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Review

Echoes of a Stressful Past: Abiotic Stress Memory in Crop Plants towards Enhanced Adaptation

Georgios Lagiotis [1,2,*], Panagiotis Madesis [1,2] and Evangelia Stavridou [2,3,*]

[1] Laboratory of Molecular Biology of Plants, School of Agricultural Sciences, University of Thessaly, 38446 Thessaly, Greece; pmadesis@uth.gr
[2] Institute of Applied Biosciences, Centre for Research and Technology—Hellas, 6th km Charilaou-Thermi Rd., Thermi, 57001 Thessaloniki, Greece
[3] Department of Botany, School of Biology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece
* Correspondence: glagiotis@certh.gr (G.L.); estavrido@bio.auth.gr (E.S.)

Abstract: Plants can develop stress memory as a response to various abiotic stresses, but the underlying mechanisms are not yet fully understood. Most of the knowledge concerning the mechanisms of stress memory development and inheritance in plants is primarily based on research in the model plant Arabidopsis. While shared mechanisms exist across plant species, it is crucial to expand our understanding of epigenetic regulation in crops. Stress priming, or prior exposure to mild stress, can enhance a plant's adaptation to future stress events and the development of stress memory. During stress priming, plants undergo physiological, biochemical, molecular, and epigenetic changes that can be transient or maintained throughout their lifespan, and in some cases, these changes can also be inherited by the offspring. In this review, we present the current state of knowledge on the development of priming-induced stress memory in agronomically important crops towards stress resilience. The most prominent abiotic stresses, namely, heat, cold, salt, drought, and waterlogging, are highlighted in relation to stress cis-/trans-priming and memory development at the intra-, inter-, and transgenerational levels. The cost for developing stress memory in plants along with the duration of these memory imprints and stress memory fading are also discussed. This review is particularly important in the era of climate change, which necessitates the development of agricultural sustainability strategies.

Keywords: somatic memory; transgenerational memory; priming; abiotic stresses; epigenetic regulation; crop plants

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1. Introduction

Adverse environmental conditions can negatively impact plant growth, reproduction potential, and yield, thus ultimately affecting plant diversity and distribution. Climate change and global warming exacerbate abiotic stress incidents, which are predicted to become more frequent and severe within the century, posing a serious challenge for crop cultivation and production [1]. Abiotic stresses, such as drought, salinity, heat, and cold are amongst the major constraints for crop production that could cause a great loss of crop yield [2–4]. To cope with such adverse environmental conditions, plants can reprogram their regular development at the expense of reproductive potential, favouring stress response mechanisms. Such responses to stress are usually tissue-specific and dependent on the ontogenetic stage of the plant, as well as their adaptive response related to the tolerance level of the genotype [5]. It is well-established that both abiotic and biotic stresses can induce genome reprogramming by modulating gene expression at the transcriptional and posttranscriptional level in different plant species [6–8]. Indeed, plants have evolved complex regulatory networks to perceive and respond to stress via the allocation of resources for minimizing stress-induced damage, and the preservation of resources for development and reproduction [9]. Therefore, the development of adaptation strategies is essential for enhanced crop stress resilience, especially during the reproductive phase, to sustain yield under variable climates.

The prior exposure of a plant to mild yet non-lethal stress stimuli, also known as priming, may enhance the adaptation to subsequent stress events, towards developing stress memory. This acquired stress memory can prepare plants for a more rapid and effective response to future stress events during their development, and in some cases, it can also be maintained in the offspring [10]. To date, the research on the field has identified that plant stress priming involves three distinct phases: (i) the pre-challenge priming phase, (ii) the post-challenge stress response phase of primed plants, and (iii) the inter-/transgenerational priming phase [11,12]. The pre-challenge priming phase is characterized by the perception of the stimulus, while the strong modulation of gene expression and genome reprogramming are only observed during the post-challenge stress response phase. During stress priming, changes take place at the physiological, biochemical, molecular, and epigenetic levels, and these changes can be transient or maintained throughout the lifespan of a plant [13] or inherited by future generations [14,15]. Intragenerational memory helps plants respond swiftly to immediate stressors, while intergenerational memory ensures that the offspring inherit a degree of resilience, enhancing their chances of survival. Moreover, transgenerational memory contributes to the long-term evolution of stress resistance in crop populations.

There is increasing evidence that epigenetic mechanisms may play a prominent role in both natural stress occurrence and the application of stress stimuli that induce priming towards developing stress tolerance. Both DNA methylation and histone modifications are the most prevalent changes that mediate epigenetic regulation and consequently the regulation of gene expression. These modifications are heavily present on transposons and other repetitive sequences [16], and it has been shown that various abiotic and biotic stresses can interfere with the epigenetic regulation machinery [17–19]. In plants, the DNA methylation of cytosine residues is mediated by DNA methylases via the small interfering RNAs (siRNAs)-directed DNA methylation (RdDM) pathway [20,21] in both symmetrical (CG and CHG) and non-symmetrical (CHH) patterns [16]. Although DNA methylation is a relatively stable epigenetic modification, it can be reverted by the activity of DNA demethylases [17]. Along with DNA methylation, the N-terminal tails of the nucleosomal histones (H2A/2B, H3 and H4), which have been extensively studied in plants, can also be subjected to epigenetic modifications, such as acetylation, biotinylation methylation, phosphorylation, and ubiquitination [22,23]. Such covalent modifications can affect the structure and function of the nucleosomes and ultimately influence gene expression through interfering with the accessibility of the transcription machinery [24].

Epigenetic regulation has been shown to play a central role in plant stress responses [10,25]. For instance, heat stress may alter the structure of the chromocenters [26–28] and cause broader changes to the composition of nucleosomes [29]. Additionally, salinity and drought can induce the histone acetylation and methylation of related stress-responsive genes [30–32], while loss-of-function mutations in demethylase genes leads to the down-regulation of such genes [33]. The salinity-induced DNA demethylation of certain loci in the plant genome has also been reported [34]. It has also been demonstrated that the application of stress priming can induce epigenetic modifications, such as different histone methylation patterns for several responsive genes [35,36]. Although there has been extensive research on plant stress memory induction, the term is mainly used as a concept or idea; however, there is enough evidence to support the theory that plant memory is a biological phenomenon, as was interestingly reviewed by Galviz et al. (2020) [37].

Plant stress memory has great potential for agricultural applications, especially for the development and cultivation of crop varieties with enhanced tolerance to various abiotic stresses. Discovering plants' epigenetic and transcriptional memory of stress may be an alternative tool for improved agriculture in challenging regions, reducing the need for transgenic crop plants, which are controversial for the consumers [38]. The manipulation of epigenetic stress memory mechanisms, especially those that are transgenerationally inherited, can have a great impact on breeding programs for the development of climate-resistant crops and crop improvement [39–41]. Various gene editing technologies are readily available and the use of gene editing technology may broaden the understanding of plant transcriptional memory mechanisms under abiotic stress. CRISPRa epigenome editing in plants has shown great potential as an application in crop improvement, albeit it is still one of the greatest challenges in the field [42]. The future exploitation of CRISPRa in crop improvement programmes will significantly reduce economic losses from the devastating effects of abiotic stresses on plant growth and productivity. Other approaches in achieving plant stress memory include seed priming, which is widely used in agriculture [43–45] and grafting in perennial species, such as in citrus species, which have long life cycles and are typically non-amenable to conventional biotechnological procedures [46].

Research on priming and the associated stress memory development has mainly focused on the model plant Arabidopsis, yet our knowledge on the relevant epigenetic stress adaptation mechanisms and biological processes in crop plants is rather limited, requiring further investigation for different economically important crops [47,48]. Herein, we attempt to review the present state of knowledge on the priming-induced development of stress memory in agronomically important crop plants towards the stress tolerance that may occur after priming. We focused on the effects of the most prominent abiotic stresses affecting crop production, including extreme temperatures, water availability, and salinity, in relation to stress priming and memory development. Additionally, the cross-tolerance effects induced by stress priming were examined. In this review, we attempt to answer questions such as: how is the effective memory associated with an altered physiological, transcriptional and/or epigenetic state? How are abiotic stress priming-induced changes inherited in more than one generation in crop plants? How long can the stress memory imprints last?

