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Review

Priming crops for the future: rewiring stress memory

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The agricultural sector must produce resilient and climate-smart crops to meet the increasing needs of global food production. Recent advancements in elucidating the mechanistic basis of plant stress memory have provided new opportunities for crop improvement. Stress memory-coordinated changes at the organismal, cellular, and various omics levels prepare plants to be more responsive to reoccurring stress within or across generation(s). The exposure to a primary stress, or stress priming, can also elicit a beneficial impact when encountering a secondary abiotic or biotic stress through the convergence of synergistic signalling pathways, referred to as cross-stress tolerance. 'Rewired plants' with stress memory provide a new means to stimulate adaptable stress responses, safeguard crop reproduction, and engineer climate-smart crops for the future.

Highlights

Plants have stress memories that lead to epigenetic, transcriptomic, proteomic, and metabolomic changes, enabling enhanced responses to additional stress exposure.

Multi-omic studies have identified previously unrecognised regulators, metabolites, and pathways as key components of priming-induced thermotolerance.

Successful acclimation for drought and flooding-induced stress memory is linked to changes in antioxidative capacity, biochemical modifications, and hormone pathways.

Cross-stress tolerance can be elicited by pre-exposure of a primary stress to improve crop performance under subsequent stress. Application of priming agents is another effective cross-priming approach, particularly for seed priming or commercial seed production.

Cross-stress priming success relies on synergistic stress signalling pathways being shared across stresses varying in nature and intensity.

Adapting to a changing climate: what does the future look like for crops?

Crop production and quality are frequently challenged by environmental stresses, such as drought, heat, salinity, and frost. With global climate change, both the magnitude and the frequency of severe weather events, such as extreme temperatures and reduced precipitation, are predicted to increase [1]. Repeated and increasing occurrence of droughts, floods, heat waves, and frost events present a substantial threat to crop production and global food security, and may lead to fundamental changes in germplasm composition [2,3]. Given the ever-increasing world population, new effective plant breeding strategies to fortify stress resilience, enhance yield production, improve crop quality, and establish more adaptable and sustainable germplasm pools for future climate challenges are needed.

A significant body of research has investigated the intricate adaptation mechanisms and coordinated stress response networks of high-economic value broad-acre crops, such as rice (*Oryza sativa*), bread wheat (*Triticum aestivum*), maize (*Zea mays*), and soybean (*Glycine max*) [4–7]. Recently, advances in understanding the genetic and epigenetic regulation of **plant stress memory** (see Glossary) have provided new insights and strategies for improving crop resilience [8–14]. Stress memory is based on mechanistically directed epigenetic modifications and genetic rearrangements made in plants after the initial stress occurrence [15,16]. **Stress priming**, also called stress hardening, training, or conditioning, can induce short-term or long-term stress memory that enables plants to be more tolerant to an additional stress in the current or even subsequent generations [17–20]. By pre-exposing crops to eliciting factors at early developmental stages or in parent/grandparent generations, stress priming can lead to enhanced adaptation and the expression of favourable traits. When epigenetic variation is maintained across many generations, genetic assimilation may occur [21] and will likely enable fixed stress memory phenotypes longer term [22]. Here, we focus on the mechanistic basis of stress memory and the application of stress priming in agronomically important crops especially for significant, yet challenging, breeding priorities (such as thermotolerance).

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Stress memory: the multi-omics landscape

In recent times, an increasing number of reports have described the phenomenon of plant stress memory, which describes the sustained effect and imprint of stress, in which previous abiotic and/or biotic stress exposures have had a significant impact on subsequent stress responses in the current or future generation(s) [8,13,14,23–26]. Previously, stress memory had largely been described under two categories: mitotic stress memory (somatic memory, affecting the current generation) and meiotic stress memory (transgenerational memory, influencing future generation(s)) [27–29]. The Bäurle lab proposed to distinguish single-generation stress memory as intergenerational memory, while multiple generation stress memory is referred to as transgenerational memory [30–32]. This is in alignment with animal research, in which intergenerational (parent) and transgenerational (grandparent or great-grandparent) influences are clearly distinguished and are discussed separately. Although there is limited adoption distinguishing such events in the plant community [33–36], it now appears necessary because more and more studies suggest that the molecular basis of intergenerational and transgenerational stress memory is different, and that the stress imprint fades across generations [23].

Somatic memory is generally transient and activated upon exposure to an acute stress but can be reactivated within a limited period (typically hours to days). However, somatic memory can also be sustained long term across multiple developmental stages within the current life cycle. Intergenerational memory is directly transmitted from the parents to the first-generation progeny but can reset in the second-generation offspring. When the stress imprint is passed beyond the first-generation progeny (i.e., inherited in, and further than, second-generation offspring), it is considered transgenerational memory [30,31,37,38]. With the development and deployment of various omics approaches (e.g., **transcriptomics**, **epigenomics**, **degradomics**, **proteomics**, and **metabolomics**) using high-throughput processing pipelines, a substantial volume of large-scale data has been generated and interrogated to link molecular function with agronomic performance, thus providing new insights into the mechanistic basis of plant stress memory [13,14,24,39,40].

Current evidence suggests that stress memory is heavily epigenetic based and involves mechanisms including chromatin remodelling, DNA methylation, nucleosome positioning, histone modification, and noncoding RNA-mediated regulation (Figure 1). Epigenetic regulators include, but are not limited to, chromatin remodellers [e.g., ATP-dependent switch/sucrose nonfermentable (SWI/SNF) complex; imitation SWITCH (ISWI) complex; chromodomain helicase DNA-binding (CHD) family and INO80 complex ATPase subunit (INO80) family], histone modifiers (e.g., histone acetyltransferases, methyltransferases, and demethylases), DNA methyltransferases, and DNA-demethylating enzymes [30,41,42]. Stress memory depends on imprints left on the physical structure (e.g., chromatin) that affect future gene transcription events after the initial stress onset, or the retained abundance of regulators controlling functional gene expression post-transcriptionally to promote or suppress the accumulation of transcription factors, signalling metabolites, and stress-response proteins via gene silencing and/or activation [11,27,43]. These regulators interact with each other to fine-tune their molecular functions, with the feedback loop usually mediated by small noncoding RNAs (sRNAs) such as **small-interfering RNAs** (**siRNAs**) and **miRNAs** [5,33,44], across different abiotic stress examples, such as heat, cold, drought, and flooding; these pathways are detailed in the following text.

