few reviews presenting it from all possible perspectives including underlying mechanisms, regulatory factors, and application of PSM in enhancing the crop adaptation towards climate change. In this review, we delineate the underlying regulatory mechanisms involved in PSM establishment and activation at the later stages. Furthermore, we synthesize the recent findings pertaining to priming strategies as potential means of initiating PSM and enhancing the plants' ability to withstand recurrent biotic and abiotic stresses.

Regulations of plant stress memory

PSM is the outcome of crosstalk among multiple physiological, metabolic, hormonal, molecular, and epigenetics processes that are involved in stress memory establishment, reactivation, and transfer to the later phase in the same life cycle, and/or to the next generations (Fig. 2). Plants perceive the stresses, learn from the stress stimuli, store, and recall the previous responses in later phase to the recurrent stresses and collectively establish the PSM (Demongeot et al. 2019). Thus, stress perception, transduction of signal through different pathways, and activation of defense pathway are the beginning step in establishing the PSM. The other aspects of PSM are the maintenance and reactivation during the recurrent stress which involves epigenetics, transcriptomics, metabolites, and hormonal regulations in complex manners.

Perception and signal transduction of stresses

A diverse range of regulatory networks are involved in the perception and transduction of stress stimuli from the environment to the plant cell to induce a proper response. Plants' responses toward the stress stimuli are constituted through the organized and programmed events including stress signal perception through primary and secondary receptors and messengers, signal transduction, activation of transcriptional factors (TFs) and gene regulatory network, and protein synthesis for specific functions (Fig. 3).

Cellular events including phosphorylation, dephosphorylation, and transcriptional modulations act as a first line of defense that involve the enzymes (Gupta et al. 2013). For instance, type 2C protein phosphatase (PP2C), and FORGETTER2 (FGT2) have been identified as important enzymes that regulate the membrane lipid dynamics during stress conditions. Another example is calcium (Ca^{2+}) signaling which is involved in the perception and transduction of stress stimuli and signaling cascade (Bhar et al. 2022). Reactive oxygen species (ROS) is overproduced by various biotic and abiotic stresses which act in transducing the stress signal (Mittler 2022). ROS is generated due to the stress-mediated imbalance in metabolic pathway and acts as signaling molecule by affecting the influx of Ca^{2+} and phosphorylation of downstream target by stress-responsive kinase (Mittler 2022). However, ROS brings cellular damage and causes a detrimental impact on plants which is minimized by several antioxidative enzymes. During the priming or primary stresses, these enzymes are involved in mitigating the negative impact of ROS overproduction and subsequently show rapid regeneration in the recurrent stress exposure (Sun et al. 2022).

Integration of Ca^{2+}, plant growth regulators or phytohormone, ROS, and kinase shape the perception and transduction of signal. Intriguingly, calcium-dependent protein kinase (CDPK) signaling regulates both biotic and abiotic stress response, which is associated in hormone signaling pathways, especially the abscisic acid (ABA) (Li et al. 2008; Shi et al. 2018). Priming or the induced primary stress produces calcium memory through the regulation of the stress

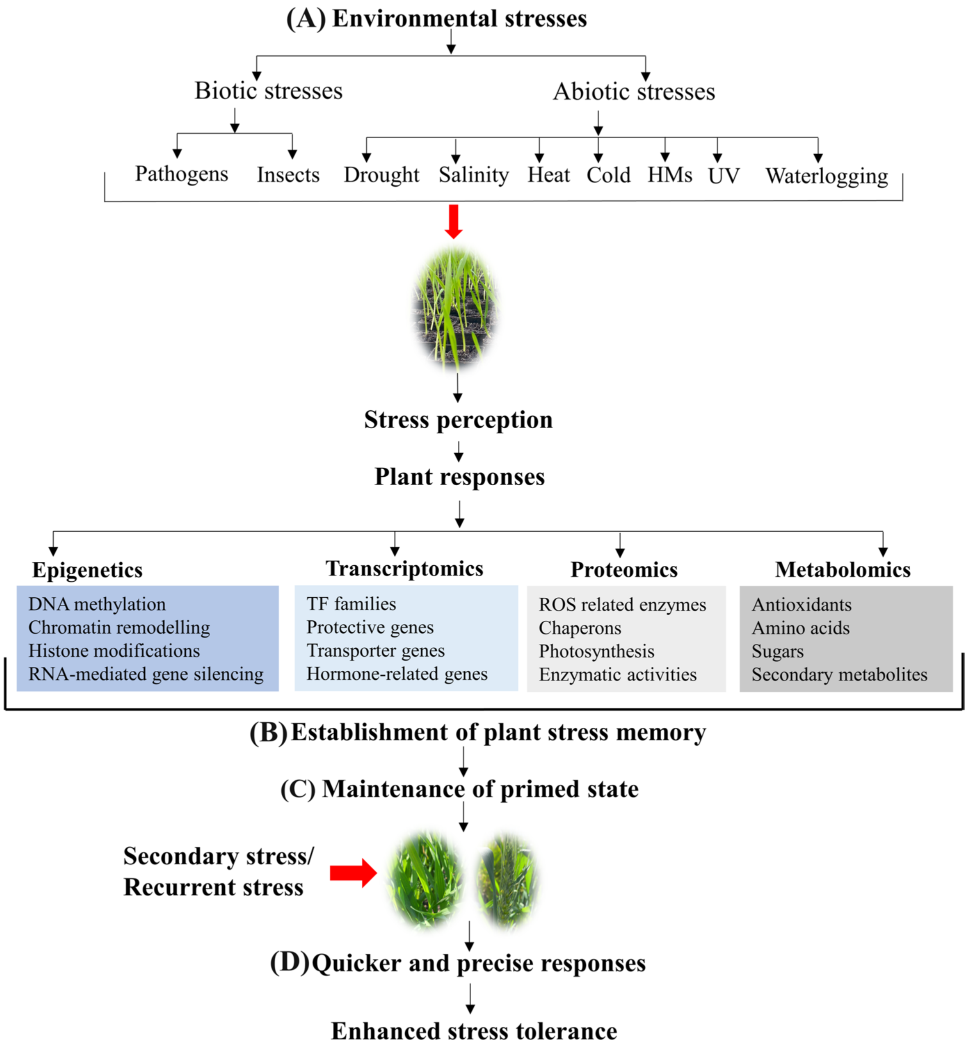

Fig. 2 Schematic diagram showing the regulatory mechanisms involved in PSM establishment, maintenance, and transfer to the later phase **A** Plant faces diverse biotic and abiotic stresses which are perceived by plants through specific features such as ROS, Ca^{2+}, and MAPK (details in Fig. 3). Plant implies a diverse set of molecular, physiological, metabolic, and epigenetic mechanisms to minimize the negative impact. **B** Several mechanisms establish the stress memory and **C** maintain it during the favorable or recovery phases. **D** Upon exposure to stresses at the later phases and recurrent stresses, plants reactivate the defense mechanisms which are faster and more precise, resulting in enhanced stress tolerance

related gene expression. Calcium-dependent protein kinase (CDPK) is involved in Ca^{2+} signaling and subsequent physiological processes including biosynthesis and homeostasis of phytohormones that regulate the plant responses towards stresses (Xu and Huang 2017). Most importantly, calcium -dependent protein kinase 5 (CPK5) has been demonstrated for signal propagation and manifestation of immune memory in systemic acquired resistance through NHP- and SARD1-dependent pathway (Guerra et al. 2020). However, the mechanistic explanation of CDPK in establishing the PSM is still obscure.

Mitogen-activated protein kinase (MAPK) cascades regulate the ROS generation and immune responses of plants towards adverse conditions (Rasmussen et al. 2012). MAPK is notably involved in multiple stress responses such as hormone signaling pathways including auxin, jasmonic acid (JA), brassinosteroid (BR), ethylene (ET), salicylic acid (SA), and abscisic acid (ABA) (Jagodzik and Tajdel-Zielinska 2018). MAPK regulates hormonal biosynthesis and stability under different stress conditions. As an example, mitogen-activated protein kinase 3 (MPK3) and MPK6 control the stability and activity of 1-Aminocyclopropane-1-carboxylic acid synthase (ACS) which determines the ethylene biosynthesis and their regulation at the protein level under pathogen attack (Li et al. 2012). ABA is involved in multiple stress responses including stomatal and photosynthetic regulations. Overexpressing of Calcium/calmodulin dependent protein kinase 1 (CaAMK1) in pepper plants exhibited drought tolerant phenotype mediated by ABA-regulated physiological responses such as lower water loss due to decreased stomatal aperture, and molecular responses such as higher stress responsive gene expression (Jeong et al. 2020). Arabidopsis MPK4 is a regulator of pathogen defense responses, and it is required for repression of SA- and JA-dependent gene expression. Transgenic *mpk4* plants failed to display JA defense marker gene with more sensitivity to pathogen which is an evident of that MPK4 regulates the hormonal biosynthesis under biotic stress (Brodersen et al. 2006). MPK4 also interacts with WRKY TFs and regulate pathogenesis-related (PR)