2. Development of Abiotic Stress Memory

The development of stress memory in plants and its underlying mechanisms, as a unique response to various abiotic stresses, are not yet fully understood and it is evident that many interacting pathways are involved. In many cases, the metabolic and transcriptional changes occurring in an organism in response to an environmental stimulus are usually transient or exhibit short-term effects towards its acclimation [49–51]. However, plants can remember stress cues either via somatic memory retained through mitosis in the same generation (somatic memory), and/or long-lasting memories transmitted across generations (inter- and transgenerationally). There is research evidence of epigenetic stress memory transmission during vegetative propagation, indicating the existence of different types of somatic memory. DNA methylation inheritance after vegetative propagation has been previously confirmed in Arabidopsis plants regenerated in vitro, retaining some original epigenetic traits [34]. Similar findings were observed in poplar [52], white clover [53,54], and dandelion [55]; however, the distribution and functional implications of these inherited epigenetic marks and their long-term stability requires further investigation.

Different stress-inducible molecular mechanisms may play different roles in establishing stress memory, such as the transcriptional (transcription factors, stress-related genes, and signalling pathways) and post-transcriptional (alternative splicing and RNA silencing) regulation of gene expression, as well as epigenetic factors (DNA methylation and chromatin modifications) [56–58]. Concerning transcriptional regulation, genes related to memory are categorized into two groups: those maintaining an altered expression pattern during the recovery phase, and those that exhibit a modified response upon second stress exposure, as discussed in Bäurle (2018) [59] and Bäurle and Trindade (2020) [60], which is typically more robust and rapid [61,62]. Evidence suggests that stress memory and the associated response mechanism are epigenetically based and involve post-transcriptional regulation [63].

Considering the associations between abiotic stresses and epigenetic regulation, it is possible that genes involved in the epigenetic machinery could ultimately be regulated by stress-responsive transcription factor (TF) activity and vice versa [17]. The expression of a MYB transcription factor in maize, which is influenced by epigenetic regulation [64], was reported to regulate the expression of other MYB transcription factors [65]. The elucidation of such direct associations of transcription factor machinery and epigenetic regulation becomes even more complex when considering that DNA methylation can strongly influence a large proportion of transcription factors in their ability to bind genomic DNA [66]. Besides epigenetic regulation, the accumulation of protein-coding transcripts and microRNAs (miRNAs), as well as TF activity, the priming memory can also be stored in the form of downstream regulatory stress signalling cascades [67].

Most of the research on stress tolerance and the induction of stress memory in crop plants has been mainly focused on seed priming as a pre-sowing treatment with chemical agents, inducing a mild stress-like cue, similar to an acclimation response [68,69]. This approach has served as a tool to ameliorate plant survival and fitness in one generation [67,70–72]. However, recent research has focused on abiotic stress-induced memory and transgenerational inheritance in crop plants, which we present in the following sections.

3. Transgenerational Stress Memory

It is well-known that most plant epigenetic modifications last only during one generation; however, plants can pass on the stress-induced acquired memory to subsequent generations [73] through inter-/transgenerational epigenetic inheritance [14,74,75]. Intergenerational memory usually lasts for only one generation and may be the result of environmental cues affecting the offspring during embryo development or “signals” transmitted to the embryo by the mother plant [51]. In contrast, transgenerational stress memory can be inherited over two generations, and it is mediated by stably inherited epigenetic modifications [41,49,76]. Although the inheritance of epigenetic modifications is still a largely unexplored field [17,77], a certain level of sustained epigenetic inheritance over many generations may be present, given that the silencing of transposable elements and some epigenetic modifications seem to escape genome resetting during gametogenesis [78,79].

The potential underlying mechanisms of epigenetic inheritance in plants have been linked to both differential DNA methylation and stress-responsive histone modifications [17]. Stably inherited DNA methylation patterns through several generations are considered the primary epigenetic mechanism underlying plant stress memory that results in an enhanced stress response [17,80–83]. A study by Mathieu et al. (2007) showed that, specifically, CG methylation is an integral component of transgenerational epigenetic inheritance in Arabidopsis [84]. DNA methylation was also reported to affect other important processes in plants such as the expression of genes, genome stability, heterosis, imprinting, and transposable element regulation [85].

The epigenome, which is sensitive to environmental perturbations and the epigenetic regulation, play an important role in plant stress memory development induced by priming [80] for plants to rapidly acclimate [80,85–88]. DNA methylation has been previously involved in the regulation of stress response genes [89–91], which may allow plants to transgenerationally adapt to the stress conditions [92–95]. However, the intensity and duration of the abiotic stress stimulus (priming) can variably affect the intra- and trans-generational memory of stress tolerance [96].

Changes in DNA methylation caused by osmotic stress were transgenerationally inherited through the female gametes in Arabidopsis [34], while multigenerational exposure to heat stress enhanced offspring phenotypic acclimation to high temperatures and epigenetic variations [97]. This increase in epigenetic variation was also observed in nearly isogenic Arabidopsis recombinant inbred lines (RILs) that were exposed to drought stress [98], suggesting that epigenetic changes may provide the necessary transcriptional plasticity required for plants to respond to environmental changes irrespective of genetic diversity. Nonetheless, it becomes apparent that the intensity of the priming stimulus may be of integral importance in drought stress memory development, given that mild drought stress application in Arabidopsis failed to induce strong transgenerational effects and DNA methylation changes were only intergenerationally inherited [99].

4. Abiotic Stress-Induced Memory of Crop Plants

By studying stress-induced memory in crop plants, researchers aim to develop strategies to enhance crop resilience leading to more sustainable and productive agriculture. This section is dedicated to the current research of priming-induced abiotic stress memory development and inheritance mechanisms, focusing on crop plants, which have an enormous untapped potential for plant science and agriculture. The most prominent abiotic stresses (heat, low temperatures, drought, waterlogging, and salinity) are presented (Figure 1 and Table 1). In each subsection, the effect of the corresponding abiotic stress on crop plants is presented. The available and relatively recent research on stress-induced memory development either somatically or inter-/intragenerationally in various crop plants is discussed. Stress-primed induced memory entails the induction of acclimation, or even in some cases, the adaptation to recurrent stress either in the same or subsequent generations. Moreover, the aspects of cross-tolerance stress memory in crop plants are also discussed. Although not in the scope of this review, some mechanistic aspects that have been studied extensively in Arabidopsis were included to emphasize the gap of knowledge on crop plants.