An inherent feature of stress memory is that the mechanisms are not simply repetitious activation of the same pathways that are responsive to the original stress exposure. Activation of existing imprints and feedback loops often initiates faster recruitment and efficient production of beneficial signalling compounds and metabolites. Nonetheless, stress memory effects are dependent on

Glossary

Degradomics: there are two major types of degradomics studies: (i) the proteomic approach used to establish the global profile of proteases, protease inhibitors, and protease substrates. Protease degradomics is used to analyse the proteolytic events within an organism; and (ii) mRNA degradomics, which refers to next-generation sequencing analysis (degradome-seq) used to globally identify miRNA cleavage sites within mRNAs and mRNA degraded post-transcriptionally.

Epigenomics: analysis of the global epigenetic state or modifications within an individual (i.e., epigenome). The epigenome governs changes in the genetic material and regulates gene activities in the absence of changing the gene sequence.

Metabolomics: qualitative and quantitative analysis of small-molecule metabolic products (metabolome) within living organisms. Metabolomics analysis provides the biochemical footprint of specific biological processes within a single cell, tissue, or whole plant.

miRNAs: single-stranded small ncRNAs (mostly 21–24 nucleotides) that function in post-transcriptional gene silencing by binding to their mRNA targets, causing mRNA cleavage or translational inhibition. miRNAs are highly conserved across the plant kingdom and are epigenetic regulators that control gene expression.

Plant stress memory: ability of plants to retain changes and store information after stress exposure(s). The information or imprint is utilised by the plants (or the offspring) to cope with a reoccurrence, thereby responding and/or adapting more efficiently.

Proteomics: large-scale characterisation of the entire set of proteins (proteome) produced by an organism; can exhibit high levels of variation and is spatiotemporal, subject to environmental conditions and development stages.

Small-interfering RNAs (siRNAs): ncRNA molecules produced by the processing of long double-stranded RNA precursors. siRNAs function in the RNA interference pathway by binding to complementary mRNA sequences, causing mRNA cleavage and degradation. siRNA can also lead to DNA methylation.

Stress priming: strategy/process whereby exposing plants to a single or

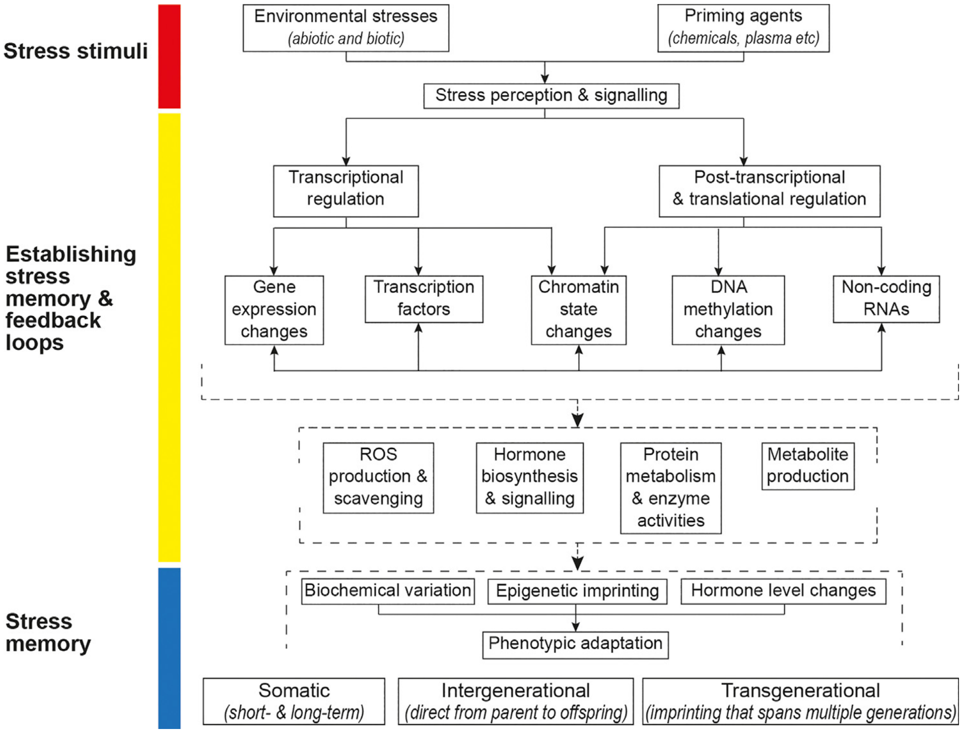

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Figure 1. Plant stress memory overview. The molecular and physiological framework of stress memory, highlighting the stimuli (red), elements and feedback loops (yellow), and stress memory (blue) required to attenuate stress responses. Abbreviation: ROS, reactive oxygen species.

the stress type, intensity, duration, and the plant species/genotype, as demonstrated by recent research in agronomically important, crops such as rice, bread wheat, durum wheat (*Triticum turgidum durum*), and soybean [13,14,19,26,45–47]. Therefore, the identification of shared stress memory mechanisms may provide potential for plant improvement.

Thermopriming: regulating the body temperature of plants

To mitigate the impact of extreme temperature events that are predicted to increase in frequency and intensity, enhancing crop thermotolerance has become a primary objective for many plant breeding programs. Different crop species have evolved a range of complex mechanisms to perceive ambient temperature signals, regulate their growth and reproduction, or store temperature memories to facilitate adaptation and the subsequent formation of desired agronomic traits. Recent research exploring the principles of thermopriming and stress memory have provided valuable new information on previously unrecognised regulators, proteins, metabolites, and pathways that are key components of priming-induced temperature resilience (Table 1) [12,14,48–50]. The discovery and characterisation of these new regulators will facilitate the development of novel genetic and epigenetic markers. Germplasm that can be acclimated or primed to tolerate a wider range of temperature regimes will significantly enhance the geographical distribution of a crop and, therefore, crop productivity.