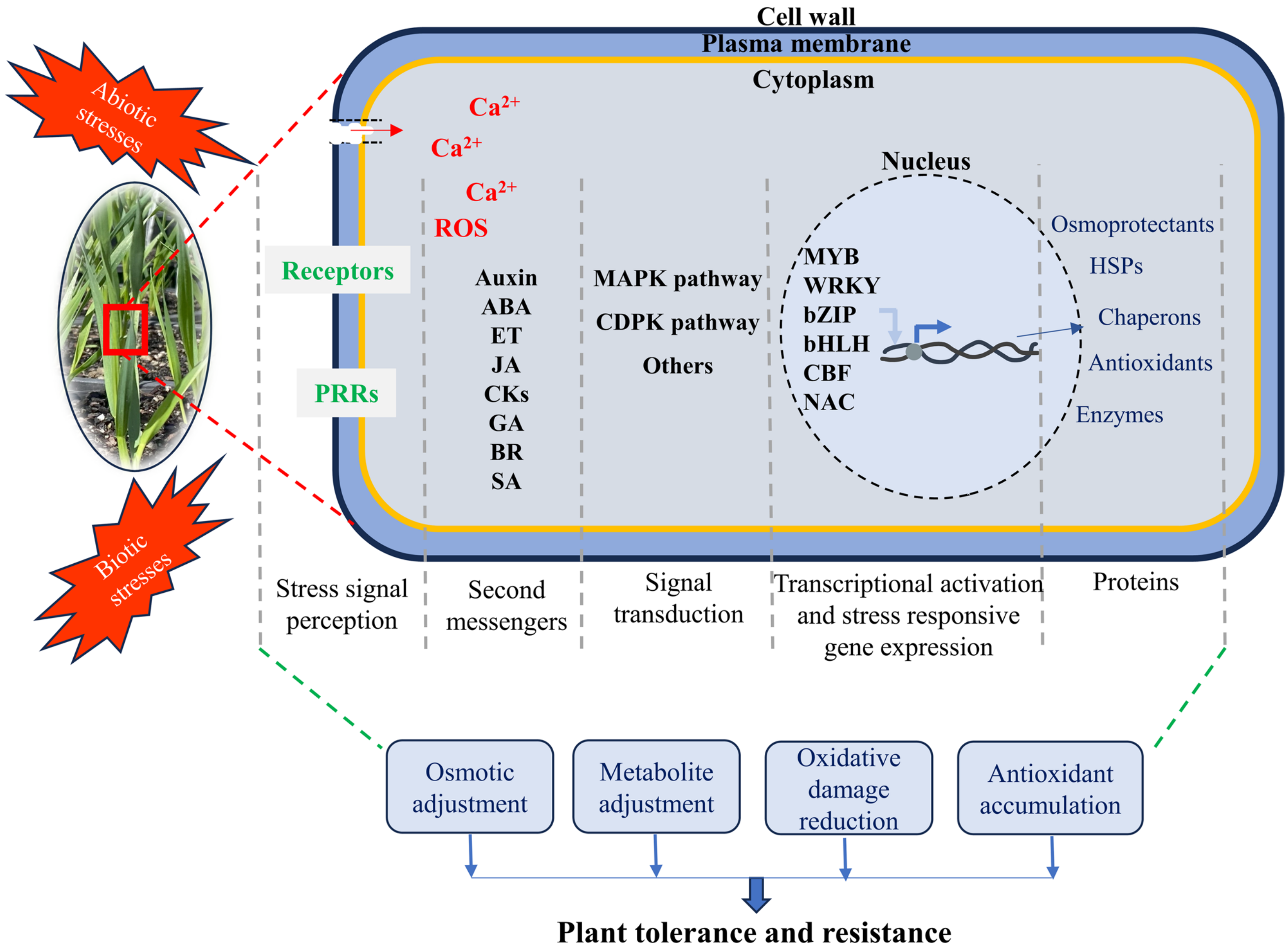

Fig. 3 Regulatory network involved in stress signal perception, transduction, and activation of defense systems. Stress stimulus is perceived through the receptors in cell wall which are received by both primary and secondary messengers. Signaling cascades transduce the signal and activate the transcriptional events resulting in gene expression which shape the plant responses

gene expression (Andreasson et al. 2005). Additionally, MPK3 and MPK6 are associated with higher expression of Pr1 and PAL1 defense gene and is involved in the activation of SAR in Arabidopsis (Beckers et al. 2009). In addition to CDPK and MAPK, there are other kinases involved in transduction and activation of TFs including the target of rapamycin (TOR) and sucrose non-fermenting-1-related protein kinase-1 (SnRK1) (Chen et al. 2022; Wurzinger et al. 2018; Tateda et al. 2014; Jaskiewicz et al. 2011). The kinase cascades activate several TFs including myeloblastosis viral oncogene homolog (MYB), WRKY, basic leucine zipper (bZIP), C-repeat binding factors (CBF), and NAC consists of no apical meristem (NAM), Arabidopsis thaliana transcription activator factor1/2 (ATAF1/2), and cup-shaped cotyledon 2 (CUC2) (Baillo et al. 2019). These TFs regulate stress responsive gene expression, resulting in biosynthesis of proteins, acts as osmoprotectant, molecular chaperons, heat shock proteins, antioxidants, and enzymes which shape plant resistance and tolerance towards the biotic and abiotic stresses (Baillo et al. 2019). These responses are quicker during the recurrent stresses in plants and form the PSM.

Establishment of plant stress memory

A diverse regulatory mechanism has been reported in establishing the PSM. Recent studies have shown that PSM is mainly regulated by epigenetic mechanisms which involve DNA methylation, chromatin and histone modifications, and non-coding RNA (Ramakrishnan et al. 2022). Epigenetic mechanisms refer to the heritable changes in chromatin levels, do not bring any changes in DNA sequence and play crucial roles in plant responses and adaptations to stresses (Kotkar and Giri 2020). Additionally, epigenetics is involved in the establishment and transfer of stress memory to the next generation (Mozgova et al. 2019; Kotkar and Giri 2020).

DNA methylation

The involvement of DNA methylation in epigenetic changes has been studied intensively under environmental stimuli which is relatively stable and heritable. Both N6-methyladenine (6-mA) and 5-methylcytosine (5-mC) DNA methylation have been reported which involves the addition of methyl group to different positions (Liu and He 2020).

DNA methylation occurs due to abiotic and biotic stress response that could be repaired during the recovery phase or remains dormant during the favorable conditions. Upon exposure to similar stress at the later phase, the process is activated quickly and precisely (Sun et al. 2022; Liu and He 2020). As an example, primed rice with short term drought stress exhibited quicker responses during the recovery and recurrent stress involving the DNA methylation as the regulator of PSM (Ou et al. 2012). Salinity stress mediated DNA methylation remained stable during the recovery stage and activated in later stage, possibly passed to the daughter cell through mitosis (Wang et al. 2015). DNA methylation has roles in transferring the responses mitotically in the same generation and meiotically to the next generation, building both SSM, ISM, and TSM through the gene expression, genomic imprinting, and transposable element activity (Sun et al. 2022; Wang et al. 2016). As an example, Ou et al. (2012) reported that CHG demethylation observed in rice leaf tissue treated with heavy metals, can be transferred to the next generation indicating the meiotic-based inheritance. Heavy metal-induced alterations in the 5-mC state of Tos17 retrotransposons transfer to the next generation of rice, indicating their role in the establishment and transfer of stress memory (Cong et al. 2019). Though the involvement of DNA methylation in establishing the PSM cannot be neglected, they show differential behavior in terms of persistence which requires further study. Additionally, the integration of 5-mC and 6-mA methylation with other epigenetic alterations needs to be targeted.

Histone modifications

Histone modification is involved in integrating the PSM into the offspring. Histone is a DNA packaging protein that influences the structure and accessibility of chromatin and thereby manipulates the biological functions (Nguyen et al. 2022). Changes in histone tails through methylation, acetylation, phosphorylation, ubiquitination, sumolytation, glycosylation, and ADP-ribosylation constitute the epigenetics code that regulate the stress-responsive transcriptional activities and gene expression (Kang et al. 2022).

Structural changes in chromatin are recognized as the backbone of the epigenetic regulations in plants for several developmental processes, stress responses, and the remembering of past experiences. Several epigenetic modifications in histones such as H3K4me3, H3K4me2, H3K9ac, H4K5ac, and H4K12ac regulate the PSM through the modifications at the promoter regions of TFs (Halder et al. 2022). For example, pathogen-mediated modification of histone at the promoter site of WRKY genes promotes the defense priming and results in tolerance during later phase, suggesting the histone-based memory establishment (Fabrizio et al. 2019). H3K4me3 has roles in epigenetic modification to the DNA packaging protein Histone H3 and is involved in the tri-methylation at the 4th lysine residue of the histone H3 protein, and subsequently modifies the gene expression. Genes responsive to water deficit such as RD20 and RD29A with clear enrichment of H3K4me3 in their coding regions were found to be maintained during the recovery phase (Kim et al. 2017).

One of the most reported phenomena of the roles of chromatin regulations in epigenetics is vernalization in cold stress where plants memorize the previous prolonged low temperatures and flower only when the available condition is available (Bäurle and Trindade 2020; Friedrich et al. 2018). Floral repressor FLOWERING LOCUS C (FLC) is repressed due to the continuous cold stress and activates when the temperature rises during spring. Histone marks H3K4me3 and H3K36me3 are involved in activation of FLC positively whereas H3K27me3 acts oppositely (Mozgova and Hennig 2015). Under prolonged cold exposure, H3K27me3 switches off FLC expression which is maintained during the cold temperature and this state is remained stable and epigenetically regulated (Friedrich et al. 2018; Jing et al. 2018; Sheldon et al. 2008). However, LEAFY COTYLEDON1 (LEC1), an embryonic pioneer TFs reset this phenomenon in early embryogenesis, and FLC turns into activate chromatin state (Tao et al. 2017). This classic phenomenon is reviewed in detail by He and Li (2018). However, the independent mechanism of histone and chromatin modifications in regulating stress memory is yet to be understood. Besides, the integration of histone modifications with other stress response cellular mechanisms needs to be studied.

Non-coding RNAs (ncRNAs)

ncRNAs are kind of RNA including siRNAs, and miRNAs which do not encode a protein. However, they are involved in regulating the plant responses and building up the stress memory for both the biotic and abiotic stresses (Yang et al. 2023; Liu et al. 2021c; Liu and He 2020). In addition to the DNA methylation and chromatin remodeling, RNA-mediated gene silencing either by siRNA or miRNA, play critical roles in epigenetic basis of PSM as observed in many species including soybean (Liu et al. 2021a; Chen et al. 2022). The progeny of UV-C-stressed plants showed an increase in transposon expression which is dependent on the DCL2-4 proteins. However, the DCL proteins are involved in long-term stress memory through the modulation of siRNA biosynthesis. Plants with compromised epigenetics machinery due to the RNA-directed DNA methylation affect the priming efficiency and transgenerational stress memory (Crisp et al. 2016). siRNA-mediated DNA methylation and transcriptional gene silencing are also observed in Arabidopsis (Zheng et al. 2013). These findings demonstrate the involvement of siRNA- and miRNA-mediated gene silencing in shaping the epigenetics regulated PSM.

Long-term memory, particularly TSM are mainly regulated through the heritable changes in sRNAs metabolism, methylation, and chromatin remodeling. Bilichak et al. (2015) reported that sRNA is involved in the heat shock-induced intergenerational stress memory in the somatic and reproductive tissues of stressed parents and their progeny of *Brassica rapa* through the miR168-AGO1 messenger module. sRNA-mediated gene silencing controls the methylation and histone modifications which activates the systemic acquired resistance towards the pathogen attack at later phases (Rebolledo-Prudencio et al. 2022). Parental line of durum wheat primed with drought stress exhibit an improved tolerance in progeny through the miRNA-mediated gene expression which regulates the photosynthesis, hormonal signaling, and ROS scavenging (Liu et al. 2021a, c). Involvement of miRNAs in regulating the ISM for heat stress has been also reported through regulating the hormonal, ROS detoxification, and photosynthetic process (Liu et al. 2021b). The regulation of antioxidative enzymes such as SOD and CAT suggested these as candidates for developing epigenetic markers especially for heat stress memory. miR156 isoforms are highly inducive by heat stress (HS) and promote sustained expression of HS-responsive genes. miR156 plays critical roles in heat stress memory by down-regulating SQUAMOSA-PROMOTER BINDING-LIKE (SPL) transcription factor and thereby increases expression of heat shock memory-related gene such as *has32, HSFA2, HSP17.6A,* and *HSP22* (Stief et al. 2014). A genome-wide analysis (GWAS) revealed up-regulation of the transposon-associated 21 nucleotide siRNAs and associated transcriptional changes of the transposon and/or the proximal gene in response to salicylic acid hormone treatment (Dowen et al. 2012). siRNA together with heat shock factors regulate thermotolerance by controlling HTT genes with additional functions in flowering that provides evidence of transgenerational heat stress memory controlled by sRNAs (Liu et al. 2019).