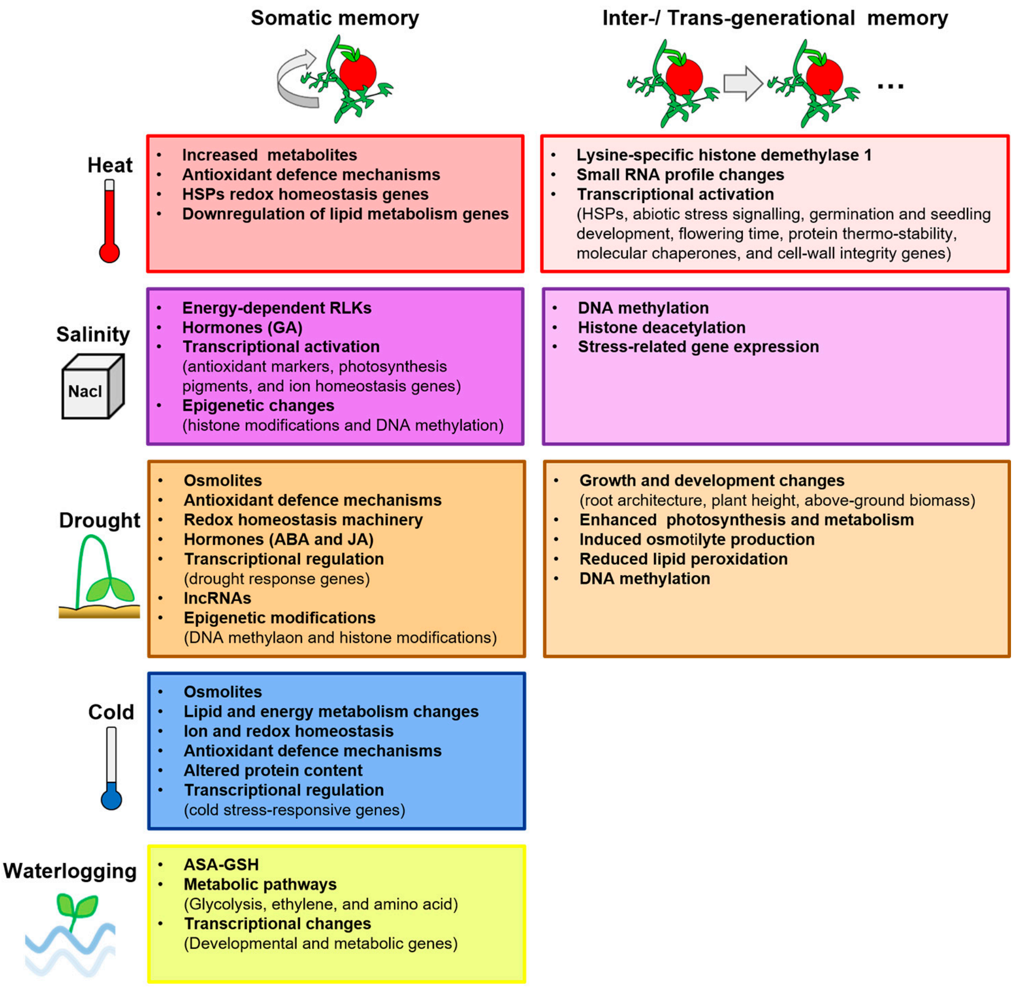

Figure 1. Graphical outline of the known biological mechanisms involved in abiotic stress-specific memory (somatic and inter-/transgenerational) in crop plants.

Table 1. An overview of recent research on abiotic stress memory (somatic and inter-/transgenerational) development in crop plants, including the corresponding mechanisms or response involved.

Stress	Type of Stress Memory	Plant Species	Stress Memory	References
Drought	Somatic	Citrus scion/rootstock combinations	DNA methylation patterns with an increase in ABA levels	[100]
Drought	Somatic	Citrus scion/rootstock combinations	Modification of methylation status and gene expression with the use of drought-primed scions	[46]
Drought	Somatic	*Glycine max*	Increased expression of drought response genes or dehydration memory genes encoding transcription factors, protein phosphatase 2Cs, and late embryogenesis rich proteins	[101]
Drought	Somatic	*Gossypium hirsutum* L.	Histone modifications	[102]
Drought	Somatic	*Olea europaea* L.	Higher photosynthetic efficiency, higher proline and sugar contents, as well as more active antioxidant machinery	[103]
Drought	Somatic	*Oryza sativa*	DNA methylation, lncRNAs, and abscisic acid (ABA) regulatory pathways induce drought-responsive genes	[104]
Drought	Somatic	*Oryza sativa*	Global DNA methylation changes regulate stress memory gene expression and transposons	[105,106]
Drought	Somatic	*Solanum tuberosum* L.	Increased expression of genes related to biosynthesis and signal transduction	[107]
Drought	Somatic	*Solanum tumberosum*	Increased antioxidant activity	[108]
Drought	Somatic	*Triticum aestivum* L.	Activation of antioxidant defence and redox homeostasis mechanisms	[109,110]
Drought	Somatic	*Triticum aestivum* L.	miRNAs induced osmoregulation	[111]
Drought	Somatic	*Triticum aestivum* L.	Phytohormones ABA and JA induced the activity of detoxifying enzymes	[112]
Drought	Somatic	*Vigna unguiculata*	Improved water status, water productivity of biomass index, photosynthesis, and plant hormones	[113]
Drought	Somatic	*Vitis vinifera* L.	Increased water status, leaf gas exchange, and berry size	[114]
Drought	Transgenerational	*Arachis hypogea* L.	Drought-resistance mechanisms, exemplified by characteristics such as enhanced rooting, seed weight, and germination efficiency	[115]
Drought	Transgenerational	*Hordeum vulgare*	Enhanced root development	[116]
Drought	Transgenerational	*Oryza sativa*	Decreasing energy dissipation, increasing ATP energy provision, reducing oxidative damage in GC	[117]
Drought	Transgenerational	*Oryza sativa*	Alteration in DNA methylation levels in guard cells, modulation of proteins involved in pathways for coping with oxidative stress and maintaining GC, enhanced photosynthesis and metabolism, improved gas exchange	[118]
Drought	Transgenerational	*Triticum aestivum* L.	Improved grain yield, preservation of photosynthetic activity and induced osmolyte production	[119]
Drought	Transgenerational	*Triticum aestivum* L.	Increased plant height, above-ground biomass, number of grains per plant, grain weight per plant, and water potential, improved osmolyte accumulation and reduced lipid peroxidation	[120,121]

Table 1. *Cont.*

Stress	Type of Stress Memory	Plant Species	Stress Memory	References
Heat	Intergenerational	*Triticum aestivum* L.	Thermo-tolerance manifested as higher yield, improved photosynthesis, enhanced antioxidant activity, energy production, and reduced cell damage, upregulation of the lysine-specific histone demethylase 1 (LSD1)	[122]
Heat	Intergenerational	*Brassica rapa* L.	Changes in small RNA profiles in pollen grain	[123]
Heat	Somatic	*Triticum aestivum* L.	Increased metabolites and antioxidant defence mechanisms	[124,125]
Heat	Somatic	*Triticum aestivum* L.	*HSPs* redox homeostasis genes and downregulation of lipid metabolism genes involved in membrane rigidity	[126–128]
Heat	Transgenerational	*Phaseolus vulgaris* L.	Increased expression of 22 genes related to biological processes involved in the heat stress response (activation of *HSPs*, abiotic stress signalling, germination and seedling development, flowering time, protein thermo-stability, molecular chaperones, and cell-wall integrity)	[129]
Low temperatures	Somatic	*Citrullus lanatus* (Thunb.) Matsum & Nakai	Osmoregulation, decrease in electrolyte leakage and MDA accumulation, activation of photoprotective mechanisms, increase in Rubisco activase (CIRCA) and in gene expression of the Benson–Calvin cycle	[130]
Low temperatures	Somatic	*Oryza sativa*	Altered protein content and induction of selective protein degradation in the anthers	[131]
Low temperatures	Somatic	*Pisum sativum*	Increased enzyme activities in the Calvin cycle, higher resistance to photoinhibition of PSII, a more oxidised electron transport chain, less oxidative damage, and less impaired metabolite synthesis	[132]
Low temperatures	Somatic	*Prunus persica* L.	Accumulation of proteins related to energy metabolism	[133]
Low temperatures	Somatic	*Solanum comersonii* Poir.	Reduction in linoleic acid and sterol phospholipid ratios	[134]
Low temperatures	Somatic	*Solanum melongena* L.	Enhanced morphological and physiological parameters, increased pigment content and chlorophyll fluorescence parameters and enhanced max. quantum yield of PSII (Fv/Fm) and performance index (PI)	[135]
Low temperatures	Somatic	*Triticum aestivum* L.	Activation of the sub-cellular antioxidant systems, reduction in oxidative burst in photosynthetic apparatus	[136]
Low temperatures	Somatic	*Triticum aestivum* L.	Increased photosynthetic rate and stomatal conductance, enhanced antioxidant enzyme activities, and altered stress-related gene expressions	[137]
Salinity	Somatic	*Brassica napus*	Seed priming induced changes in transcriptome (mainly in *MYB*, *DREB* and *NAC* genes) and proteome (eIF4A, eIF3 subunit K, eIF6, eEF1) corresponding to translation initiation, elongation factors, seed storage proteins (SSPs) and management of oxidative stress. Higher expression of genes and proteins involved in water transport, cell wall modification, cytoskeletal organization, and cell division was linked to the advanced germination of primed seeds	[138]
Salinity	Somatic	*Brassica napus*	Higher genotype-dependent growth rates, stabilization of cell membranes integrity, increased chlorophyll content	[139]
Salinity	Somatic	*Capsicum annuum* L.	Seed-halopriming improved total germination, germination index, germination speed, vigour index, plumule and radicle length, and dry weight of the seedlings	[140,141]