Heat priming for hotter environments

The global average ambient temperature is predicted to increase by up to 6°C by the end of the 21st century [51]. Each degree increase in the average temperature is estimated to reduce yield

multiple stress prepares the plant for subsequent stress that occurs in later developmental stages, or future generations. Primed plants generally exhibit modified responses (molecular and physiological) compared with their nonprimed counterparts.

Transcriptional memory (TM): long-lasting changes in the expression level of genes after the exposure and recovery period of the initial stress. TM is mainly regulated by a combination of epigenetic mechanisms, such as histone modification, DNA methylation, and chromatin remodelling.

Transcriptomics: quantitative analysis of the set of all RNA transcripts (i.e., transcriptome) produced by an organism. The high-throughput sequencing pipeline is called transcriptome sequencing (transcriptome-seq) or RNA-seq.

Water use efficiency (WUE): amount of plant production (grain yield or any harvested parts) divided by the amount of water used by the plant. WUE reflects the relationship between leaf photosynthetic activities and transpiration activities.

Table 1. Summary of thermopriming approaches in crop and model plant species, and the identification of genetic and epigenetic regulators involved

Stress priming treatment	Stress retest treatment	Type of stress memory	Species name	Priming impact and pathways affected	Regulators/factors for consideration	Refs
7 days of recurrent heat stress (HS) for 2 h, from 21 days after sowing	Recurrent HS	Somatic stress memory (short term)	Arabidopsis (*Arabidopsis thaliana*)	Constitutive photomorphogenesis 5A (CSN5A) controls expression of HS memory genes (*APX2* and *HSP22*) and is required to reset gene expression to the baseline. CSN5A is also required for the deposition of H3K4me3 after recurrent HS	CSN5A, a subunit of the constitutive photomorphogenesis 9 (COP9) signalosome	[94]
1 h of heat acclimation, followed by 90 min recovery, followed by 45 min heat shock	After 2 d of recovery, HS tester (lethal to nonacclimated plants) was applied for 90 min	Somatic stress memory (short term)	Arabidopsis	Chromatin protein BRUSHY1 (BRU1) mutant plants were defective in HS memory (reduced growth and lower survival rate). BRU1 is specifically required for HS memory and to maintain transcriptional induction of heat stress-associated 32-kD protein (HSA32)	BRU1	[10]
Four cycles of repeated HS priming, each cycle includes a short HS treatment for 4 h and a recovery period for 44 h	Short HS treatment for 4 h after final recovery period	Somatic stress memory (short term)	Tall fescue (*Festuca arundinacea*)	Genes such as *Fa-heat shock protein 17.8 Class II* (*FaHSP17.8-CII*) obtained transcriptional memory (TM), which lasted for more than 4 days. TM of FaHSP17.8-CII is regulated by H3K4me3 modification. FaHSP17.8-CII helped to reduce ROS accumulation, prevented degeneration of chloroplast structure and regulated ROS–PSII signalling-related genes	FaHSP17.8-CII and H3K4me3	[50]
1 h of HS acclimation, with or without 2 d recovery	7 d of long HS (LHS)	Somatic stress memory (short term)	Azalea (*Rhododendron hainanense*)	HS acclimation with or without recovery both improved thermotolerance of primed plants under LHS, as shown by less phenotypic damage, improved photosynthetic rate, and membrane stability. Recovery further enhanced positive effects. HS-protective proteins maintained high protein levels rather than gene transcript levels after recovery	Chloroplast-localised heat shock proteins (HSPs), Rubisco activase 1 (RCA1), beta-subunit of chaperonin-60 (CPN60β), and plastid transcriptionally active chromosome 5 (pTAC5)	[48]
High temperature, high light intensity, and their combination applied to 27-day-old plants	High temperature applied after 2 days of recovery	Somatic stress memory (short term)	Tomato (*Solanum lycopersicum*)	HS priming improved stress avoidance via increased evaporation and decreased leaf temperature; high light intensity potentially aggravated damage of reoccurring HS	Chlorophyll pigments and protective compounds, such as carotenoids	[95]
35°C HS treatment for 5.5 days (starting with 5-day-old plants)	No retest, stressed plants were returned to 22°C to recover for 24 h	Somatic stress memory (short term)	Arabidopsis	H3K4 methyl transferases SDG25 and ATX1 were required for maintaining stress-responsive gene expression during stress	SDG25 and ATX1	[56]

Table 1. (continued)