The intricate relationships among the RNAi, histone modifications, and DNA methylation play crucial roles in transcriptional gene silencing and shape the epigenetics basis of PSM. The RNAi-guided methylation has been observed in fission yeast through the recruitment of RNAi transcriptional silencing and histone modifications (Heard and Martienssen 2014; Castel and Martienssen 2013). In plants, RNA-mediated DNA methylation and DNA-demethylation pathways mediate the ISM in response to osmotic stress (Wibowo et al 2016). This result suggests that RNAi in collaboration with DNA methylation orchestrates the heritable transcriptional gene silencing.

Involvement of other molecular factors

Besides epigenetics regulations, several other factors such as transcriptional factors, metabolites, and plant hormones participate in building up the priming state of plants and activate the defense quicky and precisely.

Transcriptional factors

Transcriptional factors (TFs) are usually involved in plants' acclimatization to adverse environmental conditions. Several TFs including bHLH, MYB, WRKY, and HSF are commonly associated with stress response mechanisms. DNA methyltransferase and chromatin remodeling bring changes in TFs expression and thus regulate the plant stress memory machinery.

DNA methylation can affect the gene expression required for TFs under stress conditions (Xu et al. 2015). Speechless (SPCH) and FAMA are two bHLH TFs that are required for the differentiation of stomatal guard cells. Recurrent water deficit stress in terms of high vapor pressure deficit resulted in DNA methylation at the loci of these two genes regulating the stomatal development and remained stable consecutive two generations (Davies and Bergmann 2014). Higher tolerance with quicker responses to water stress in the next generation suggested the role of DNA methylation-mediated TFs regulations involving the establishment and transferring the PSM. In another study, transgenic lines overexpressing MYB74 upregulate the stress marker genes which contain the conserved MYB recognition sites. Xu et al. (2015) reported that DNA methylation and siRNA regulate the MYB74 promoter region which are master TFs for ABA signaling implying that MYB TFs might be involved in PSM. Priming plants with priming agents such as SA, and primary stresses such as cold and pathogen resulted in higher expression of different TFs including WRKY19, CBF3, and COR410 TFs in rice, Arabidopsis, and wheat (Cui et al. 2021; Wang and Li 2020; Luna et al. 2012a). Jaskiewicz et al. (2011) reported that plants primed with pathogens can establish the SAR with the higher primed level of WRKY TFs in systemic leaves, associated with higher augmentation of H3K4me3 and H3k4me2 on the promoter regions of TFs. Higher accumulation of H3K9ac on the promoter regions of *PR1* and WRKY TF leads to establish the TSM as they remained in the state in the stress-free generation (Luna et al. 2012a). These results have shown that WRKY TFs are involved in plant responses and establishment of PSM irrespective of biotic and abiotic stresses where epigenetic mechanisms such as histone acetylation and DNA methylation are involved. CBFs-TFs play an important role in cold stress through the upregulation of cold-responsive effector genes. Zhu et al. (2008) reported that histone methylation and deacetylation interact with CBFs-TFs to upregulate the genes PICKLE (PKL). PKL is involved in chromatin remodeling and promotes the H3K27me3 enrichment required for the TFs silencing in RdDM which serves as cold-induced freeze-tolerance (Park et al. 2018). These studies suggest that CBF-TFs-directed chromatin remodeling is essential for cold stress-resistant mechanisms.

Light signaling transcription factor HY5 has been found essential to maintain salt induced H3K4me3 in *P5CS1* during the recovery stage (Feng and Li 2016). The thermomemory of plants is mainly regulated by heat shock proteins (HSP) and heat stress transcription factors (HSFs) (Lin et al. 2014). Priming plants with heat stress led to H3K4me3 accumulation at the loci of HSP which is retained during the recovery stage and elevated during the recurrent heat stress (Lämke and Brzezinka 2016). HSFs also cooperate with other regulators such as histone methyltransferase and acetylase and maintain heat stress memory. JUMNJI (JMJ) regulates the H3K27me3 demethylation at the HSP loci and provides heat stress memory (Yamaguchi et al. 2021). Additionally, prolonged HS resulted in increased level of HSPs which are maintained by a peptidyl prolyl cis/trans isomerase ROF1, ROF1 and HSP90.1. In the presence of the transcription factor HsfA, ROF1 and HSP90.1 move to the nucleus which is essential for thermotolerance (Meiri and Breiman 2009). HSFs function in the interaction of thermomemory with the glucose signaling pathway which promotes the H3K4me3 at thermomemory-related loci (Sharma et al. 2019). Concurrently HSFA1s positively regulates HLP1 transcription which regulates the heat stress responsive gene expression, suggesting the cooperation of HSFs and methylation for maintenance of heat stress memory.

Hormonal regulations

Plant growth regulators or phytohormones are endogenous low molecular compounds that regulate seed germination, growth, development, and stress adaptation (Liu et al. 2021c). Hormonal signaling is intrinsically associated with plant stress and the stress-mediated memory. As a priming agent, phytohormones equip plants with stress responses and tolerance for both biotic and abiotic stresses and prepare plants for future stresses (Liu et al. 2021c). Hormones can directly establish the PSM probably through chromatin regulations and gene expression. For instance, ABA treatment triggered histone deacetylation which resulted in the upregulation of gene expression accompanied with hypersensitive responses leading to freezing tolerance (Zhu et al. 2008). ABA-mediated HOS15 expression regulates ABA homeostasis through chromatin remodeling and provides tolerance to drought and heat stress in both Arabidopsis and tall fescue (Zhang et al. 2019). A SWI/SNF chromatin remodeling protein, BRAHMA (BRM), along with a putative helicase (FGT1) is specifically required for heat stress memory where BRM is regulated by ABA-dependent phosphorylation (Han et al. 2020). Thus, it implies that ABA treatment can be the nexus to establish drought and heat stress memories. It is also reported that priming plants with SA resulted in elevated occupancy of H3K4me3 around the transcription start site which is associated with defense-related gene expression. (Mozgová and Hennig 2015). Furthermore, polycomb repressive protein LHP1 mediated H3K27me3 controls the expression of stress-responsive genes, and responses to the stress hormones SA and ABA as well as pathogen susceptibility (Ramirez-Prado et al. 2019).

Conversely, environmental stresses can also regulate the hormonal biosynthesis and homeostasis by bringing epigenetic changes which is essential to withstand stress conditions (Mladenov et al. 2021). ABA and JA levels were found to be associated with strong memory in drought-stress primed rice seedlings in a cyclic changing pattern with increased expression of the genes regulating photosynthesis, metabolic, and hormonal biosynthesis (Li et al. 2019). Insect herbivores and/or mechanical damage has exhibited JA-mediated TSM in Arabidopsis. Tomato plants showed higher resistance to earworms in the progeny through the MeJA-mediated histone modifications occurred in the parental line (Rasmann et al. 2012). Plants having dysfunction in JA perception and siRNA biogenesis failed to activate this inherited resistance in Arabidopsis which confirmed the JA involvement in TSM. Similar results have been reported for rice primed with MeJA and wounding (Kim et al. 2017). Acetic acid priming could induce increased survivability under subsequent drought stress in rice through the induction of JA signaling (Ogawa et al. 2021). SA is involved in plant response to biotic stress including roles in chromatin remodeling during the recovery stage period (Dowen et al. 2012). An increased expression of SA-dependent *PR1* gene has been reported in Arabidopsis mutants impeded with DNA methylation with the display constitutive priming of SA (Luna and Ton 2012). Moreover, Choi et al. (2012) reported that histone deacetylase mutant *hda19* had higher expression of SA biosynthesis genes with higher SA content which concluded that HDA19 controls the deacetylation and repression of SA-related genes. Biosynthesis of another stress-responsive hormone ethylene was found to be associated with the water logging tolerance during the second stress event in bread wheat (Hartman et al. 2019). Other than major stress hormones, cytokinin (CK), and auxin signaling are also reported to embroil chromatin changes in response to environmental cues. Therefore, it is suggestive that hormonal signaling, and their interconnection play a pivotal role in environmental cue-responsive epigenetic changes.

Metabolic regulations

Unfavorable environmental conditions can bring a major alteration in primary metabolites such as amino acid and sugar, and metabolic precursors such as acetyl-CoA and S-Adenosyl methionine (SAM) which are associated with plant responses and adaptation (Mladenov et al. 2021). Several sugar and sugar derivatives comprise the sugar signaling and are involved in plant growth and stress responses. For example, primary carbohydrate metabolisms are regulated by FRUCTOSE-BISPHATE ALDOLASE 6 (FBA6) gene which participates in heat stress memory at the shoot apical meristem where HSFA2A directly control the expression of FBA6 in Arabidopsis (Olas et al. 2021). Sucrose regulates genes expression of HSI2 and HSL1 which are involved in seed maturation and flowering together with the H3K27me3 mediated FLC control (Zeng et al. 2020; Kouznetsova and Tchekanov 2019; Chhun et al. 2016). In addition to regulating the developmental process, sugar signaling is involved in shaping the plant responses to biotic and abiotic stresses, for instance thermotolerance in Arabidopsis. Higher glucose led to the higher expression of HSFA1S and HSP70 which enhance the plant tolerance to heat stress (Kose et al. 2012). Sharma et al. (2019) suggested that histone marks are involved in this process. The involvement of glucose in mediating histone acetylation process through these genes have been also reported in Zhou et al. (2013). However, there is a tight engagement of epigenetic modifications with sensing and transmitting sugar signals. Therefore, it would be interesting to find out whether sugar-induced epigenetic modifications can create ISM and TSM.

Regulations of ROS through ROS scavenging, and maintenance of cell turgor pressure are important features to enhance adaptation in plants. Proline accumulation enables plants to regulate the ROS, maintain cell turgor pressure, and can also act as a signaling molecule (Uzal 2022). Proline acts as an osmoprotectant under stress conditions which mitigates stresses including heat and cold stress (Mattioli and Palombi 2020). Arabidopsis primed with salinity stress showed upregulation of proline biosynthesis genes with an increase of H3K4me3 resulting in histone methylation which was retained during the recovery stage. Recurrent salinity stress showed stronger induction of proline accumulation which supports the role of proline in the establishment of stress memory through chromatin remodeling (Szabados and Savouré 2010). These findings suggest that changes in metabolic features influence the epigenetic mechanisms which are the key players in the establishment of stress memory.