Table 1. *Cont.*

Stress	Type of Stress Memory	Plant Species	Stress Memory	References
Salinity	Somatic	*Glycine max*	Alterations in the transcriptional landscape of salt stress responsive genes through methylation and acetylation	[142–145]
Salinity	Somatic	*Leguminous species*	Seed-halopriming elevated activities of nitrate assimilatory enzymes resulting in improved nitrate uptake, reduced ammonium accumulation and glutamate dehydrogenase activity. The efficacy of halopriming was more effective in salt sensitive cultivars	[146]
Salinity	Somatic	*Leguminous species*	Improved catalase activity, higher water contents, lower accumulation of ROS, MDA and proline, reduced DNA damage, and enhanced growth	[147]
Salinity	Somatic	*Lolium perenne* L.	Reduced accumulation of Na+, BPSP, and sucrose synthase showed a high level of transcriptional memory	[148]
Salinity	Somatic	*Nicotiana tabacum*	Reduced level of DNA methylation in the promoter and coding regions of flavonoid biosynthesis and antioxidant genes	[149]
Salinity	Somatic	*Oryza sativa*	Seed-halopriming increased expression of ion homoeostasis genes	[150]
Salinity	Somatic	*Physalis angulata* L.	Seed osmopriming increased transcript levels of salt stress responsive genes (*GST*, *TXN* and *APX*)	[151]
Salinity	Somatic	*Solanum lycopersicum*	Seed-halopriming induced the upregulation of Gibberellic Acid (GA) biosynthesis genes, while improving germination and NaCl tolerance	[152]
Salinity	Somatic	*Solanum lycopersicum*	Greater partitioning of biomass to roots, higher growth rate, yield, maintenance of K+ selectivity in the developing leaves, priming-induced adaptation capacity is growth stage- and stress priming level dependent	[153]
Salinity	Somatic	*Triticum aestivum* L.	Seed-halopriming increased expression of salt responsive genes related to improved biosynthesis of photosynthetic pigments and decreased levels of oxidative stress markers	[154]
Salinity	Somatic	*Triticum aestivum* L.	Enhanced osmotic and antioxidant potential	[155]
Salinity	Transgenerational	*Brassica napus*	Demethylation promotes the expression of stress-related genes and induces salt resistance in these species	[156]
Salinity	Transgenerational	*Gossypium hirsutum*	Demethylation promotes the expression of stress-related genes and induces salt resistance in these species	[157]
Waterlogging	Somatic	*Cucumis sativus* L.	Investment in adventitious roots and up-regulated expression of genes related to the activation of amino acid metabolism, plant hormone biosynthesis, and glycolysis pathway	[158]
Waterlogging	Somatic	*Oryza sativa*	Alteration in expression and chromatin level of flooding-responsive genes	[159]
Waterlogging	Somatic	*Triticum aestivum* L.	Increased activities of antioxidant enzymes and photosynthetic capacity, higher chlorophyll content, and light usage efficiency	[160]
Waterlogging	Somatic	*Triticum aestivum* L.	Enzymatic and non-enzymatic processes involved in ascorbic acid-glutathione (ASA-GSH) cycle, increased plant biomass, maintenance of root growth, induction of ethylene biosynthesis and formation of aerenchyma in roots	[161]

4.1. Heat Stress

High temperature incidents, as a result of global warming, have been a major detrimental factor to several crops, affecting many critical biological processes, such as photosynthesis, cell membrane stability, RNA splicing, and protein synthesis [162]. Therefore, the development of adaptation strategies for more resilient plants is necessary. To cope with heat stress, plants have evolved sophisticated mechanisms of complex physiological and molecular networks that are not yet fully understood [163]. A sudden increase in temperature activates transmembrane proteins, which regulate calcium levels required for reactive oxygen species (ROS) production that subsequently activates heat-shock responsive genes, such as heat shock factors (HSFs), heat shock proteins (HSPs), and several detoxifying enzymes, associated with acquired thermo-tolerance [164,165]. Although the epigenetic response of crop plants during extreme temperature conditions is rather limited, heat stress was reported to induce epigenetic de-condensation of rDNA loci in rice [26], as well as rDNA chromatin re-organizations and transcriptional changes in rye (*Secale cereale* L.) [166].

The development of thermo-memory in plants involves a variety of cellular processes, including signalling molecules [167], plasma membrane structure and function [168], plastidic gene expression [169], phytohormone activity [170], along with transcriptional, post-transcriptional, and epigenetic modifications [164]. Specifically in crop plants, recent studies have shown that epigenetic modifications (chromatin remodelling and (de-) methylation), the transcriptional activation of heat stress response genes, along with lipid metabolism and redox homeostasis genes, the alteration of small RNA profiles, metabolite regulation, and signal cascade coordination are overall involved in the development and inheritance of heat stress memory (Figure 1 and Table 1), whilst improving yield under high temperatures [122,124–129,166,171,172].

The differential regulation of epigenetic mechanisms between initial and subsequent exposures to heat stimuli has been associated with the maintenance of acquired thermo-tolerance [60]. Recent studies in seagrasses and Arabidopsis demonstrated a strong association of heat stress with active DNA de-methylation, resulting in active transcriptional plasticity in these organisms under high temperature stress [173,174]. Furthermore, a multi-generational study in Arabidopsis exposed to heat stress over 25 consecutive generations revealed decreased levels of DNA methylation and overall higher epigenetic variation in the treated progeny [97]. Nevertheless, it has been previously shown that high temperature can either induce or repress the epigenetic stress response mechanisms in plants, which demonstrates the complexity of the phenomenon [4,175].

Heat priming has proven to be an efficient approach in understanding the underlying mechanisms of stress priming and stress memory development in plants [176], and most importantly, was shown to confer improved tolerance to heat stress in several plant species [122,124,126,127,171]. Regarding crop plants, heat priming has been extensively studied in wheat (*Triticum aestivum*), given its sensitivity to high temperature stress (>35 °C) during the ripening stage, which has detrimental effects on yield [122,124]. More specifically, heat priming, especially when applied at the stem elongation stage, significantly enhanced heat stress tolerance via an increase in metabolites and antioxidant defense mechanisms, which improved grain yield during subsequent heat stress exposure [124,125]. Furthermore, *HSP*s redox homeostasis genes were strongly induced by heat priming in wheat, whilst lipid metabolism genes involved in membrane rigidity were down-regulated, thus alleviating the effects of heat stress during grain filling [126–128]. The heat priming of the parental wheat plants can induce transgenerational thermo-tolerance by heritable epigenetic modifications in successive generations, which is represented by higher yield, improved photosynthesis, enhanced antioxidant activity and energy production, as well as reduced cell damage [122]. Notably, the lysine-specific histone demethylase 1 (LSD1) was significantly up-regulated in the offspring of primed wheat plants, which further strengthens the notion that epigenetic modifications could be involved in transgenerational stress memory development in wheat [122]. Despite the obvious advantages in using heat priming as a tool to confer intra- and/or transgenerational tolerance to heat stress, repeated exposure to the stress stimulus may have the exact opposite effect [172]. This finding reveals the hidden complexity of the priming mechanisms in plants and necessitates a more thorough investigation of the intricacies for each stress stimulus and species/cultivar combination.

Apart from wheat, transgenerational heat stress priming mechanisms were also investigated in other crop plants, such as rapeseed (*Brassica rapa* L.), which exhibited significant changes in pollen grain small RNA profiles in response to heat stress and were inherited by the next generation [123]. In another important horticultural crop, the heat-sensitive common bean (*Phaseolus vulgaris* L.), genome–environment associations revealed 22 genes related to biological processes involved in the heat stress response, such as the activation of HSPs, abiotic stress signalling, germination and seedling development, flowering time, protein thermo-stability, molecular chaperones, and cell-wall integrity [129]. Nevertheless, to date, stress priming studies in the common bean have mainly focused on the morpho-physiological effects of heat stress [177] and the development of preliminary epigenomic maps linked to important agronomic traits [178,179]; hence, to what extent such epigenetic changes are inter-/or transgenerationally inherited in the common bean is still a largely unexplored field.