Stress priming treatment	Stress retest treatment	Type of stress memory	Species name	Priming impact and pathways affected	Regulators/factors for consideration	Refs
				recovery. Mutations of SDG25 and ATX1 decreased histone H3K4me3 levels, increased DNA cytosine methylation, and inhibited HS-responsive gene expression during stress recovery		
5-day heat stress priming applied at stem-elongation, booting, and anthesis	5-day severe HS during grain fill (15 days after anthesis)	Somatic stress memory (long term)	Bread wheat (*Triticum aestivum)*	HS priming led to: reduced loss in grain yield and biomass; higher sucrose contents and sucrose-phosphate activity; increased photosynthetic capacity; enhanced activities of antioxidant enzymes; and reduced reactive oxygen species (ROS). Positive influence was most pronounced for HS priming at booting stage	Sucrose-phosphate synthase (SPS), superoxide dismutase (SOD), peroxidase (POD)	[19]
42°C for 3 h per day for 7 d, starting 2 weeks post germination	No retest, progeny not treated with stress	Intergenerational stress memory	Field mustard (*Brassica rapa*)	Progeny of HS parents exhibited significant changes in expression of tRNA fragments (tRFs) and small nucleolar RNA fragments (snoRFs), but not small nuclear RNA fragments (snRFs) or ribosomal RNA fragments (rRFs)	tRFs targeting genes involved in brassinosteroid metabolism, and isoacceptor tRNA that regulate cellular component endoplasmic reticulum	[96]
5 days of HS, starting at 1 week post germination in F_0 plants	Same HS applied to F_1 plants	Intergenerational stress memory	Arabidopsis	Progeny of primed parents had larger leaves and delayed bolting. HS priming increased transposon expression in progeny, while progeny HS decreased global genome methylation. Memory gene expression was positively correlated with acH3K9 and negatively correlated with repressive marks (me2H3K9)	Heat stress transcription factor A2 (HSFA2), Mut-S homolog (MSH6), repressor of silencing 1 (ROS1), and Su(var)3-9 homologs (SUVH)	[97]
Cyclic HS applied from flowering to harvest in parents	Cyclic HS applied from flowering to harvest in progeny	Intergenerational stress memory	Durum wheat (*Triticum turgidum durum*)	Parental HS priming had positive impact on leaf physiological traits, grain yield, and grain quality traits in less stress-tolerant genotype. Significant number of miRNAs and their target genes showed differential expression subject to the priming factor	Key miRNA–gene modules responsive to HS priming, such as miR528-F-box protein, miR398-Cu/Zn SOD, and miR5054-catalase	[14]
2 weeks of HS, starting at 10 days post germination	Second and third generation were grown unstressed	Transgenerational stress memory	Arabidopsis	HS priming induced post-transcriptional gene silencing (PTGS), and maintained for three generations with fading impact. Memory-driven RELATIVE OF EARLY	HSFA2, REF6, SUPPRESSOR OF GENE SILENCING 3 (SGS3)-INTERACTING PROTEIN 1 (SGIP1), HTT5	[23]

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Table 1. (continued)

Stress priming treatment	Stress retest treatment	Type of stress memory	Species name	Priming impact and pathways affected	Regulators/factors for consideration	Refs
				FLOWERING 6 (REF6)-HSFA2 regulatory loop and suppression of tasiRNAs induced HEAT-INDUCED TAS1 TARGET 5 (HTT5), which promoted early flowering		

by ~6.0% for wheat, ~3.2% for rice, ~7.4% for maize, and ~3.1% for soybean [52]. When the air temperature exceeds the safe threshold, heat stress (HS) induces irreversible cellular damage that negatively affects photosynthetic capacity, nutrient transport, **water use efficiency** (**WUE**), floral viability, embryo development, yield production, and grain quality [53–55]. HS-induced epigenetic changes are central to establishing HS memory that is later retrieved to modify stress perception, signalling processes, and gene expression to improve plant fitness [23,56,57]. Other important mechanisms of HS memory include reactive oxygen species (ROS) scavenging, membrane stabilisation, metabolite production, and coordination of signalling cascades [8,9].

Recently, the heritable regulatory feedback loop of *REF6-HSFA2*, which functions in the transgenerational adaptation of HS, was characterised in arabidopsis (*Arabidopsis thaliana*) [23]. *RELATIVE OF EARLY FLOWERING 6* (*REF6*) is an H3K27me3 demethylase directly activated by HS-induced HEAT SHOCK TRANSCRIPTION FACTOR A2 (*HSFA2*). *REF6* in turn derepresses and promotes the expression of *HSFA2*, establishing a positive feedback loop that is capable of transmitting epigenetic memory by maintaining the active state of HSFA2 *trans*-generationally. *HSFA2* activates the expression of an E3 ligase, SUPPRESSOR OF GENE SILENCING 3 (SGS3)-INTERACTING PROTEIN 1 (SGIP1), which mediates SGS3 degradation to repress biosynthesis of *trans*-acting siRNA (tasiRNA) and results in the release of the tasiRNA target *HEAT-INDUCED TAS1 TARGET 5* (*HTT5*). Transgenerational degradation of SGS3 and the upregulation of *HTT5* to promote early flowering in thermomemory phenotypes was confirmed in the progeny. Subsequent research has also demonstrated that *FORGETTER3/ HEATSHOCKTRANSCRIPTION FACTOR 3* (*FGT3/HSFA3*) directly induces transcription of memory-related genes during the recovery phase after HS. HSFA3 also binds HSFA2 to form heterotrimeric complexes that enable maximal HS memory via the sustained recruitment of H3K27me3 demethylase [58]. Heat memory also appears to be maintained by H3K27me demethylases, with REF6 and the Jumonji proteins (especially JMJ30) specifically controlling the level of histone modification of *HEAT SHOCK PROTEIN 22* (*HSP22*) and *HSP17*.6, to alter their re-induction during fluctuating HS [59].

The chromatin regulatory protein BRUSHY1 (BRU1) [10] not only ensures the faithful inheritance of chromatin structure and organisation after HS exposure, but is also essential to sustain the transcriptional induction of HS-responsive genes *HEAT STRESS-ASSOCIATED 32* (*HSA32*), *ASCORBATE PEROXIDASE 2* (*APX2*), *HSP22.0*, and *HSP21* [11,60] after the removal of HS. Together with previous evidence that BRU1 functions in transcriptional gene silencing, chromatin reconstitution, and DNA damage repair [61,62], transcriptome analysis has demonstrated that BRU1 was mainly required for the memory phase to promote the expression of BRU1-dependent genes, rather than for the acute response phase. Sustained gene expression during HS memory may also be regulated by *FORGETTER1* (*FTG1*) [57], which interacts with the ATP-dependent chromatin remodeller families SWI/SNF and ISWI to help maintain low relative nucleosome occupancy at memory genes (*HSA32*, *HSP22.0*, *HSP18.2*, and *HSP101*) after HS acclimation.