Application of PSM concept for stress tolerance

Plants are exposed to a range of abiotic and biotic stress conditions frequently and intensively which are predicted to be increased in the future. Hence, new strategies for enhancement of plant tolerance to multiple stresses need to be developed. Considering the potential roles of stress memory in providing better tolerance at later phase, priming the plants by using priming agents, biotic, and abiotic stresses have been explored (Table 1). Plants' experience of primary stress elicits the positive impact on secondary biotic, and abiotic stress through the synergistic signaling pathways. Priming the plants provides a new means to stimulate adaptable stress responses, safeguard crop production and engineer climate resilient crops for the future (Liu et al. 2021a). This section summarizes the recent progress of exploitation of stress memory concept through the application of priming agents for better tolerance to biotic and abiotic stresses.

Priming agents for PSM and tolerance to biotic stress

Biotic stress such as pathogenic microbes and insect pests cause severe damage to growth resulting in a significant loss of crop production. Among all other strategies in disease and insect management, the enhancement of plant resistance by priming agents has been exploited. Pretreating the plants with biological, physical, and chemical agents activates and enhances the defense systems resulting in the primed state that exhibits resistance toward the pathogens and pests (Table 1).

Several studies have reported that priming agents lead to the development of the primed state and respond quickly upon exposure to pathogens and insects (Yang et al. 2023). Among the chemical priming agents, SA, MeJA, BABA, chitosan, INA, and nanomaterial formulated from membrane lipids of *Trichoderma brevicompactum* have been mostly used. Treating the seeds or seedlings with priming agents provided better tolerance towards a diverse range of pathogenic microbes including powdery mildew, *Fusarium* wilt, *Ralstonia, Alternaria, Pseudomonas,* bacterial wilt, and spot, *Cercospora*, and *Fusarium* root rot in different plant species (Kelbessa et al. 2023; Chakraborti et al. 2022; Kappel et al. 2022; Yang et al. 2023; Martínez-Aguilar et al. 2021; Yadav et al. 2021; Westman et al. 2019). Besides, priming the plants with chemical and biological priming

Table 1 Reported studies of priming agents in establishment of stress memory for enhanced biotic and abiotic stress tolerance in crop plants

Primary stress/priming agents	Secondary stress	Mechanisms	Plant species	References
High temperature and high light intensity	After 2 days of recovery application of high temperature	Secondary metabolites formation in chlorophyll pigments	Tomato	Zhou et al. (2020)
Application of high temperature for 7 consecutive days	No secondary stress is required	Small RNA assisted epigenetic modification	Mustard	Byeon et al. (2019)
Heat stress application on booting and anthesis stage for 5 consecutive days	Heat application for 5 days after 15 days of anthesis	Formation of protective compounds and activation of superoxide dismutase and peroxidase	Bread wheat	Fan et al. (2018)
Cyclic application of temperature stress from flowering till harvest in parents	Cyclic application of temperature stress from flowering till harvest in progeny	Small RNA assisted epigenetic modification	Durum wheat	Liu et al. (2021b)
Restrictions of water supply after germination	Again 4 days drought stress application, after rewatering for 1 day	Altered gene expression and formation of protective compounds	Soybean	Kim and Chae (2020)
Continuous drought or water-logged stress for several seasons	Application of more stress followed by recovery	Altered gene expression and formation of protective compounds	Foxtail millet	Lukić et al. (2023)
Application of drought stress (DS) for several days after 20 days of germination	Subsequent DS cycle for 50 days after 6 days of the recovery from 1st stress	Higher quantity synthesis of IAA and ABA	Cow pea	Tankari et al. (2021)
Water deficit	Water deficit followed by rewatering (7 cycles)	DNA methylation	White clover	González and Oreite (2018)
Cutting down water supply from the beginning till full flowering	Repeated drought stress in next several generations	Secondary metabolites formation and store in seeds	Oilseed rape	Hatzig et al. (2019)
Drought stress is applied in parents from tilling to grain filling	Repeated drought stress in next several generations	Transgenerational epimutation due to stress	Rice	Zheng et al. (2013)
Application of drought stress (DS) for 10 days for first several generations	Application of DS in same pattern at fourth generation	Accumulation of proline and glycine betaine	Bread wheat	Wang et al. (2018)
Withdrawal of water in parents during reproductive stage	Withdrawal of water in progeny during the reproductive stage	DNA methylation	Durum wheat	Liu et al. (2021a)
Salt shock to the seeds at lower concentration	Higher salt treatment later stage	Higher antioxidative activities	Faba bean	Nasrallah and Atia (2022)
PEG mediated seed treatment before sowing	Salinity treatment at later phage	Higher photosynthetic activities and superior fruit quality	Tomato	Habibi et al. (2023)
Salinity treatment during five leaf stage	Withold of water during reproductive stage	Higher tolerance at physiological, transcriptional, and hormonal levels	Rice	Rossatto et al. (2023)
Salinity treatment to the trifoliate stage of seedlings	Higher salinity treatment to the late vegetative stage	Histone marks mediated ion homeostasis, cell wall modification, and stress responses	Soybean	Yung et al. (2021)
Waterlogging at the seven-leaf stage	Waterlogging during the reproductive stage	Higher energy metabolism and stress defense due to hormonal biosynthesis	Wheat	Wang et al. (2016)
Seed treatment with H_2O_2	Waterlogging at the V3 stage	Higher waterlogging tolerance through the stomatal activities and higher photosynthesis	Maize	Wang and Hu (2022)
Waterlogging priming for one, two, and three generations	Hypoxia stress at the next generation	Enhanced tolerance through the photosynthetic efficiency and hormonal biosynthesis	Wheat	Feng and Wang (2022)
Seed priming using different concentration of P and Zn	Seedlings were grown under lower P and Zn	Enhanced seed germination, higher uptake of nutrient, and improved growth	Barley	Ajouri et al. (2004)
Seed priming using Zinc	Plants were grown under Zn deficient soil	Enhanced early growth and grain yield	Maize	Tamindžić et al. (2021)

Table 1 (continued)

Primary stress/priming agents	Secondary stress	Mechanisms	Plant species	References
Micronutrient seed priming	Seedlings were grown under micronutrient deficient soil	Higher seed germination and better plant growth	Maize	Nciizah et al. (2020)
Seed priming using Selenium	Drought stress at multiple leaves, flowering, and seed filling stage	improved biochemical and photosynthetic performance	Quinoa	Raza et al. (2024)
Suckers were treated with salicylic acid	Plants at 30 days after planting were treated with higher dose of cadmium (Cd)	Antioxidative mediated tolerance to Cd	Mint	Zaid et al. (2022)
Seed priming using water, SA, proline, and combination of SA and proline	Seeds were grown in media containing Cd in two different concentrations	Higher germination and root growth with lower Cd accumulation	Rice	Karalija et al. (2021)
BABA	*Botrytis cinerea*	BABA established the stress memory through DNA methylation at the promotor regions of stress responsive genes and conferred resistance	Tomato	Catoni et al. (2022)
JA and/or BABA	Spider mites, caterpillars, aphids, *Botrytis cinera*, powdery mildew	Primed seedlings exhibited higher resistance to insects and pests for a few weeks after treatment	Tomato	Worrall et al. (2011)
Rutin (flavonoid)	Whitefly	Priming enhanced resistance to whitefly by increasing the flavonoid accumulation, callose deposition, and JA dependent gene expression	Tomato	Tang et al. (2023)
1,2,4-triazolyldithiocarbamate silver nano conjugate	Bakanae disease of rice	Primed plant exhibited improved resistance to pathogen	Rice	Sharma et al. (2022)
ROS-generating nanoparticles	Salinity and blast pathogen	Primed plants exhibited better tolerance associated with metabolic and transcriptional reprogramming, activation of hormonal and MAPK signal pathway	Rice	Yan et al. (2023)
Heavy metals (copper and cadmium)	Herbivory insects	Priming enhanced the synthesis of volatile organic compounds and increased jasmonic acid	Rice	Winter et al. (2012)
Botanical, chemical, and biological priming agents	Root rot nematode	Primed plants exhibited reduced nematode infestation	Bread wheat	Arshad et al. (2022)
Hydro- and osmotic priming	*Aspergillus niger*	Primed plants exhibited better resistance to disease with upregulation of PR-protein related gene expression	Bread wheat	Gul et al. (2022)
Micromonospora spp	*Botrytis cinerea*	Induction of jasmonate-regulated defense upon exposure to fungal pathogen and the resistance last longer	Tomato	Martínez-Hadalgo et al. (2015)
Trichoderma atroviride	Root knot nematode	Primed plants exhibited systemic resistance to nematode in both parental and progeny without compromising the growth	Tomato	Medeiros (2017)

Table 1 (continued)

Primary stress/priming agents	Secondary stress	Mechanisms	Plant species	References
Colletotrichum tropicale	Leaf cutting insect	Endophytes altered the leaf chemistry and decreased the damage caused by the leaf cutting insect	Cucumber	Estrada et al. (2013)
Foliar spray of *Trichoderma atroviride*	No secondary stress is required	Secondary metabolites formation and store in cells	Beet	Kappel et al. (2022)
Foliar spray of *Trichoderma logibrachiatum* during vegetative growth stage	No secondary stress is required	Formation of protective compounds in cells	Onion	Abdelrahm-an et al. (2016)
Ensifer meliloti	Aphid	Priming induced the systemic resistance towards aphids	Barley	Wehner et al. (2021)

agents improves plant's ability to protect them from major insect pests (Luna et al. 2012a, b; Rasmann et al. 2012).

Priming-mediated activation of defense mechanisms includes biosynthesis of metabolites, phytohormones, antioxidant production, accumulation of proteins, and upregulation of stress-responsive gene expression (Catoni et al. 2022; Slaughter et al. 2012). These led to the construction of a primed state in treated plants and response quicker upon exposure to pathogens and insects which establish the stress memory for both short-term and long-term (Kappel et al. 2022; Luna et al. 2012b) . Besides, priming agents mediated epigenetic changes such as DNA methylation have also been reported to enhance the plant resistance towards the pathogens and insects. For instance, Catoni et al. (2022) treated tomato plants with β-aminobutyric acid (BABA) which resulted in increased resistance to the fungal pathogen, *Botrytis cinerea*. The establishment of primed state through BABA treatment led to CHH hypomethylation and subsequently enhanced the tolerance to pathogens. This study concluded that the application of BABA can establish stress memory through the epigenetic changes that enhance the plant resistance to pathogens at later phage. In addition to short-term stress memory, chemical, and biological priming agents have also been reported to establish long-term transgenerational stress memory (Luna et al. 2012a; Slaughter et al. 2012). BABA-treated Arabidopsis plants exhibited enhanced resistance to biotic stress through the faster and higher accumulation of stress-responsive genes at both parental and offspring lines (Slaughter et al. 2012). BABA treatment enhanced epigenetic marks 3K4me2/3 on defense gene promotors and enhanced the gene expression to establish the primed state, demonstrating that priming agents can also establish the stress memory through epigenetic changes resulting in a better resistance to biotic stress.