4.2. Low Temperatures

Low temperature stress occurring at various developmental stages during crop cultivation can repress plant metabolism, development, and growth, which result in yield reduction [180]. Nonetheless, mild cold stress application can have beneficial effects for plant acclimation and is a requirement in some plant species for proper development. For some plant species, exposure to non-freezing cold temperatures is required to acclimate to subsequent cold stress events [181], while vernalisation, an extended exposure to low temperatures, is essential for the induction of flowering [182]. Studies in the field suggest a strong epigenetic basis in plant cold stress responses. Cold stress-induced histone modifications were shown to alter cold-responsive gene expressions [183–186]. For instance, the induced expression of histone deacetylases (HDACs) were shown to repress several cold-responsive genes both in *Zea mays* L., via the deacetylation of the H3 and H4 histone lysine residues [187], and in rice (*Oryza sativa* L.) [188,189]. Furthermore, the cold-induced H3K9 histone acetylation was implicated in regulating the *DEHYDRATION-RESPONSE ELEMENT BINDING FACTOR* 1 (*DREB*1) genes in rice [190,191]. Apart from histone modifications, DNA methylations were also shown to play a prevalent role in cold stress responses [20,185,192,193].

Cold stress has also been investigated as a priming stimulus for the development of abiotic stress memory in crop plants that can effectively improve the crop's tolerance to low temperatures. Despite the recent advances in uncovering priming mechanisms associated with cold stress tolerance, research on the field is rather limited, especially for crop plants. Cold-primed plants (i.e., cereals, pea, and spinach) have shown increased enzyme activities in the Calvin cycle and sucrose accumulation [132,194] and gene regulation corresponding to improved cell membrane stability, ion homeostasis, and photosynthesis [125]. In wheat, cold stress has been one of the major constraints for crop yield [195] and cold priming for a week during the tillering stage was shown to alleviate the negative effects of cold stress [136]. Moreover, cold-primed wheat plants showed higher photosynthetic rates and stomatal conductance under subsequent cold stress exposures [137]. Imin et al. (2004) reported that priming early in microspore development can alter anther protein content and induce selective protein degradation in rice anthers [131]. Rice is a very sensitive crop to cold stress, especially during the microspore development stage, and pollen sterility can be easily induced by low temperature exposure in that developmental stage [131,196,197]. Therefore, cold priming at the gametophyte stage could be a very effective approach in improving cold stress tolerance in rice and other crop plants.

In horticultural crops, such as eggplants (*Solanum melongena* L.), cold priming in early stages improved the acclimation to chilling stress in later stages [135]. Given that cold stress can primarily damage cell membrane structure and integrity, cold priming could effectively improve membrane stabilisation during cold stress [198]. Cold priming inducing the accumulation of osmolytes, such as sucrose and proline, has been proposed as one of such mechanisms in watermelon [130]. Furthermore, cold-primed *Solanum comersonii* Poir. plants showed a decrease in linoleic acid and sterol phospholipid ratios [134], and given that cold-resistant plants accumulate unsaturated fatty acids in their plastid membranes [199,200], this indicates that cell membranes may have a central role in cold stress tolerance. Cold priming research in peach (*Prunus persica* L.) showed an increased accumulation of proteins related to energy metabolism, such as triose-phosphate isomerase and glyceraldehyde-3-phosphate dehydrogenase [133]. Moreover, subcellular processes associated with the production and scavenging of ROS may also be involved in cold stress priming [201,202].

Overall, based on the limited research related to the mechanisms that underlie cold stress memory development in crop plants, the main pathways involved include the accumulation of osmolites, transcriptional regulation, lipid and energy metabolism, ion and redox homeostasis, as well as the alteration of protein content (Figure 1 and Table 1). Nevertheless, it is still largely unknown to what extent somatic and/or transgenerational epigenetic mechanisms are implicated in cold stress priming in crop plants (Figure 1 and Table 1).

4.3. Drought

Drought stress can severely affect crop plant development and yield by inhibiting growth and photosynthetic activity, inducing ROS production and stomatal closure, as well as inducing root growth as a counter-response to limited water supply [203–205]. Acclimating plants in water-deficit environments can prevent yield loss to drought by inducing changes in root architecture, water usage efficiency, photosynthetic adjustments, as well as the production of osmotic and antioxidant factors [206]. In this context, pre-treatment with drought stress as a priming approach could be efficient for the development of drought memory towards drought tolerance.

Evidence suggests that drought stress memory establishment in crop plants is a rather complex process that can be manifested either somatically or/and inherited transgenerationally. Regarding somatic memory development, drought priming in wheat during the seedling stage was shown to effectively alleviate drought stress damage occurring in later growth stages [109], similar to drought priming applied at the sixth leaf and stem elongation stages, which alleviated the effects of drought stress during grain filling [110], through activating the antioxidant defense and redox homeostasis mechanisms. Drought memory miRNAs were shown to induce soluble sugar and proline accumulation towards improving drought resistance in wheat seedlings [111]. Drought memory in *Glycin max* L. manifested as an increase in the expression of drought response genes and dehydration memory genes encoding transcription factors, protein phosphatase 2Cs, and late embryogenesis rich proteins after recurring drought stress [101]. Drought-primed cowpea plants were more tolerant to subsequent drought stress, as indicated by an improved water status, water productivity of biomass index, photosynthesis, and plant hormones [113]. Long-term drought stress enhanced the stress tolerance and tuber yield in potato (*Solanum tuberosum* L.) [108], with somatic memory development being associated with the increased expression of genes related to biosynthesis and signal transduction [107]. Drought priming has also been applied as an effective approach for inducing stress tolerance in perennial species, such as olive trees (*Olea europaea* L.), which showed a higher photosynthetic efficiency, higher proline and sugar contents, as well as more active antioxidant machinery compared to non-primed trees [103]. Similarly, unirrigated grapevines (*Vitis vinifera* L.) improved drought-resilience due to long-term drought stress adaptation manifested as increased water status, leaf gas exchange, and berry size [114].

The epigenetic mechanisms in drought-induced somatic memory development have been extensively studied in Arabidopsis, showing that drought priming led to DNA methylation changes and the upregulation of histone modifications [30,32,74,207]. In crop plants, specifically, histone modifications were shown to play an important role in regulating the expression of drought stress memory genes in cotton (*Gossypium hirsutum* L.) plants exposed to recurring drought stress [102]. Relatively recently, the transcriptome analysis of rice plants treated with mild drought stress revealed that DNA methylation, lncRNAs, and abscisic acid (ABA) regulatory pathways may underlie the development of drought stress memory in rice by inducing drought-responsive genes after subsequent drought stress [104]. Moreover, drought stress was shown to induce global DNA methylation changes during the vegetative development of rice [105], while drought stress-responsive differentially methylated regions (DMRs) were shown to be involved in the regulation of stress memory genes and transposons [106] during recurring exposures to drought stress. The involvement of phytohormones in drought stress memory development is further supported by the work of Wang et al. (2021), who demonstrated that in drought-primed wheat, ABA and jasmonic acid (JA) are involved in the enhancement of plant drought tolerance by inducing the activity of detoxifying enzymes [112]. In concordance, research in citrus plants demonstrated an association of DNA methylation patterns with an increase in ABA levels after multiple exposures to drought stress [100]. Notably, epigenetic memory was also shown to be stored and transmitted in citrus trees using drought-primed scions [46]. This was achieved through the modification of methylation status and gene expression, which is expected to facilitate the development of new drought-tolerant crop varieties [46].

Several studies of drought priming in crop plants show that there is a very strong transgenerational component associated with the acquired drought memory in plants. The progeny of drought-primed barley developed longer roots compared to the non-primed plants, which is a typical defence mechanism for drought stress acclimation [116]. Similarly, in wheat offspring, improved grain yield along with enhanced photosynthetic activity, proline production, and reduced oxidative stress were associated with transgenerational stress memory due to the priming of the parental plants at the grain filling stage [119]. Research on the responsiveness of the progenies of non-primed and primed peanut (*Arachis hypogea* L.) genotypes under contrasting water regimes revealed the high variability of transgenerational drought-resistance mechanisms, exemplified by characteristics such as enhanced rooting, seed weight, and germination efficiency [115]. Furthermore, DNA methylation patterns in drought-primed rice indicated a transgenerational effect with variable drought resistance levels [117,118]. Evidence suggest that drought memory development is a rather complex process, involving both intra-, inter-, and transgenerational mechanisms. A study performed recently in winter wheat showed that inter- and transgenerational drought stress memory development seem to have an additive effect towards offspring tolerance to drought stress, while variable effects were observed when both types of drought memory inheritance were considered separately [120]. This is also supported by the study by Tabassum et al. (2018), who demonstrated that both terminal drought in wheat parental plants and seed osmopriming, either in combination or independently, improved drought tolerance in the offspring [121].