Regulation of ROS signalling, associated antioxidative capacity, and enhanced membrane stability are also important for maintenance of HS memory. In heat-sensitive tomato (*Solanum lycopersicum*) [9], the respiratory burst oxidase homologue-dependent H_2O_2 (*RBOH*-H_2O_2) responded to HS acclimation, and acted to promote the expression of HS-responsive genes and antioxidant enzyme activities. By contrast, chloroplast-generated H_2O_2 enhanced the expression of programmed cell death (PCD) genes [63]. However, both sources of H_2O_2 were beneficial to the maintenance of HS memory, contributing to a lower and stable H_2O_2 level under reoccurring HS after the initial HS recovery period. The regulation of membrane lipid dynamics and lipid signalling by *FORGETTER2* (*FGT2*), a type 2C protein phosphatase (PP2C), also appears important in HS memory [8]. FGT2 interacts with PHOSPHOLIPASE D (PLDα2) to mediate production of the signalling molecule phosphatidic acid (PA). Both *FGT2* and *PLDα2* are required for the maintenance of HS memory, because *FGT2* and *PLDα2* mutants were memory-defective when exposed to reoccurring HS that was lethal.

sRNAs are also significant in establishing HS memory through epigenetic inheritance. In *Brassica rapa*, the contribution of sRNAs to heat shock-induced intergenerational inheritance was elucidated by sequencing the transcriptome and sRNAome in the somatic and reproductive tissues of stressed parents and their untreated progeny [12]. After HS priming, substantial transcriptional changes were observed in the embryo and endosperm tissues, with significant alterations in the sRNAome found in tissues that were not directly exposed to stress (pollen and endosperm of the parents, and progeny leaf tissue). tRNA-derived sRNA fragments (tRFs) that were intergenerationally transmitted and induced by HS priming were also discovered for the first time. The study suggested that miR168-AGO1 is an epigenetic messenger module that mediates meiotic HS memory inheritance through a negative feedback loop. In another study in durum wheat [14], parental HS treatment post anthesis had a positive impact on the stressed offspring for traits such as chlorophyll content, grain weight, grain number, and total starch content. Integrated analysis of the sRNAome, mRNA transcriptome, and mRNA degradome showed that miRNA–mRNA modules associated with ROS scavenging, photosynthesis, and hormone signal transduction had important roles in intergenerational HS adaptation. Key modules included the miR528-F-box protein, miR398-Cu/Zn SUPEROXIDE DISMUTASE (SOD) and miR5054-CATALASE (CAT), all of which are candidates for developing epigenetic markers to detect HS memory.

Cold acclimation and frost hardening

Cold stress (CS) is divided into two categories: chilling stress and freezing/frost stress [64,65]. Tropical and subtropical crops, such as rice, maize, soybean, tomato, potato (*Solanum tuberosum*), and cotton (*Gossypium hirsutum*), are sensitive to chilling stress due to the lack of cold acclimation during their evolution [66]. Crops grown in temperate climates, such as wheat, barley (*Hordeum vulgare*), and oats (*Avena sativa*), do experience low temperatures during winter and early spring and, therefore, are generally tolerant to chilling stress but vary in their frost sensitivity. CS tolerance acquisition involves a range of mechanisms, including ROS scavenging, lipid stabilisation, and the accumulation of osmolytes with cryoprotectant properties [64,66]. Although reports in crop plants and model species on CS memory are relatively low in number compared with other major stresses, epigenetic mechanisms that regulate cold-induced transcriptional events, the accumulation of cryoprotectants, plant hormones, and signalling metabolites, such as salicylic acid (SA) and ROS, appear important.

Transcriptional memory (TM) has recently been linked to CS training and is mainly induced by epigenetic regulators and chromatin marks left from the initial stress exposure. For example, combined analyses of RNA-sequencing (RNA-seq), global DNA methylation assays, chromatin immunoprecipitation, and qPCR demonstrated that, in *Brachypodium distachyon*, chromatin-associated TM changed the expression of both stress and developmental-associated genes [e.g., *C-REPEAT BINDING FACTOR1* (*CBF1*), *COLD-REGULATED410* (*COR410*), *ICE RECRYSTALLISATION INHIBITOR* (*IRI*) and *VERNALISATION10* (*VRN1*)] after repeated CS exposure, thereby providing plasticity to CS responses [67].

Agronomic and physiological evaluation as well as comparative omics analyses of the transcriptome, phenome, and methylome in Tartary buckwheat (*Fagopyrum tataricum*) after different CS priming approaches (repeated cold priming and acute cold shock) also showed that DNA methylation had a major role in CS training [68]. The CS memory group exhibited better performance, increased free proline content, and had a higher survival rate. Single base-resolution DNA methylome profiling discovered the global loss of DNA methylation, with some locally hypermethylated sites after cold priming; while transcriptome sequencing correlated the increase of hundreds of CS-induced genes, such as COPPER AMINE OXIDASE (*CuAO*), the largest subunit of RNA POLYMERASE II (*RPB1*), and DEHYDROGENASE E1 COMPONENT (*DHE1*), with the differential DNA methylation patterns in the CS memory group. Memory-induced DNA methylation affected pathways included lysine degradation, isoquinoline alkaloid biosynthesis, and pyrimidine metabolism, suggesting that CS memory affects metabolites that promote freezing tolerance.

Cryoprotectant production is also important for CS memory. Cold priming seeds from chickpea (*Cicer arietinum*), an important but highly chilling-sensitive legume, at 5°C for 30 days induced long-term memory (within the same generation) to lessen damage and enhance cold tolerance at reproduction [17]. CS memory elicited in the seeds led to improved leaf hydration status and photosynthetic ability as well as the production of osmolytes/cryoprotectants in the leaves, ultimately supporting reproductive function.

CS priming may also have positive effects on cellular redox mechanisms, mainly ROS signalling and scavenging. Melatonin application and CS priming in bread wheat enhanced CS memory and the priming effects, inducing a higher tolerance level to subsequent CS events [69]. The most significant traits improved by priming included photosynthetic rate, stomatal conductance, and antioxidant enzyme [SOD, CAT, APX, and peroxidase (POD)] activities. Cold priming and SA priming have also been shown to confer stress memory in wheat by improving antioxidant capacity protecting the photosynthetic apparatus to improve efficiency, while reducing malonaldehyde content and superoxide radical production [18]. This was mainly attributed to higher expression of CS-responsive genes [*WRKY-Type Transcription Factor 19* (*WRKY19*), *Dehydration-Responsive Element Binding Protein 2* (*DREB2*), *C-Repeat Binding Factor 3* (*CBF3*), *Cold-Regulated Protein 10* and *14* (*COR410* and *COR14*), *Heat Shock Transcription Factor 3* (*HSF3*), *HSP70*, and *Alternative Oxidase 1a* (*AOX1a*)]. The beneficial effects of cold priming on improving the antioxidant systems in chloroplasts and mitochondria, through enhanced protection of photosynthetic electron transport against subsequent CS, has also been demonstrated in winter wheat [70].