Priming agents for PSM and tolerance to abiotic stress

Climate change results in heat waves, drought, flooding, salinity, and heavy metal contaminations and has been one of the potential threats to crop production. Establishing the stress memory through either mild abiotic stresses and/or priming agents has been exploited for enhancing the abiotic stress tolerance in different crops (Table 1). For instance, treating seedlings with mild heat stress resulted in thermotolerance at later stages in different plants including Arabidopsis, tomato, and barley (Liu et al. 2021a; Singh et al. 2021; Wang and Li 2020; Brzezinka et al. 2018). Mild drought as a primary stress resulted in activation of regulatory networks, the establishment of stress memory, and improved tolerance to recurrent drought stress at a later phage as reviewed by Kambona et al. (2023). Besides, priming the seedlings with mild salinity and lower concentration of heavy metals can enhance the plant tolerance to higher salinity and higher concentration of heavy metals respectively at the later stage (Cong et al. 2019; Yan et al. 2015; Janda et al. 2016). Long-term stress memory induced by treating the parental lines leads to enhanced abiotic stress tolerance in the next generations (Yadav et al. 2022). For instance, treating the parental lines with drought stress established the stress memory linked to photosynthetic and redox-related mechanisms which enhanced the offspring's drought tolerance with increased biomass and reproductive output (Lukić et al. 2023).

Use of mild abiotic stress such as salinity, heat shock, heavy metals, nutrient deficiency, and waterlogging have been also exploited for enhancing the plant tolerance towards the moderate to high level of respective abiotic stresses in different plants as summarized in Table 1. Primed Faba bean plants with mild salinity stress exhibited higher level of tolerance due to the higher antioxidative activities and lower accumulation of ROS (Nasrallah and Atia 2022). On the other hand, non-primed plants were affected by higher level of salinity stress due to higher accumulation of ROS. Another study carried out by Yung et al. (2021) reported the positive impact of mild salt treatment in soybean. The primed plant exhibited modifications at the transcriptional levels due to the alteration in histone and provided tolerance to moderate salt treatment. Priming the seeds or seedling with short time waterlogging impacts on the plant performance under the long-time waterlogging condition at later stage. As an example, wheat seedlings primed with waterlogging exhibited better tolerance towards the waterlogging stress during the anthesis period with better yield performance compared to the non-primed plants (Wang et al. 2016).

In addition to transferring the stress memory from one stage to another stage, long term stress memory (TSM) has been reported in wheat variety for waterlogging tolerance as well. Seedlings generated from primed plants exhibited better adaptation to the waterlogging condition with improved root system architecture, antioxidative defense and better photosynthetic efficiency (Feng and Wang 2022). Priming the seeds with nutrient has been exploited for improving the plant tolerance towards the nutrient deficient soils. For an instance, Nciizah et al. (2020) reported that priming the maize seeds with lower concentration of zinc, boron, and molybdenum for longer duration enhanced the plant capacity to grow under the nutrient depleted soil. Priming the maize seeds with zinc improved plant performance in zinc depleted soil (Tamindžić et al. 2021). These results suggest that both the higher and lower concentration of micronutrient can potentially improve the plants' capacity to grow under nutrient depleted soils.

Besides the abiotic stresses as a primary stress for inducing the primed state and establishing stress memory, chemical priming agents have also been successfully exploited (Table 1). Several studies suggested the use of chemical priming agents such as H_2O_2, selenium, SA, and proline initiate and activate the defense systems against waterlogging, drought, and heavy metal stress (Raza et al. 2024; Wang and Hu 2022; Zaid et al. 2022; Karalija et al. 2021). As an example, priming the rice plants with SA enhances the antioxidative enzymes and established short-term SSM which are revealed by their higher tolerance in later phase in rice and wheat (Wang and Li 2020). Treating the seedlings results in higher antioxidative and enzymatic activities, improved photosynthetic and sugar metabolism, stress-responsive gene expression, and accumulation of osmolytes and molecular chaperon prepares the plants for the secondary stresses (Byeon et al. 2019). Besides, primary stress-induced epigenetic changes store and transfer to the later phase which build up the long-term stress memory. These imply that priming the seedlings with mild abiotic stresses and/or primary agents can be a potential strategy for improving the plants' tolerance to abiotic stresses and mitigating the negative impact of climate change.

Priming agents for PSM and cross-tolerance

Exposure to one kind of stress may lead to the development of tolerance to another type of stress due to the shared and common stress response and signaling pathway (Foyer et al. 2016). The primary stress acts as a priming agent, and activates the defense systems which acclimate, and prepare plants for secondary biotic and/or abiotic stresses (Foyer et al. 2016). As an example, short-term high temperature stress improved the salinity stress tolerance through the increased antioxidative activities, and the treated plants exhibited lower damage during the later phage (Hossain et al. 2016). Rossatto et al. (2023) reported the improvement of drought stress tolerance by priming the plants with low doses of salinity stress at an earlier stage. Additionally, priming the plants with microbes can enhance their resistance to other types of biotic stresses (Tiwari et al. 2022). As an example, priming the tomato plants with *Micromonospora* strains and *Fusarium oxysporum* improved the plant tolerance to several pathogenic fungi and wilt disease, respectively by activating the jasmonate signaling pathway (Martinez-Hadalgo et al. 2015). Priming the plants with symbiotic microbes improved the plant tolerance to insects in cucumber and barley (Wehner et al. 2021). It is also reported that abiotic stress-induced priming can improve the plant tolerance to pathogens and insects by regulating the hormonal signaling, and antioxidative activities (Tiwari et al. 2022). As an example, plants primed with heavy metal showed plant tolerance to herbivores and aphid attacks (Guo and Sun 2020). These results suggested that primary stress and/or priming agents can be used as a potential management tool to improve the plant for future climatic conditions.

Conclusion

Plant stress memory is a captivating phenomenon in the field of plant science that has generated significant attention from researchers. This review offers a comprehensive presentation of plant stress memory, PSM, and its underlying regulatory mechanisms at the molecular, physiological, and epigenetic levels. The exploration of epigenetic modifications, hormonal signaling, metabolic changes, and stress-responsive genes has yielded valuable insights into plant responses and adaptations, not only to primary stresses but also to secondary and recurrent stresses in subsequent generations.

PSM possesses the potential to enhance stress tolerance, which has been harnessed through priming techniques. Priming plants with mild primary stress and priming agents whether biological or chemical, establishes PSM and facilitates better adaptation in later stages. This approach holds promise as a strategy for developing climate-resilient crops. As we continue to unravel the intricacies of plant stress memory, this field of research will remain a fertile ground for exploration and innovation, with promising implications for sustainable crop production and environmental resilience on a broader scale.

In recent years, PSM has garnered attention among biologists for unraveling the underlying mechanisms and its potential applications in addressing climate change. However, there are still unanswered questions that need to be addressed to expand our understanding of PSM and its integration into practical applications. Some areas that could be considered for constructing new research include:

1. Unraveling the specific signaling pathways and molecules involved in memory establishment.
2. Investigating plants' strategies for retaining the established memory and identifying factors determining the duration of memory within the same generation and/or across generations.
3. Studying mechanisms in memory establishment for multiple stresses simultaneously and exploring cross-talk among signaling pathways to understand how plants prioritize one stress over another.
4. Examining PSM at the community and population levels in cropping ecosystems.
5. Conducting feasibility studies to translate the PSM concept into developing new varieties through plant breeding which are capable of coping with climate change.

Addressing these questions may lead to a better understanding of PSM as a whole and expand its applications in plant varietal development, contributing to efforts to combat climate change.

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Declarations

Conflict of interest All the authors declare no conflicts of interest regarding this study.

References

Abdelrahman M, Abdel-Motaal F et al (2016) Dissection of *Trichoderma longibrachiatum*-induced defense in onion (*Allium cepa* L.) against *Fusarium oxysporum* f. sp. *cepa* by target metabolite profiling. Plant Sci 246:128–138. https://doi.org/10.1016/j.plantsci.2016.02.008

Ajouri A, Asgedom H, Becker M (2004) Seed priming enhances germination and seedling growth of barley under conditions of P and Zn deficiency. J Plant Nutr Soil Sci 167:630–636. https://doi.org/10.1002/jpln.200420425

Arshad U, Jabran M et al (2022) Seed-priming: a novel approach for improving growth performance and resistance against root-knot nematode (*Meloidogyne incognita*) in bread wheat (*Triticum aestivum* L.). Gesunde Pflanzen 74:1041–1051. https://doi.org/10.1007/s10343-022-00672-9

Andreasson E, Jenkins T et al (2005) The MAP kinase substrate MKS1 is a regulator of plant defense responses. EMBO J 24(14):2579–2589. https://doi.org/10.1038/sj.emboj.7600737

Beckers GJ, Jaskiewicz M et al (2009) Mitogen-activated protein kinases 3 and 6 are required for full priming of stress responses in *Arabidopsis thaliana*. Plant Cell 21(3):944–953. https://doi.org/10.1105/tpc.108.062158

Baillo EH, Kimotho RN et al (2019) Transcription factors associated with abiotic and biotic stress tolerance and their potential for crops improvement. Genes 30:771. https://doi.org/10.3390/genes10100771

Bäurle I, Trindade I (2020) Chromatin regulation of somatic abiotic stress memory. J Exp Bot 71:5269–5279. https://doi.org/10.1093/jxb/eraa098

Berry S, Dean C (2015) Environmental perception and epigenetic memory: mechanistic insight through FLC. Plant J 83:133–148. https://doi.org/10.1111/tpj.12869

Bhar A, Chakraborty A, Roy A (2022) Plant responses to biotic stress: old memories matter. Plants 11(1):84. https://doi.org/10.3390/plants11010084

Bilichak A, Ilnytskyy Y et al (2015) The elucidation of stress memory inheritance in *Brassica rapa* plants. Front Plant Sci 6:1–20. https://doi.org/10.3389/fpls.2015.00005

Breusegeum FV, Remacle C (2023) Oxidative stress responses in plants. Free Radical Biol Med 204:394. https://doi.org/10.1016/j.freeradbiomed.2023.05.012

Brodersen P, Petersen M et al (2006) Arabidopsis MAP kinase 4 regulates salicylic acid- and jasmonic acid/ethylene-dependent responses via EDS1 and PAD4. Plant J 47(4):532–546. https://doi.org/10.1111/j.1365-313X.2006.02806.x

Brzezinka K, Altmann S, Bäurle I (2018) BRUSHY1/TONSOKU/MGOUN3 is required for heat stress memory. Plant Cell Environ 42:753–1086. https://doi.org/10.1111/pce.13365