Collectively, research on the somatic effects of drought priming towards drought stress memory establishment in crop plants involves the activation of antioxidant defence and redox homeostasis machinery, the accumulation of osmolites, hormonal regulatory pathways (ABA and JA), epigenetic modifications, as well as the regulation of non-coding RNAs, stress memory genes, and transposons (Figure 1 and Table 1). Regarding the transgenerational effects of drought priming, the limited research at the molecular level in crop plants implicates DNA methylation patterns in stress memory inheritance (Figure 1 and Table 1).

4.4. Waterlogging

The oversaturation of the soil with water can lead to hypoxia, which can subsequently inhibit root growth, induce root death and early leaf senescence, reduce carbohydrate metabolism, and ultimately crop yield [208,209]. In contrast to other stresses, soil waterlogging was also reported to induce stress memory in crop plants, although the mechanisms of stress memory development still require further investigation in order to better understand the adaptive potential of plants to flooding stress.

Existing studies have shown that flooding priming can help plants adapt to flooding stress and reduce yield loss. Research on waterlogging priming in crop plants has been mainly focused on wheat [160,161], which was shown to alleviate the severity of recurring waterlogging stress during grain filling by increased photosynthetic capacity, higher chlorophyll content, and light usage efficiency [160]. Additionally, enzymatic and non-enzymatic processes involved in the ascorbic acid-glutathione (ASA-GSH) cycle were highly induced by waterlogging priming in wheat [161]. Waterlogging stress memory development was also studied very recently in other plant species. For instance, the long-term waterlogging of cucumber (*Cucumis sativus* L.) genotypes revealed that the development of water stress transcriptional memory is linked to developmental changes, including the formation of adventitious roots, as well as changes to the glycolysis, ethylene, and amino acid metabolic pathways [158].

Although the mechanisms of water stress memory development are still largely understudied, both H3K4 trimethylation and H3 acetylation of the *alcohol dehydrogenase 1* (*ADH1*) and *pyruvate decarboxylase 1* (*PDC1*) genes seem to be implicated in the rice submergence response [159]. A recent study by Lukić et al., 2023, revealed that both waterlogging and drought stress can induce strong transgenerational adaptive effects in several perennial plant species through the activation of antioxidative mechanisms in the offspring of the pre-conditioned plants [210]. The limited knowledge on the priming-induced flooding both at the somatic and transgenerational stress memory development in crop plants indicates the need for further research to elucidate the implicated mechanisms (Figure 1 and Table 1).

4.5. Salinity

Salinity is a major environmental constraint for agriculture worldwide, impairing physiological, biochemical, and molecular functions, and therefore affecting plant development, growth, yield, and overall productivity. As a multifaceted stress, causing osmotic and ionic toxicity, different methods, from conventional breeding to transgenic technology and gene editing, have been employed to alleviate the unfavourable effects while improving plant yield and quality, with seed priming being one of the promising strategies [211]. The epigenetic regulation of plant salt stress responses was shown in Castor bean, *Ricinus communis*, where diverse salt responsive genes and switched histone methylation sites have been identified, indicating that modifications in bivalent H3K4me3-H3K27me3 regulate the *RSM1* transcription involved in ABA-mediated salt stress signalling [212].

Employing a pre-treatment with stress stimuli (priming) has been proven to be energetically effective in terms of plant metabolism and, in parallel, a cost-effective technique for developing plants with priming-induced memory of salinity stress to later developmental stages. Seed priming techniques, as a possible salt stress management approach for developing somatic salt stress memory, have, thus far, been investigated in major crops, such as maize, wheat, and rice [213], *Brassica napus* L. [138,139] and peppers (*Capsicum annuum* L.) [140,141]. Research on halopriming (the soaking of seeds in aerated solutions of inorganic salts prior to stress exposure [214]) of seeds with low salt concentration solution, prior to salinity stress, has shown to alleviate the negative effects of NaCl on nitrogen metabolism and DNA damage in different leguminous species [146,147] and induced the upregulation of Giberellic Acid (GA) biosynthesis genes, while improving germination and tolerance in tomato plants [152]. Similarly, halopriming increased the expression of salt-responsive genes attributed to the improved biosynthesis of photosynthetic pigments and decreased levels of oxidative stress markers in bread wheat [154], whereas in rice seeds, it increased the expression of genes associated with ion homoeostasis [150]. Osmopriming (osmotic solutions with low water potential to revive seeds [214]) with polyethylen glycol (PEG) also increased the transcript levels of salt stress-responsive genes (*GST*, *TXN* and *APX*) in *Physalis angulata* L. [151]. Nevertheless, it is not a popular technique due to the required large volume of osmotic solutions, costly temperature management and aeration systems [45].

The overall molecular mechanism of priming-mediated responses against salt stress involves the energy-dependent trans-membrane receptor-like kinases (RLK), which recognize the priming elicitors and when activated, they regulate the transcription of abiotic stress defence genes [214]. In *Lolium perenne*, short-term epigenetic salt stress/recovery treatments could change the transcriptional response to the subsequent abiotic stress inducing transcriptional and metabolic changes and improving plants' stress response via inhibiting physiological damage (such as cell membrane stability and ROS) regulated by trainable genes [148].

However, salt pre-treatment during the early growth and vegetative developmental stages for improving salt tolerance, even in salt-sensitive genotypes, and the associated transgenerational response mechanisms, have not yet been extensively studied in crop plants. The acclimation of plants to salinity can be induced not only during germination and early development, but also during late vegetative growth, and can be dependent on the stress level and the exposure period. The salt priming of young wheat plants improved their salt tolerance via enhancing the osmotic and antioxidant potential [155]. It is noteworthy that salt priming in tomato induced an adaptive response to the primed salt-sensitive genotype compared to non-primed plants of the same genotype, as well as the primed plants of the salt-tolerant genotype [153]. This suggests that the stress level necessary to trigger the adaptive response is related to the tolerance level of the genotype, indicating a possible saturating tolerance-dependent effect. Furthermore, the adaptive response induced by the salt pre-treatment observed only at the five-leaf stage might indicate that there is possibly a developmental window for adaptation [153].

Despite the limited research on salt priming memory in crop plants, the short salt priming of young Arabidopsis plants was shown to alter the response of adult plants to salt stress, mainly by causing significant genome-wide changes in histone modification profiles [36], providing evidence of the development of long-term somatic memory in plants at the physiological and molecular level. Epigenetic modification also has a key role in soybean salt tolerance by altering the transcriptional landscape of salt stress-responsive genes through methylation and acetylation [142–145]. The regulation of histone proteins can function as an epigenetic molecular tool to prime plants' response to salt stress by altering key salt-responsive genes that are maintained throughout vegetative growth [215]. The overexpression of the repressor of silencing *AtROS1* gene in tobacco plants was associated with somatic transcriptional memory by reducing the level of DNA methylation in the promoter and coding regions of flavonoid biosynthesis and antioxidant genes [149].

Epigenetic transgenerational stress memory leading to an adaptive response to salinity stress has been reported for *Arabidopsis thaliana* and *Suaeda salsa* [216,217]. In Arabidopsis, salt stress significantly altered the genome methylation level and gene expression patterns and most of the changes were transferred stably to the next generation [218]. In *Brassica napus* and *Gossypium hirsutum*, the number of demethylated sites is higher in salt-tolerant than in sensitive lines, while the number of methylated sites is lower than in sensitive lines [156,157], indicating that demethylation can promote the expression of stress-related genes and induce salt resistance in these species [219]. These changes are also a source of epigenetic memory that help plants to survive under recurrent stresses [220]. Moreover, the miRNA expression, as another epigenetically regulated event through the process of histone deacetylation, was shown to control the expression of stress-responsive genes, regulating transgenerational salt stress response memory in soybean [176].