Securing the water balance: adjusting the tap for smarter crops

With climate change impacting the variability in precipitation, water availability for crops is becoming less predictable. While drought is undoubtedly a major detrimental yield-reducing factor, flooding stress is another constraint for cropping systems. Drought and floods impact plant water homeostasis, gas exchange, water and nutrient uptake, and WUE. Water-related stress acclimation is often linked to adaptive changes in antioxidative capacity, biochemical modifications, and phytohormone-mediated pathways, with evidence now building for drought and flooding-induced stress memory in plants (Table 2).

Surviving the dry season: priming for optimal WUE

Drought stress (DS) results in stomatal closure, which inhibits photosynthesis and carbon assimilation, causing impaired plant growth, impeded reproductive development, and reduced yield [71]. DS tolerance is strongly associated with improved WUE, which is an important breeding objective to fulfil to develop climate-resilient crops [72,73]. The phenomena of DS memory, and the various biological processes involved in its acquisition, are now being reported widely [13,24,74–77]. In most cases, the initial drought occurrence (DS priming) generates transcriptional memory eliciting epigenetically mediated changes in DS-responsive gene expression that benefit plant survival in response to repeated DS [78,79].

Noncoding RNAs (ncRNAs), including long ncRNAs (lncRNAs) and sRNAs, have important roles in the formation and maintenance of DS memory, particularly those that mediate signal transduction pathways, hormone biosynthesis, and transcription factor (TF) families. A recent study in durum wheat reported that the beneficial effects of parental water deficit (WD) stress priming was genotype dependent, having a greater impact in the variety that had lower tolerance to WD stress [13]. Analysis of sRNA-omics, mRNA transcriptomics, and mRNA degradomics revealed that enhanced expression of miRNA-mediated genes in hormone signal transduction, ROS scavenging, and carbon fixation likely contributed to better adaptation to water-deficit stress in the progeny (Table 2) [13].

The roles of ncRNAs in DS memory, together with other DS-responsive regulators, has also been demonstrated in rice. Seedlings that underwent three cycles of DS training displayed strong memory under appropriate levels of WD, with significantly less reduction in water content and a cyclic changing pattern of jasmonic acid (JA) and ABA levels reported [24]. Whole-transcriptome strand-specific RNA seq (ssRNA-seq) identified clusters of DS memory-related genes and lncRNAs. The memory genes were significantly enriched in carbon fixation, carotenoid biosynthesis, arginine/proline metabolism, and hormone signal transduction pathways. Most rice memory genes, particularly those involved in secondary metabolite production and hormone signalling, were directly regulated by DNA methylation. However, DS-memory-related lncRNAs appeared to regulate the expression of genes involved in ABA and JA biosynthesis.

Similarly, multiple DS regulatory mechanisms have been shown to function simultaneously in maize, thus enabling a coordinated memory strategy for faster adaptation and increased chance of reproductive success [76]. Integrating transcriptome and chromatin omics, Forestan *et al.* studied how maize plants responded, adapted, recovered, and memorised mild WD stress before the flowering transition stage. Three major categories of DS memory genes were identified, with Type I being TM genes persistently maintained at high levels of expression after the recovery period of the initial stress, mainly due to chromatin marks that kept transcriptional potential for longer periods. Type II were epigenetic memory genes the transcriptional performance of which was affected by stress-responsive histone modifications induced by the initial stimulus. Finally, Type III were delayed memory genes enriched for TF families that regulate flowering transition and inflorescence patterning. Considering the complex nature of the stress memory mechanisms, different classes of memory gene could be used as candidates for memory inheritance screening in plant breeding programs.

The rising water table: flooding memory and better recovery

Flooding stress is generally classified into two major categories depending on the depth of the water relative to the crops: waterlogging (WL; excessive water surrounding mainly the root

Table 2. Summary of the recent identification of molecular, physiological, and proteomic regulators for drought and waterlogging priming-induced tolerance in crops and model plant species