Byeon B, Bilichak A, Kovalchuk I (2019) Transgenerational response to heat stress in the form of differential expression of noncoding RNA fragments in *Brassica rapa* plants. The Plant Genome 12(1):180022. https://doi.org/10.3835/plantgenome2018.04.0022

Castel SE, Martienssen RA (2013) RNA interference in the nucleus: roles for small RNAs in transcription, epigenetics and beyond. Nat Rev Genet 14:100–112. https://doi.org/10.1038/nrg3355

Catoni M, Alvarez-Venegas R et al (2022) Long-lasting defence priming by β-aminobutyric acid in tomato is marked by genome-wide changes in DNA methylation. Front Plant Sci 13:836326. https://doi.org/10.3389/fpls.2022.836326

Chakraborti S, Bera K et al (2022) Bio-priming of seeds: plant stress management and its underlying cellular, biochemical, and molecular mechanisms. Plant Stress 3:100052. https://doi.org/10.1016/j.stress.2021.100052

Challinor AJ, Watson J et al (2024) A meta-analysis of crop yield under climate change and adaptation. Nat Clim Change 4:287–291. https://doi.org/10.1038/nclimate2153

Charng Y, Mitra S, Yu S (2023) Maintenance of abiotic stress memory in plants: lessons learned from heat acclimation. Plant Cell 35(1):187–200. https://doi.org/10.1093/plcell/koac313

Chen Q, Zhang J, Li G (2022) Dynamic epigenetic modifications in plant sugar signal transduction. Trends Plant Sci 27(4):379–390. https://doi.org/10.1016/j.tplants.2021.10.009

Chester KS (1933) The problem of acquired physiological immunity in plants. Q Rev Biol 8:275–324. https://doi.org/10.1086/394440

Chhun T, Chong SY et al (2016) HSI2 repressor recruits MED13 and HDA6 to down-regulate seed maturation gene expression directly during Arabidopsis early seedling growth. Plant Cell Physiol 57:1689–1706. https://doi.org/10.1093/pcp/pcw095

Choi SM, Song HR et al (2012) HDA19 is required for the repression of salicylic acid biosynthesis and salicylic acid-mediated defence responses in *Arabidopsis*. Plant J 71(1):135–146. https://doi.org/10.1111/j.1365-313X.2012.04977.x

Cong W, Miao Y et al (2019) Transgenerational memory of gene expression changes induced by heavy metal stress in rice (*Oryza sativa* L.). BMC Plant Biol 19:282. https://doi.org/10.1186/s12870-019-1887-7

Crisp PA, Ganguly D et al (2016) Reconsidering plant memory: intersections between stress recovery, RNA turnover, and epigenetics. Sci Adv 2(2):e1501340. https://doi.org/10.1126/sciadv.1501340

Cui N, Chen X et al (2021) Changes in the epigenome and transcriptome of rice in response to *Magnaporthe oryzae* infection. Crop J 9(4):843–853. https://doi.org/10.1016/j.cj.2020.10.002

Davies KA, Bergmann DC (2014) Functional specialization of stomatal bHLHs through modification of DNA-binding and phosphoregulation potential. Proc Nat Aca Sci USA 111(43):15585–15590. https://doi.org/10.1073/pnas.1411766111

Demongeot J, Hasgui H et al (2019) Memory in plants: boolean modelling of the learning and store/recall memory functions in response to environmental stimuli. J Theor Biol 467:123–133. https://doi.org/10.1016/j.jtbi.2019.01.019

Dowen RH, Pelizzola M et al (2012) Widespread dynamic DNA methylation in response to biotic stress. Proc Nat Aca Sci USA 109(32):E2183–E2191. https://doi.org/10.1073/pnas.1209329109

Driedonks N, Rieu I, Vriezen WH (2016) Breeding for plant heat tolerance at vegetative and reproductive stages. Plant Reprod 29:67–79. https://doi.org/10.1007/s00497-016-0275-9

Estrada C, Wcislo WT, Bael SAV (2013) Symbiotic fungi alter plant chemistry that discourages leaf-cutting ants. New Phytol 198:241–251. https://doi.org/10.1111/nph.12140

Fabrizio P, Garvis S, Palladino F (2019) Histone methylation and memory of environmental stress. Cells 8(4):339. https://doi.org/10.3390/cells8040339

Fan Y, Ma C et al (2018) Heat Priming during early reproductive stages enhances thermo-tolerance to post-anthesis heat stress via improving photosynthesis and plant productivity in winter wheat (*Triticum aestivum* L.). Front Plant Sci 9:805. https://doi.org/10.3389/fpls.2018.00805

Feng XJ, Li JR et al (2016) Light affects salt stress-induced transcriptional memory of P5Cs1 in *Arabidopsis*. Proc Nat Aca Sci 113:E8335–E8343. https://doi.org/10.1073/pnas.1610670114

Feng K, Wang X (2022) Waterlogging priming enhances hypoxia stress tolerance of wheat offspring plants by regulating root phenotypic and physiological adaption. Plants 28:1969. https://doi.org/10.3390/plants11151969

Foyer CH, Rasool B et al (2016) Cross tolerance to biotic and abiotic stresses in plants: a focus on resistance to aphid infestations. J Exp Bot 67:2025–2037. https://doi.org/10.1093/jxb/erw079

Friedrich T, Faivre L et al (2018) Chromatin-based mechanisms of temperature memory in plants. Plant Cell Environ 42:762–770. https://doi.org/10.1111/pce.13373

Gao Z, Zhou Y, He Y (2022) Molecular epigenetic mechanisms for the memory of temperature stresses in plants. J Genet Genom. https://doi.org/10.1016/j.jgg.2022.07.004

González APR, Oreite V et al (2018) Transgenerational effects and epigenetics memory in the clonal plant *Trifolium repens*. Front Plant Sci 9:1677. https://doi.org/10.3389/fpls.2018.01677

Guerra T, Schilling S et al (2020) Calcium-dependent protein kinase 5 links calcium signaling with N-hydroxy-lpipecolic acid- and SARD1-dependent immune memory in systemic acquired resistance. New Phytol 225(1):310–325. https://doi.org/10.1111/nph.16147

Gul S, Hussain A et al (2022) Hydropriming and osmotic priming induce resistance against *Aspergillus niger* in wheat (*Triticum aestivum* L.) by activating β-1, 3-glucanase, Chitinase, and Thaumatin-like protein genes. Life 12(12):2061. https://doi.org/10.3390/life12122061

Guo H, Sun Y et al (2020) O3-induced priming defense associated with the abscisic acid signaling pathway enhances plant resistance to *Bemisia tabaci*. Front Plant Sci 11:93. https://doi.org/10.3389/fpls.2020.00093

Gupta S, Bhar A et al (2013) *Fusarium oxysporum* f.sp. *ciceri* Race 1 induced redox state alterations are coupled to downstream defense signaling in root tissues of chickpea (*Cicer arietinum* L.). PLoS ONE 8(9):e73163. https://doi.org/10.1371/journal.pone.0073163

Habibi N, Aryan S et al (2023) Potential benefits of seed priming under salt stress conditions on physiological, and biochemical attributes of micro-tom tomato plants. Plants 12:2187. https://doi.org/10.3390/plants12112187

Halder K, Chaudhuri A et al (2022) Chromatin-based transcriptional reprogramming in plants under abiotic stresses. Plants 11(11):1449. https://doi.org/10.3390/plants11111449

Han Y, Reyes AA, Malik S, He Y (2020) Cryo-EM structure of SWI/SNF chromatin remodelling complex nucleosome. Nature 579:452–455. https://doi.org/10.1038/s41586-020-2087-1

Hartman S, Liu Z et al (2019) Ethylene-mediated nitric oxide depletion pre-adapts plants to hypoxia stress. Nat Commun 10(1):4020. https://doi.org/10.1038/s41467-019-12045-4

Hatzig SV, Nuppenau J et al (2019) Drought stress has transgenerational effects on seeds and seedlings in winter oilseed rape (*Brassica napus* L.). BMC Plant Biol 18:1–13. https://doi.org/10.1186/s12870-018-1531-y

He Y, Li Z (2018) Epigenetic environmental memories in plants: establishment, maintenance, and reprogramming. Trends Genet 34:856–866. https://doi.org/10.1016/j.tig.2018.07.006

Heard E, Martienssen RA (2014) Transgenerational epigenetic inheritance: myths and mechanisms. Cell 27:95–109. https://doi.org/10.1016/j.cell.2014.02.045

Hossain MA, Burritt DJ, Fujita M (2016) Cross-stress tolerance in plants: molecular mechanisms and possible involvement of reactive oxygen species and methylglyoxal detoxification systems. Willey, Hoboken, pp 327–380. https://doi.org/10.1002/9783527694570.ch16

Jacques C, Salon C et al (2021) Drought stress memory at the plant cycle level: a review. Plants 10(9):1873. https://doi.org/10.3390/plants10091873

Jagodzik P, Tajdel-Zielinska M et al (2018) Mitogen-activated protein kinase cascades in plant hormone signaling. Front Plant Physiol 9:1387. https://doi.org/10.3389/fpls.2018.01387

Janda T, Darko É, Shehata S et al (2016) Salt acclimation processes in wheat. Plant Physiol Bioch 101:68–75. https://doi.org/10.1016/j.plaphy.2016.01.025

Jaskiewicz M, Conrath U, Peterhälnsel C (2011) Chromatin modification acts as a memory for systemic acquired resistance in the plant stress response. EMBO Rep 12(1):50–55. https://doi.org/10.1038/embor.2010.186

Jeong S, Lim CW, Lee SC (2020) The pepper MAP kinase CaAIMK1 positively regulates ABA and drought stress responses. Front Plant Sci 11:720. https://doi.org/10.3389/fpls.2020.00720

Jing Y, Guo Q, Lin R (2018) The B3-domain transcription factor VAL1 regulates the floral transition by repressing FLOWERING LOCUS T. Plant Physiol 181:236–248. https://doi.org/10.1104/pp.19.00642

Kambona CM, Koua PA et al (2023) Stress memory and its regulations in plants experiencing recurrent drought conditions. Theor Appl Genet 136:26. https://doi.org/10.1007/s00122-023-04313-1

Kang H, Fan T et al (2022) Histone modification and chromatin remodelling in plant response to pathogens. Front Plant Sci 13:986940. https://doi.org/10.3389/fpls.2022.986940

Kappel L, Kosa N, Gruber S (2022) The multilateral efficacy of chitosan and *Trichoderma* on sugar beet. J Fungi 8(2):137. https://doi.org/10.3390/jof8020137

Karalija E, Selović A et al (2021) Use of seed priming to improve Cd accumulation and tolerance in *Silene sendtneri*, novel Cd hyperaccumulator. Ecotoxicol Environ Saf 210:11188. https://doi.org/10.1016/j.ecoenv.2020.111882