Conclusively, salt stress memory establishment in crop plants has been mainly investigated at the somatic level, while any transgenerational effects are still poorly understood. Concerning somatic memory, salt stress priming memory induced the upregulation of GA, salt-responsive (antioxidant markers and photosynthesis pigments), and ion homeostasis genes, as well as energy-dependent RLKs that subsequently regulate abiotic stress-defence genes (Figure 1 and Table 1). At the epigenetic level, both global histone modifications and DNA methylation shifts were shown to enhance salt stress priming memory (Figure 1 and Table 1). Transgenerationally, salt stress memory in crop plants, thus far, is achieved through changes in genome methylation and histone deacetylation patterns, along with stress-related gene expression regulation (Figure 1 and Table 1). Nevertheless, the mechanistic basis of salt stress memory establishment via epigenetic and hormonal cues, especially in crop plants, is still poorly understood.

4.6. Cross-Tolerance and Stress Memory

Plants have the ability to counter different types of environmental stresses simultaneously, which enables them to establish a better response to future exposure [219]. Interestingly, plants exposed to single stress stimuli are more susceptible than when exposed simultaneously to different abiotic stresses [221]. Cross-tolerance or "trans priming" is the inherent tolerance potential of primed plants to cope with subsequent stress exposure when the stimulus is different from the initial stress factor [211]. This acquired resistance has a positive impact on plant vitality and profound implications for agriculture [201]. To achieve cross-stress acclimation and memory, it is essential that both stress perception, stress effects, and the associated molecular response mechanisms are compatible among the different stresses [221–223]. Previous studies on cross-tolerance provided evidence of the molecular and physiological processes occurring in signal initiation and transduction. Plant responses to abiotic stresses are mediated by common signals, such as reactive oxygen and nitrogen species (ROS and RNS) [224], calcium gradients [225], heat-shock proteins (HSPs) [226], and plant hormones [227], and the interplay among these signalling pathways is a key component in regulating cross-tolerance [228].

Abiotic stress priming could stimulate specific stress response memory and induce cross-tolerance to the subsequent exposure to stresses [12,229–231]. However, cross-tolerance induced by priming requires a stress-free lag phase between the priming and the triggering stress stimuli in order for plants to recover from the initial stress [232,233]. Whether a short stress-free lag phase is sufficient to trigger priming-induced memory, such as the period allowed between priming and the different abiotic stresses [171], requires further experimentation. Another important aspect of cross-tolerance is that the response to priming is genotype-dependent, and thus, phenotypical variation should be expected when studying the effects of abiotic stress priming [172].

Evidence of cross-tolerance has been reported in cereals, when short-term drought priming during the early vegetative stages showed improved tolerance to cold, salinity, and heat stresses [234–238]. Drought priming-induced cross-tolerance in cereals is mediated by the activation of antioxidant mechanisms in the chloroplasts and mitochondria as a result of the upregulation of the Cu/Zn *SOD*, Mn *SOD*, and t*APX* encoding genes under low temperature stress [239,240] or the activation of the AP endonuclease (*Ape1*L) gene under heat stress [241], which indicate a strong involvement of antioxidant machinery and DNA repair mechanisms in cross-tolerance priming. Notably, the progeny of drought-primed wheat plants can develop cross-tolerance to heat stress during grain filling, indicating putative transgenerational effects [236]. Additionally, osmoprimed offspring of parental wheat plants exposed to terminal drought showed improved salt tolerance [121], which indicates that stress memory can be triggered by environmental factors with a similar effect basis. Nevertheless, this adaptation could be the result of the cumulative effect of adaptation induced by drought and osmopriming; however, this necessitates further investigation to elucidate these effects. Aside from annual crops, drought stress priming in grapevine was reported to improve freezing tolerance in shoot and root tissues of both drought-tolerant and -sensitive grapevine cultivars, which is indicative of established stress memory [242]. Cross-tolerance has also been recently reported for *Coffea* spp. when previous exposure to water shortage helped to mitigate the impact of subsequent low temperatures due to an increase in plant antioxidative defences [243].

Moreover, salt-primed rice plants at the vegetative stage showed an enhanced tolerance to drought stress during the reproductive stage manifested at the physiological, hormonal, metabolic, and transcriptional levels [244]. In tomato, salt [245] and low temperature [246] priming induced drought stress tolerance, mainly by enhancing the photosynthetic efficiency and inducing physiological acclimation. Inversely, the drought priming of tomato seedlings induced the acclimation of adult plants to salinity stress [247]. In perennial plants, such as the olive tree, salt priming induced cross-tolerance to subsequent drought by modulating the physiological and biochemical responses and employing beneficial metabolic adjustments and antioxidant mechanisms [248].

Regarding cross-stress tolerance induced by temperature priming, short-term cold shock in mustard (*Brassica campestris* L.) seedlings stimulated ROS detoxification mechanisms, leading to cross-tolerance against both drought and salt stresses [249]. Heat priming of rice and young eggplants resulted in better plant acclimation to low temperature stresses in later developmental stages [135,250], which further supports the commonality of abiotic stress mechanisms. This idea that mechanistic commonality between stresses is required to achieve cross-tolerance is reinforced by the observation that cold-primed plants showed distinct expression patterns under cold and light intensity stresses [251]. Similarly, as was reported on the absence of cross-tolerance between drought and waterlogging stress conditions observed in several perennial plant species [210], is evidence of the notion that exposure to stress factors with different mechanistic effects may not be able to induce stress memory.

5. Stress Memory Trade-Offs

Plants grow in complex environments exposed to multiple abiotic and biotic stresses, which necessitate the constant balancing of a trade-off between defence mechanisms and growth. It has already been demonstrated that plants can allocate resources for immediate defence requirements, without permanently reducing their capacity and productivity for photosynthetic activity [252,253], while the shift from plant development and reproduction to defence may eventually reduce plant productivity and yield [254–256]. Moreover, depending on the nature, degree, and timing of the stress, the combination of stresses may have positive, negative, or even neutral effects [257–259].

The adverse impacts of stress memory on breeding relate to the fact that the acquired stress memory may inhibit the normal growth of plants [260]. In a notable demonstration of the phenotypic trade-offs arising from different levels of stress intensity, Skirycz et al. (2011) observed that the growth of Arabidopsis genotypes under moderate water-deficit stress did not correlate with their ability to endure severe drought stress [261]. This phenomenon extends to priming responses and hereditary traits as well. Specifically, drought priming has generated responses that, in some cases, are unlikely to provide any benefit or could even be detrimental to tolerance against other forms of stresses, as exemplified by the development of deeper roots in peanut [262,263] or increased water consumption in potato [264] in response to priming, which may not necessarily enhance tolerance to salinity or cold stress [206]. Morphological alterations may sacrifice other responses, such as water conservation to maintain carbon fixation, or plant growth [265]. Water-deficit priming reduced the yield of primed plants when no subsequent stress stimulus occurred, possibly due to the energetic costs, which cannot be compensated by the enhanced tolerance [237,266]. As such, successful priming is only beneficial when there is no yield loss with or without subsequent stress [267].

Alternative response mechanisms have also been reported between cross- and cis-tolerance adaptation. For example, acclimating plants in water-deficit environments can induce a plant response to high light intensity through oxidation avoidance, rather than antioxidant activity occurring during shade-to-light acclimation [206]. Hence, to create more resilient plants to the effects of climate change, it is necessary to identify breeding targets that are involved in balancing a plant's response to various stresses while maintaining growth fitness [268–270]. Overall, while stress priming can confer tolerance to specific stress conditions, it may also lead to trade-offs and limitations. The allocation of resources towards defence mechanisms may reduce plant productivity and yield. Moreover, the effectiveness of stress priming responses can vary depending on the nature, degree, and timing of the stress, as well as the specific genotype or species.

6. The Art of Forgetting

Memory of a once-experienced environmental cue may last for months until retrieved later and affect plant stress responses or development. For instance, it is well-known that plants can “remember” a cold exposure that happened months ago and are thus vernalized and induced to start flowering. The duration of the memory may vary widely. In general, memory based on the increased levels of metabolites and transcription factors probably mediates more transient or short-term effects and its duration can last from days to weeks [49,51]. For instance, the physiological benefits of heat stress memory may last for at least three days, whilst at the molecular level the enhanced re-induction was still detected after six days [271,272]. In addition, memory may also last for months, or even years, as in perennial plants, which usually requires the mitotic stability of the information and involves chromatin-based processes [51,273–275], or can even contribute to adaptation, as transgenerational stress memory [82]. Nevertheless, the mechanisms that limit the duration of the memory are still unresolved [176]. In theory, having an infinite capacity for somatic stress memory may not be advantageous for evolution, given that in nature, plants are exposed to multiple different stresses over a season and developing memory for all the stresses is energetically ineffective compared to the actual benefits of stress priming [176]. Therefore, both establishing the stress memory and erasing it are coordinated by fine-tuned mechanisms relying on the orchestrated interaction of a broad spectrum of mediators [276].