Stress priming treatment	Stress retest treatment	Type of stress memory	Species name	Priming impact and pathways affected	Regulators/factors for consideration	Refs
6 h of DS treatment at three-leaf stage, followed by 6 days of recovery	DS for 24 h after recovery period	Somatic stress memory (short term)	Bread wheat (*Triticum aestivum)*	Priming promoted root growth and biomass accumulation, and increased levels of protective proline and glycine betaine. Root zone-specific priming effects observed for DS-responsive gene expression	Betaine aldehyde dehydrogenase (BADH), YUC, ABA aldehyde oxidase (AAO), cytokinin oxidases/dehydrogenases (CKX), A-type arabidopsis response regulator (A-ARR), 12-oxo phytodienoic acid (OPDA) reductase (OPR), jasmonic acid ZIM-domain proteins (JAZ)	[98]
DS applied for 4 days, starting at 7 days after germination	After 1 d of recovery (rewatering), DS applied for another 4 days	Somatic stress memory (short term)	Soybean (*Glycine max*)	Over 1000 genes displayed significantly altered expression in primed plants compared with initial stress	DS-induced memory genes included transcription factors (e.g., MYB), protein phosphatase 2Cs, late embryogenesis abundant (LEA) protein genes, and PSII light-harvesting complex genes	[99]
DS at four- and six-leaf stages, with or without chemical applications (ABA inhibitor, H_2O_2 scavenger, NADPH oxidase inhibitor)	DS at grain-fill (7 days after flowering), with or without chemical applications (ABA inhibitor, H_2O_2 scavenger, NADPH oxidase inhibitor)	Somatic stress memory (long term)	Bread wheat	ABA-induced H_2O_2 production when primed. NADPH oxidase-mediated H_2O_2 production regulated function of ABA in osmotic adjustment. Both ABA and H_2O_2 were necessary for priming-induced DS tolerance at grain fill	9-*cis*-epoxycarotenoid dioxygenase (NCED), respiratory burst oxidase homologs (RBOHs), NADPH oxidase	[100]
DS at four- and seven-leaf stages	Post-anthesis DS from 10 days after flowering	Somatic stress memory (long term)	Bread wheat	Reduced yield loss, less reduction in leaf photosynthetic rate and stomatal conductance, lower osmotic potential associated with higher proline and sucrose content	*RuBisCo activase* (*RcaB*), *Δ1-pyrroline-5-carboxylate synthetase* (*P5CS*), *sucrose-phosphate synthase* (*SPS*)	[101]
DS for 12 days, starting at 20 days post germination	Subsequent stress at various intensity for 52 days, after 6 days of recovery post-initial DS priming	Somatic stress memory (long term)	Cowpea (*Vigna unguiculata*)	Priming increased WUE, grain yield, water productivity of biomass and of yield. Primed plants had lower ABA levels and higher IAA levels in leaves than nonprimed plants, due to better water status	Not identified	[102]
2 years of DS or WL stress	3 weeks of recovery in third year, followed by DS applied for 2 weeks	Somatic stress memory (long term)	Meadow foxtail (*Alopecurus pratensis*)	DS-primed plants had less tissue senescence, and increased RuBisCo content, antioxidative enzymes (SOD and POD) and chlorophyll content under rechallenged DS. WL-primed plants not stressed by WL treatment, and showed no significant difference to nonprimed plants	Not identified	[103]

Table 2. (continued)

Stress priming treatment	Stress retest treatment	Type of stress memory	Species name	Priming impact and pathways affected	Regulators/factors for consideration	Refs
DS applied by withholding watering from beginning of flowering until onset of full flowering	Repeat of DS treatment in next generation	Intergenerational stress memory	Oilseed rape (*Brassica napus* L.)	DS priming caused decrease in seed quality, but stressed seeds had higher seedling vigour. Seedling metabolite patterns under DS also affected by parental DS priming	Not identified	[104]
WD stress applied from emergence to 50 days after planting for five genotypes	No retest	Intergenerational stress memory	Peanut (*Arachis hypogaea* L.)	Intergenerational WD priming affected seed quality, seed size, seedling vigour and root architecture. Significant interaction with genotype factor identified	Genotype variability can affect intergenerational effect of parent stress history, presenting opposing adaptation strategies in offspring	[47]
WD applied from booting to harvest in parents	WD applied from booting to harvest in progeny	Intergenerational stress memory	Durum wheat (*Triticum turgidum durum*)	Parental WS priming had positive impact on leaf physiological traits, grain yield and grain quality traits in less stress-tolerant genotype. Significant number of miRNAs and their target genes showed differential expression subject to priming factor	Key miRNA–gene modules responsive to priming, such as miR394-glutathione reductase, miR167b-cytidylate kinase, and miR827-EamA-like transporter, reported	[13]
DS applied from tilling to grain fill (G0), seeds harvested from G0 is G1	Repeated DS for another 10 generations to obtain G11 seeds. Final recovery generation by watering G10 plants to get G10R1 in 11th generation	Transgenerational stress memory	Rice (*Oryza sativa*)	DS tolerance improved (less cell damage and increased antioxidant enzymes) in advanced generations. Multigenerational priming induced significant epimutations, of which their altered DNA methylation status was stably maintained in advanced generations. Epimutation-related genes directly function in DS response pathways	Genes related to transgenerational epimutations (e.g., lactate/malate dehydrogenase gene, DNA mismatch repair protein gene)	[105]
DS applied from tilling to grain fill for G0	DS applied for another five generations until generation six (G6)	Transgenerational stress memory	Rice	DS had significant cumulative effects on DNA methylation pattern. Stress training had significant effect on DS-sensitive variety, as evidenced by higher percentage of total differentially methylated loci (DML) and stably transmitted DML	Genes with remethylated and demethylated patterns, such as *cyclin-T1-2-like* and *Empty Pericarp5* (*EMP5*), reported	[106]
7 days of DS applied (starting at 10 days after anthesis) for one, two, or three generations	5 days of DS applied (starting at 10 days after anthesis) in fourth generation	Transgenerational stress memory	Bread wheat	DS priming improved photosynthetic rate, leaf water status, antioxidant enzyme levels, and grain yield regardless of the priming generation.	Priming induced proline and glycine betaine, regulated by key enzymes, such as Δ1-pyrroline-5-carboxylate synthetase (P5CS), proline dehydrogenase (PDH), and BADH; may have critical	[107]

(continued on next page)

section of plants), and submergence (excessive water causing partial or complete submergence of plants) [80,81]. The direct impact of water-immersed soil to plants is a deficiency of oxygen and carbon dioxide resulting in hypoxia and oxidative stress, which reduces photosynthesis, impedes growth, accelerates senescence, and ultimately reduces yield [80,81]. Adaptation mechanisms to flooding stress include changes in plant morphology and architecture (e.g., the formation of adventitious roots), alternative energy production pathways (e.g., pyruvate fermentation), metabolic modifications (e.g., enhanced anaerobic respiration), and adjustments to phytohormone biosynthesis and signalling [82,83].

In cucumber (*Cucumis sativus*), long-term WL memory included enhanced glycolysis, adventitious root development, ethylene biosynthesis, and amino acid metabolism [40]. Comparative transcriptomics uncovered a significant number of differentially expressed genes that were activated in the long-term WL recovery after WL priming, in both WL-tolerant and WL-sensitive germplasm. Differential responses to repeated WL treatment were also observed. In particular, differential expression of the ethylene biosynthesis-associated gene, *AMINOCYCLOPROPANE-1-CARBOXYLATE* (*ACC*) *OXIDASE* was confirmed via qRT-PCR in primed plants at the recovery stage, supporting a previous suggestion that it has a beneficial role in regulating plant hypoxia adaptation [84].