Kelbessa BG, Dubey M et al (2023) Potential of plant growth-promoting rhizobacteria to improve crop productivity and adaptation to a changing climate. CABI Rev. https://doi.org/10.1079/cabireviews.2023.0001

Kim YK, Chae S et al (2020) Recurrent drought conditions enhance the induction of drought stress memory genes in *Glycine max* L. Front Genet 11:576086. https://doi.org/10.3389/fgene.2020.576086

Kim JM, To TK et al (2017) Acetate-mediated novel survival strategy against drought in plants. Nature Plant 3(7):1–7. https://doi.org/10.1038/nplants.2017.97

Kose S, Furuta M, Imamoto N (2012) Hikeshi, a nuclear import carrier for Hsp70s, protects cells from heat shock-induced nuclear damage. Cell 149:578–589. https://doi.org/10.1016/j.cell.2012.02.058

Kotkar H, Giri A (2020) Plant epigenetics and the ‘intelligent’ priming system to combat biotic stress. Elsevier, Amsterdam

Kouznetsova VL, Tchekanov A et al (2019) Polycomb repressive 2 complex-molecular mechanisms of function. Protein Sci 28:1387–1399. https://doi.org/10.1002/pro.3647

Lämke J, Brzezinka K et al (2016) A hit-and-run heat shock factor governs sustained histone methylation and transcriptional stress memory. EMBO J 35(2):162–217. https://doi.org/10.15252/embj.201592593

Lämke J, Bäurle I (2017) Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. Genome Biol 18:124. https://doi.org/10.1186/s13059-017-1263-6

Li G, Meng X et al (2012) Dual-level regulation of ACC synthase activity by MPK3/MPK6 cascade and its downstream WRKY transcription factor during ethylene induction in *Arabidopsis*. PLoS Genet 8(6):e1002767. https://doi.org/10.1371/journal.pgen.1002767

Li P, Yang H et al (2019) Physiological and transcriptome analyses reveal short-term responses and formation of memory under drought stress in rice. Front Genet 10:00055. https://doi.org/10.3389/fgene.2019.00055

Li A, Wang X et al (2008) Biotic and abiotic stress responses through calcium-dependent protein kinase (CDPK) signaling in wheat (*Triticum aestivum* L.). Plant Signal Behav 3(9):654–656. https://doi.org/10.4161/psb.3.9.5757

Lin MY, Chai KH et al (2014) A positive feedback loop between HEAT SHOCK PROTEIN101 and HEAT STRESS-ASSOCIATED 32-KD PROTEIN modulates long-term acquired thermotolerance illustrating diverse heat stress responses in rice varieties. Plant Physiol 164(4):2045–2053. https://doi.org/10.1104/pp.113.229609

Liu J, He Z (2020) Small DNA methylation, big player in plant abiotic stress responses and memory. Front Plant Sci 11:595603. https://doi.org/10.3389/fpls.2020.595603

Liu J, Feng L et al (2019) An H3K27me3 demethylase-HSFA2 regulatory loop orchestrates transgenerational thermomemory in Arabidopsis. Cell Res 29(5):379–390. https://doi.org/10.1038/s41422-019-0145-8

Liu H, Able AJ, Able JA (2021a) Priming crops for the future: rewiring stress memory. Trends Plant Sci 27(7):699–716. https://doi.org/10.1016/j.tplants.2021.11.015

Liu H, Able AJ, Able JA (2021b) Small RNAs and their targets are associated with the transgenerational effects of water-deficit stress in durum wheat. Scie Rep 11(1):1–17. https://doi.org/10.1038/s41598-021-83074-7

Liu H, Able AJ, Able JA (2021c) Small RNA, transcriptome and degradome analysis of the transgenerational heat stress response network in durum wheat. Int J Mol Sci 22(11):5532. https://doi.org/10.3390/ijms22115532

Lukić N, Schurr FM et al (2023) Transgenerational stress memory in plants is mediated by upregulation of the antioxidative system. Environ Exp Bot 205:105129. https://doi.org/10.1016/j.envexpbot.2022.105129

Luna E, Ton J (2012a) The epigenetic machinery controlling transgenerational systemic acquired resistance. Plant Signal Behav 7(6):615–618. https://doi.org/10.4161/psb.20155

Luna E, Bruce TJA et al (2012b) Next-generation systemic acquired resistance. Plant Physiol 158(2):844–853. https://doi.org/10.1104/pp.111.187468

Martínez-Aguilar K et al (2021) Priming of seeds with INA and its transgenerational effect in common bean (*Phaseolus vulgaris* L.) plants. Plant Sci 305:110834. https://doi.org/10.1016/j.plantsci.2021.110834

Martinez-Hadalgo P, Garcia JM, Pozo MJ (2015) Induced systemic resistance against *Botrytis cinerea* by *Micromonospora* strains isolated from root nodules. Front Microbiol 6:922. https://doi.org/10.3389/fmicb.2015.00922

Mattioli R, Palombi N et al (2020) Proline accumulation in pollen grains as potential target for improved yield stability under salt stress. Front Plant Sci 11:582877. https://doi.org/10.3389/fpls.2020.582877 de Medeiros HA et al (2017) Tomato progeny inherit resistance to the nematode *Meloidogyne javanica* linked to plant growth induced by the biocontrol fungus *Trichoderma atroviride*. Sci Rep 7:40216. https://doi.org/10.1038/srep40216

Meiri D, Breiman A (2009) Arabidopsis ROF1 (FKBP62) modulates thermotolerance by interacting with HSP90.1 and affecting the accumulation of HsfA2-regulated sHSPs. Plant J 59(3):387–399. https://doi.org/10.1111/j.1365-313X.2009.03878.x

Mittler R (2022) ROS and redox signalling in cell-to-cell and systemic responses of plants. Free Radical Biol Med 189:1. https://doi.org/10.1016/j.freeradbiomed.2022.06.015

Mladenov V, Fotopoulos V et al (2021) Deciphering the epigenetic alphabet involved in transgenerational stress memory in crops. Int J Mol Sci 22(13):7118. https://doi.org/10.3390/ijms22137118

Mozgova I, Hennig L (2015) The polycomb group protein regulatory network. Ann Rev Plant Biol 66:269–296. https://doi.org/10.1146/annurev-arplant-043014-115627

Mozgova I, Mikulski P et al (2019) Epigenetic mechanisms of abiotic stress response and memory in plants. Epigenet Plants Agron Import Fundam Appl Transcr Regul Chromatin Remodell Plants. https://doi.org/10.1007/978-3-030-14760-0_1

Nasrallah AK, Atia MAM (2022) Salt priming as a smart approach to mitigate salt stress in faba Bean (*Vicia faba* L.). Plants 11(12):1610. https://doi.org/10.3390/plants11121610

Nciizah AD, Rapetsoa MC et al (2020) Micronutrient seed priming improves maize (*Zea mays*) early seedling growth in a micronutrient deficient soil. Heliyon 6:e04766. https://doi.org/10.1016/j.heliyon.2020.e04766

Nguyen NH, Vu NT, Cheong JJ (2022) Transcriptional stress memory and transgenerational inheritance of drought tolerance in plants. Int J Mol Sci 23(21):12918. https://doi.org/10.3390/ijms232112918

Nishad A, Nandi AK (2021) Recent advances in plant thermomemory. Plant Cell Rep 40:19–27. https://doi.org/10.1007/s00299-020-02604-1

Ogawa D, Suzuki Y et al (2021) Acetic-acid-induced jasmonate signalling in root enhances drought avoidance in rice. Sci Rep 11:6280. https://doi.org/10.1038/s41598-021-85355-7

Olas JJ, Apelt F, Annunziata MG et al (2021) Primary carbohydrate metabolism genes participate in heat-stress memory at the shoot apical meristem of *Arabidopsis thaliana*. Mol Plant 14(9):1508–1524. https://doi.org/10.1016/j.molp.2021.05.024

Ou X, Zhang Y et al (2012) Transgenerational inheritance of modified DNA methylation patterns and enhanced tolerance induced by heavy metal stress in rice (*Oryza sativa* L.). PLoS ONE 7(9):e41143. https://doi.org/10.1371/journal.pone.0041143

Park J, Lim CJ et al (2018) Epigenetic switch from repressive to permissive chromatin in response to cold stress. Proc Natl Acad Sci USA 115(23):E5400–E5409. https://doi.org/10.1073/pnas.1721241115

Pandey P, Irulappan V et al (2017) Impact of combined abiotic and biotic stresses on plant growth and avenues for crop improvement by exploiting physio-morphological traits. Front Plant Sci 8:537. https://doi.org/10.3389/fpls.2017.00537

Radha B, Sunita NC et al (2022) Physiological and molecular implications of multiple abiotic stresses on yield and quality of rice. Front Plant Sci 13:996514. https://doi.org/10.3389/fpls.2022.996514

Ramakrishnan M, Zhang Z et al (2022) Epigenetic stress memory: a new approach to study cold and heat stress responses in plants. Front Plant Sci 13:1075279. https://doi.org/10.3389/fpls.2022.1075279

Ramirez-Prado JS, Latrasse D et al (2019) The Polycomb protein LHP1 regulates *Arabidopsis thaliana* stress responses through the repression of the MYC2-dependent branch of immunity. Plant J 100(6):1118–1131. https://doi.org/10.1111/tpj.14502

Rasmann S, De Vos M et al (2012) Herbivory in the previous generation primes plants for enhanced insect resistance. Plant Physiol 158(2):854–863. https://doi.org/10.1104/pp.111.187831

Rasmussen MW, Roux M et al (2012) MAP kinase cascades in *Arabidopsis* innate immunity. Front Plant Sci. https://doi.org/10.3389/fpls.2012.00169

Raza MAS, Aslam MU et al (2024) Seed priming with selenium improves growth and yield of quinoa plants suffering drought. Sci Rep 14:886. https://doi.org/10.1038/s41598-024-51371-6

Rebolledo-Prudencio OG, Estrada-Rivera M et al (2022) The small RNA-mediated gene silencing machinery is required in Arabidopsis for stimulation of growth, systemic disease resistance, and suppression of the nitrile-specifier gene NSP4 by *Trichoderma atroviride*. Plant J 109:873–890. https://doi.org/10.1111/tpj.15599

Reimer-Michalski EM, Conrath U (2016) Innate immune memory in plants. Semin Immunol 28:319–327. https://doi.org/10.1016/j.smim.2016.05.006

Rossatto T, Souza GM et al (2023) Cross-stress memory: salt priming at vegetative growth stages improves tolerance to drought stress during grain-filling in rice plants. Environ Exp Bot 206:105187. https://doi.org/10.1016/j.envexpbot.2022.105187

Sharma M, Banday ZZ et al (2019) Glucose-regulated hlp1 acts as a key molecule in governing thermomemory. Plant Physiol 180(2):1081–1100. https://doi.org/10.1104/pp.18.01371