However, plants can also “forget” the once-acquired information. The mechanisms for resetting the heritable epigenetic memory in plant paternal chromatin have been previously described [79]. As each generation faces a different combination of environmental challenges, the loss of most stress memories could allow for a fresh start in the next generation [277]. It is reasonable to suggest that the duration of the memories is not a simple result of the mechanism underlying the memory, but probably of the resetting mechanisms involved [37]. One way of erasing stress memory stored in the form of proteins requires protein degradation [278]. For example, it is known that the acquisition of heat memory dependent on DNA methylation involves the activation of HSFs that induce the expression of heat shock proteins [35]. A mechanism described for resetting such heat memory is the autophagy of stress-induced proteins in a target-oriented manner, rather than unselectively degrading cellular contents. This selective autophagy induced by abiotic stress is closely interacting with phytohormones, metabolites, and reactive oxygen species (ROS) [279]. Autophagy may contribute to resetting the memory, for instance, of heat stress at later stages of the thermo-recovery phase, compromising heat tolerance after a second heat shock, as shown in Arabidopsis [280–282]. By contrast, selective autophagy was also shown to induce the turnover of heat stress memory in Arabidopsis by NBR1-mediated targeting of HSP90.1 and ROF1 during the recovery phase, and thus the shortening of stress memory [283].

7. Conclusions and Outlook

This paper provides a comprehensive review of stress priming in agronomically important crop plants and its implications for plant adaptation to stress conditions (Figures 1 and 2). It presents the current knowledge on the mechanisms involved in the development and inheritance of abiotic stress priming-induced memory, as well as the duration of these memory imprints. The paper also highlights the need for further research to understand how plants regulate transgenerational and intergenerational memory, as well as optimize tradeoffs between stress response and growth. Thus, the question raised is why priming-induced stress memory for achieving plant stress tolerance is important? In nature, a plant’s ability to efficiently acclimate under various stresses is critical for survival, especially in the frame of a changing climate. To date, the present state of knowledge on abiotic stress memory in crop plants induced by priming has mainly focused on the morpho-physiological and biochemical aspects of the phenomenon. There is still much to elucidate regarding the precise signalling pathways and the molecular mechanisms underlying stress memory acquisition, as well as any putative intra-, inter-, and transgenerational epigenetic effects towards stress tolerance in crop plants.

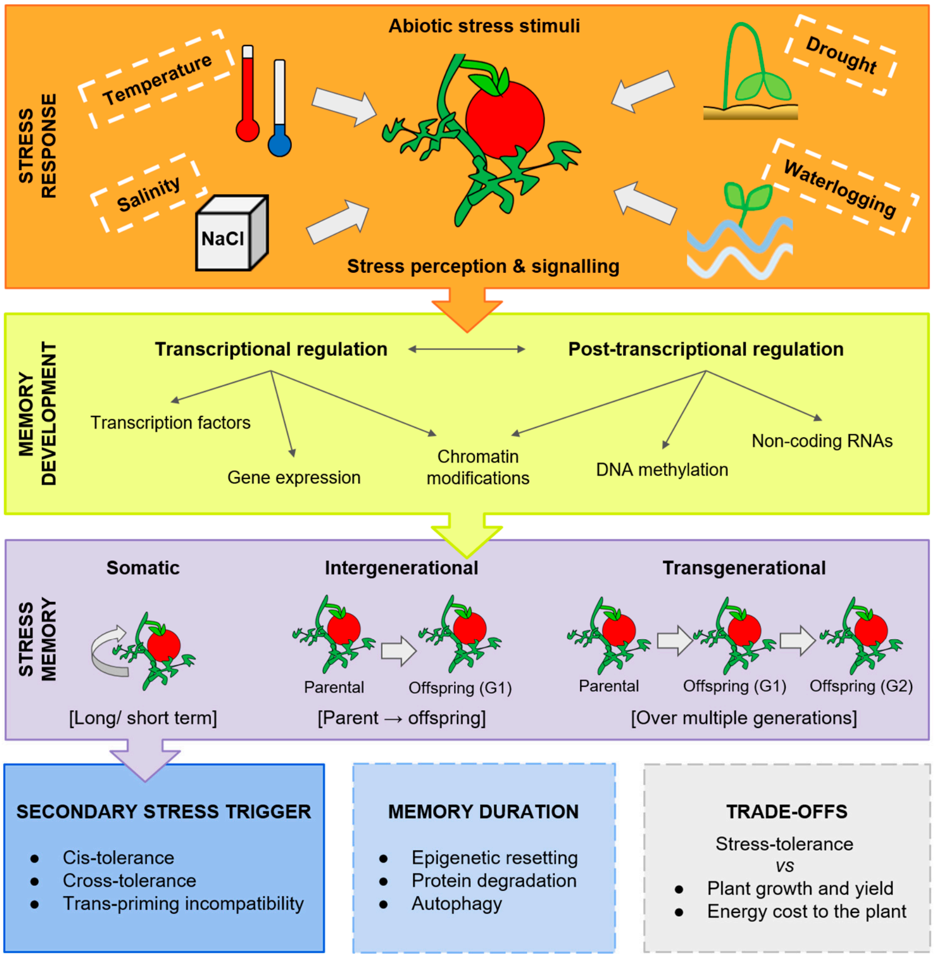

Figure 2. Graphical outline of abiotic stress memory development induced by priming in crop plants. The top panel represents the stress response to the most prominent abiotic stress stimuli that are used as priming factors to induce stress memory. The middle panel represents the memory development at transcriptional and post-transcriptional levels leading to stress memory acquisition. The third panel represents the different types of stress memory imprints (somatic, intergenerational, and transgenerational). The boxes in the fourth panel indicate from left to right the different types of developed tolerance under secondary stress exposures, along with the most prevalent mechanisms implicated in the maintenance or fading of stress memory, and the potential quid pro quo costs of acquired stress tolerance.

Plant stress responses involve dynamic interactions between thousands of genes and epigenetic mechanisms. While we understand how epigenetic stress memory is inherited in Arabidopsis, these mechanisms remain unknown in crop plants, and questions persist regarding their inheritance and maintenance. Numerous epigenetic changes are linked to stress memory after priming, but it is unclear if they form a unified pathway or act independently at the same or on different stress-responsive genes. Transgenerational stress memory can safeguard offspring from previous stressors but may also increase their susceptibility to other stressors. Investigating this relationship is crucial to understand the shared and distinct pathways among environmental stresses and the impact of spatiotemporal epigenetic responses on stress memory specificity. Interestingly, while diverse stressors trigger similar epigenetic patterns, the underlying mechanisms may differ, suggesting the involvement of multiple mechanisms in stress memory formation. Therefore, the mechanistic synergy or divergence between stress-stimuli and stressors towards enhanced stress tolerance and yield requires methodical investigation. Another aspect to consider is how stress memory is transmitted through vegetative reproduction.

In this context, the utilization of effective strategies to enhance crop productivity amidst shifting environmental conditions is paramount. One relatively new approach involves abiotic stress epi-breeding, a strategy that delves into epigenetic variations and the manipulation of the epigenome to enhance plants' acclimation to diverse environmental challenges, thereby leading to increased yields and improved overall quality. Hence, the establishment of a comprehensive database encompassing information on stress responses and the impact of the energetic state of primed plants becomes indispensable for identifying key elements crucial to the functional association between acquired epialleles and improved stress resilience. By transferring these advantageous traits to crops, we can enhance their stress resilience, while minimizing cultivation expenses, which is advantageous for both the agricultural sector and the environment. This review may ultimately contribute to the growing body of knowledge on stress resilience in crop plants and encourage future research on heritable stress memory development in non-model plant organisms.

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