Sharma AB, Sidhu A et al (2022) 1,2,4-triazolyldithiocarbamate silver nano conjugate: potent seed priming agent against bakanae disease of rice (*Oryzae sativa*). Eur J Plant Pathol 162:825–841. https://doi.org/10.1007/s10658-021-02439-w

Sheldon CC, Hills MJ et al (2008) Resetting of FLOWERING LOCUS C expression after epigenetic repression by vernalization. Proc Natl Acad Sci USA 105:2214–2219. https://doi.org/10.1073/pnas.0711453105

Shi S, Li S et al (2018) The Arabidopsis calcium-dependent protein kinases (CDPKs) and their roles in plant growth regulation and abiotic stress responses. Int J Mol Sci 19(7):1900. https://doi.org/10.3390/ijms19071900

Singh AK, Dhanapal S et al (2021) CSN5A subunit of COP9 signalosome is required for resetting transcriptional stress memory after recurrent heat stress in *Arabidopsis*. Biomolecules 11(5):668. https://doi.org/10.3390/biom11050668

Slaughter A, Daniel X et al (2012) Descendants of primed *Arabidopsis* plants exhibit resistance to biotic stress. Plant Physiol 158:835. https://doi.org/10.1104/pp.111.191593

Stief A, Altmann S et al (2014) Arabidopsis miR156 regulates tolerance to recurring environmental stress through SPL transcription factors. Plant Cell 26(4):1792–1807. https://doi.org/10.1105/tpc.114.123851

Sun M, Yang Z et al (2022) DNA methylation in plant responses and adaptation to abiotic stresses. Int J Mol Sci 23:6910. https://doi.org/10.3390/ijms23136910

Szabados L, Savouré A (2010) Proline: a multifunctional amino acid. Trends Plant Sci 15(2):89–97. https://doi.org/10.1016/j.tplants.2009.11.009

Tamindžić G, Ignjatov M et al (2021) Seed priming with zinc improves field performance of maize hybrids grown on calcareous chernozem. Ital J Agro 16:1795. https://doi.org/10.4081/ija.2021.1795

Tang J, Shen H et al (2023) Seed priming with rutin enhances tomato resistance against the whitefly *Bemisia tabaci*. Pest Bioc Physiol 194:105470. https://doi.org/10.1016/j.pestbp.2023.105470

Tankari M, Wang C et al (2021) Drought priming improved water status, photosynthesis, and water productivity of cowpea during post-anthesis drought stress. Agric Water Manag 245:106565. https://doi.org/10.1016/j.agwat.2020.106565

Tao Z, Shen L et al (2017) Embryonic epigenetic reprogramming by a pioneer transcription factor in plants. Nature 551:124–128. https://doi.org/10.1038/nature24300

Tateda C, Zhang Z et al (2014) Salicylic acid regulates *Arabidopsis* microbial pattern receptor kinase levels and signalling. Plant Cell 26(10):4171–4187. https://doi.org/10.1105/tpc.114.131938

Teshome DT, Zharare GE, Naidoo S (2020) The threat of the combined effect of biotic and abiotic stress factors in forestry under changing climate. Front Plant Sci 11:1874. https://doi.org/10.3389/fpls.2020.601009

Tiwari M, Pati D et al (2022) The impact of microbes in plant immunity and priming induced inheritance: a sustainable approach for crop protection. Plant Stress 4:100072. https://doi.org/10.1016/j.stress.2022.100072

Trewavas A (2003) Aspects of plant intelligence. Ann Bot 92:1–20. https://doi.org/10.1093/aob/mcg101

Uzal O (2022) Effects of proline treatments on plant growth, lipid peroxidation and antioxidant enzyme activities of tomato (*Solanum lycopersicum* L.) seedlings under chilling stress. Gesunde Pflanzen 74(3):729–736. https://doi.org/10.1007/s10343-022-00648-9

Wang X, Huang M et al (2016) Physiological and proteomic mechanisms of waterlogging priming improve tolerance to waterlogging stress in wheat (*Triticum aestivum* L.). Environ Exp Bot 132:175–182. https://doi.org/10.1016/j.envexpbot.2016.09.003

Wang X, Zhang X et al (2018) Parental drought-priming enhances tolerance to post-anthesis drought in offspring of wheat. Front Plant Sci 9:261. https://doi.org/10.3389/fpls.2018.00261

Wang S, Hu J et al (2022) Effects of hydrogen peroxide priming on yield, photosynthetic capacity and chlorophyll fluorescence of waterlogged summer maize. Front Plant Sci 13:1042920. https://doi.org/10.3389/fpls.2022.1042920

Wang W, Huang F et al (2015) Comparative analysis of DNA methylation changes in two rice genotypes under salt stress and subsequent recovery. Biochem Biophysic Res Commun 465(4):790–796. https://doi.org/10.1016/j.bbrc.2015.08.089

Wang X, Li Z et al (2020) Combined proteome and transcriptome analysis of heat-primed azalea reveals new insights into plant heat acclimation memory. Front Plant Sci 11:1278. https://doi.org/10.3389/fpls.2020.01278

Wehner G, Schikora A et al (2021) Priming negatively affects feeding behaviour and aphid biomass of *Rhopalosiphum padi* on barley. J Pest Sci 94:1237–1247. https://doi.org/10.1007/s10340-021-01329-8

Westman SM, Kloth KJ et al (2019) Defence priming in arabidopsis-a meta-analysis. Sci Rep 9:13309. https://doi.org/10.1038/s41598-019-49811-9

Wibowo A, Becker C et al (2016) Hyperosmotic stress memory in Arabidopsis is mediated by distinct epigenetically labile sites in the genome and is restricted in the male germline by DNA glycosylase activity. Elife 21:e44302. https://doi.org/10.7554/eLife.13546

Winter TR, Borkowski L et al (2012) Heavy metal stress can prime for herbivore-induced plant volatile emission. Plant Cell Environ 35:1287–1298. https://doi.org/10.1111/j.1365-3040.2012.02489.x

Wolf DM, Fontaine-Bodin L et al (2008) Memory in microbes: quantifying history-dependent behaviour in a bacterium. PLoS ONE 3:e1700. https://doi.org/10.1371/journal.pone.001700

Worrall D, Holroyd GH et al (2011) Treating seeds with activators of plant defence generates long-lasting priming of resistance to pests and pathogens. New Phytol 193:770–778. https://doi.org/10.1111/j.1469-8137.2011.03987.x

Wurzinger B, Nukarinen E et al (2018) The SnRK1 Kinase as central mediator of energy signaling between different organelles. Plant Physiol 176(2):1085–1094. https://doi.org/10.1104/pp.17.01404

Xu W, Huang W (2017) Calcium-dependent protein kinase in phytohormone signalling pathways. Int J Mol Sci 18:2436. https://doi.org/10.3390/ijms18112436

Xu R, Wang Y et al (2015) Salt-induced transcription factor MYB74 is regulated by the RNA-directed DNA methylation pathway in *Arabidopsis*. J Exp Bot 66(19):5997–6008. https://doi.org/10.1093/jxb/erv312

Yadav NS, Totov V et al (2022) Multigenerational exposure to heat stress induces phenotypic resilience, and genetic and epigenetic variations in *Arabidopsis thaliana* offspring. Front Plant Sci 13:728167. https://doi.org/10.3389/fpls.2022.728167

Yadav M, Dubey MK, Upadhyay RS (2021) Systemic Resistance in Chilli Pepper against Anthracnose (Caused by *Colletotrichum truncatum*) Induced by *Trichoderma harzianum, Trichoderma asperellum and Paenibacillus dendritiformis*. J Fungi 7(4):307. https://doi.org/10.3390/jof7040307

Yamaguchi N, Matsubara S et al (2021) H3K27me3 demethylases alter HSP22 and HSP17.6C expression in response to recurring heat in *Arabidopsis*. Nat Commun 12(1):3480. https://doi.org/10.1038/s41467-021-23766-w

Yan K, Xu H et al (2015) Salt priming improved salt tolerance in sweet sorghum by enhancing osmotic resistance and reducing root Na^+ uptake. Acta Physiol Plant 37:203. https://doi.org/10.1007/s11738-015-1957-x

Yan X, Chen S et al (2023) AgNPs-triggered seed metabolic and transcriptional reprogramming enhanced rice salt tolerance and blast resistance. ACS Nano 17:492–504. https://doi.org/10.1021/acsnano.2c09181

Yang H, Cui Y et al (2023) Long non-coding RNAs of plants in response to abiotic stresses and their regulating roles in promoting environmental adaptation. Cells 12:729. https://doi.org/10.3390/cells12050729

Yung WS, Wang Q et al (2021) Priming-induced alterations in histone modifications modulate transcriptional responses in soybean under salt stress. Plant J 109:1575–1590. https://doi.org/10.1111/tpj.15652

Zaid A, Mohammad F, Siddique KHM (2022) Salicylic acid priming regulates stomatal conductance, trichome density and improves cadmium stress tolerance in *Mentha arvensis* L. Front Plant Sci 13:895427. https://doi.org/10.3389/fpls.2022.895427/full

Zhang X, Wang X et al (2019) Abscisic acid mediation of drought priming-enhanced heat tolerance in tall fescue (*Festuca arundinacea*) and Arabidopsis. Phys Plant 167(4):488–501. https://doi.org/10.1111/ppl.12975

Zhang Y, Zhou Y et al (2022) Non-coding RNAs fine-tune the balance between plant growth and abiotic stress tolerance. Front Plant Sci 13:965745. https://doi.org/10.3389/fpls.2022.965745

Zeng X, Gao Z et al (2020) HISTONE DEACETYLASE 9 functions with Polycomb silencing to repress *FLOWERING LOCUS C* expression. Plant Physiol 182:555–565. https://doi.org/10.1104/pp.19.00793

Zheng X, Chen L et al (2013) Transgenerational variations in DNA methylation induced by drought stress in two rice varieties with distinguished difference to drought resistance. PLoS ONE 8(11):e80253. https://doi.org/10.1371/journal.pone.0080253

Zhou Y, Tan B et al (2013) HISTONE DEACETYLASE19 interacts with HSL1 and participates in the repression of seed maturation genes in *Arabidopsis* seedlings. Plant Cell 25(1):134–148. https://doi.org/10.1105/tpc.112.096313

Zhou R, Yu X et al (2020) Combined high light and heat stress induced complex response in tomato with better leaf cooling after heat priming. Plant Physiol Bioch 151:1–9. https://doi.org/10.1016/j.plaphy.2020.03.011

Zhu J, Cheol J et al (2008) Involvement of *Arabidopsis* HOS15 in histone deacetylation and cold tolerance. Proc Natl Acad Sci USA 105:4945–4950. https://doi.org/10.1073/pnas.0801029105