In bread wheat, physiological and proteomic analyses revealed that pre-anthesis WL priming improved the response of primed plants to post-anthesis WL stress [85], more than likely due to enhanced ROS-scavenging capacity in the ascorbate-glutathione cycle (AsA-GSH) and significantly higher expression of ethylene biosynthesis proteins (such as *S*-adenosylmethionine synthase). Increased ethylene biosynthesis (from priming or from an exogenous source, such as ethephon) alleviated the negative effects of WL on leaf photosynthetic activity, which was achieved by higher stomatal conductance due to the inhibition effects of ethylene on H_2O_2 and nitric oxide (NO) that cause stomatal closure. Being able to maintain photosynthesis is critical for cereal crops such as wheat, because the accumulation and redistribution of dry matter during the reproductive stage contribute to overall grain yield. An additional study in bread wheat [86] showed that repeated WL priming exposure during vegetative growth effectively enhanced the tolerance of primed plants to reproductive WL stress. Priming improved the efficiency of photosynthetic light and carbon use, antioxidant enzyme activities, and dry matter redistribution to the grain mass. However, to date, the epigenetic regulatory pathways of WL memory and the likely involvement of transcriptional memory in the WL recovery period remain unexplored.

Cross-stress tolerance: rewiring to translate knowledge of different stresses

Plants are exposed to multiple stresses differing in nature, duration, and intensity throughout their life cycle. Interactions between abiotic (drought, heat, salinity, etc.) and biotic (pathogen, herbivore attack, etc.) stresses can be dramatically different when considering the impact on plant growth and reproductive performance. The converging nature of many stress response pathways [e.g., auxin signalling, antioxidant metabolism, or mitogen-activated protein kinase (MAPK) cascades] also means that the distribution of limited resources and beneficial metabolites could be more efficient under the crosstalk of multiple stresses [87–89]. Here, cross-stress tolerance refers to the phenomenon where pre-exposure of a primary stress in a plant improves the efficiency and performance of such individuals (or even their offspring) under a secondary stress. Eliciting adaptive changes in crops is typically referred to as cross- or *trans*-priming (compared with *cis*-priming, in which the initial and subsequent stress factors are the same). The success of cross-stress priming is underpinned by the hierarchical interaction of synergistic stress signalling pathways being shared between stresses of a different nature (Figure 2). In recent times, considerable progress has been made in this dynamic field, particularly in crop species in which new solutions for enhancing cross-stress or multistress resilience are being explored.

ROS homeostasis is one of the key factors contributing to cross-stress tolerance. In wheat seedlings, a HS treatment (3 h at 45°C) induced cross adaptation to aluminium (Al) stress by enhancing the AsA-GSH cycle in the roots of both Al-tolerant and Al-sensitive wheat genotypes [90]. The changes were correlated with the upregulation of key enzymes, including ascorbate peroxidase, monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). In chickpea, priming seedlings with mild DS induced tolerance to heat during later stages of development [91]. Electrolyte leakage and lipid peroxidation were reduced in cross-primed plants under HS to improve membrane integrity, while higher SOD and CAT activity likely enabled greater scavenging of the ROS produced during HS. Moreover, the primed plants had a higher expression of small heat shock protein (sHSP) genes, which maintain cellular homeostasis by protecting proteins from aggregation and incorrect folding under higher temperatures.

sRNA-mediated regulation can also be used to promote cross-stress tolerance. In crops, miRNAs can rapidly respond to almost all environmental and developmental signals, having a central, regulatory role in the cross-talk of antagonistic and synergistic response pathways to multiple stresses [5]. Parental water-deficit and heat (WH) stress treatments in durum wheat can improve the performance of progeny seedlings under nitrogen (N) starvation [26]. As a yield limiting factor, N deficiency significantly affects plant growth and production through its impact on nutrient uptake, enzyme activity, water balance, and metabolic processes, such as photosynthesis and respiration. Parental WH stress helped to reduce the negative impact of N starvation on seedling performance in the WH-tolerant variety, but exacerbated the influence of N starvation in the WH-sensitive variety. sRNA sequencing discovered the miRNA candidates contributing to the positive influence of parental cross-priming, including miRNA families that are ‘hub regulators’ controlling cellular homeostasis, hormone signalling, and the mediation of TF families. Key miRNA-mRNA modules identified included miR164-NITRATE TRANSPORTER 2.1 (NRT2.1), which functions in the high-affinity transport system that enhances the efficiency of nitrogen uptake; and miR169-leucine-rich repeat receptor kinase (LRR-RK), which mediates shoot-to-shoot N-demand signalling under N stress.

Plant hormones, such as ABA, also have significant roles in establishing cross-stress tolerance. For example, ABA was shown to promote HS tolerance through drought priming in the perennial grass species tall fescue (*Festuca arundinacea*) and arabidopsis [92]. Primed plants had improved relative leaf water content, photochemical efficiency, and membrane stability as well as increased ABA levels and stress-responsive gene expression [including *calcium-Dependent Protein Kinase 3* (*CDPK3*), *Mitogen-Activated Protein Kinase 3* (*MPK3*), *Dehydration-Responsive Element Binding A2* (*DREB2A*), *ABA-Responsive Element 3* (*AREB3*), *MYB Proto-Oncogene Transcription Factor 2* (*MYB2*), *MYC Proto-Oncogene 4* (*MYC4*), *BHLH* transcription factor, *HSFA2*, *HSP18*, and *HSP70*]. Interestingly, a foliar spray of ABA also resulted in similar positive priming effects, while the application of fluridone (an ABA inhibitor) diminished the priming effects of ABA and DS, thus suggesting the essential role of ABA in establishing and maintaining cross-stress tolerance.

The application of priming agents [such as ABA, JA, SA, beta aminobutyric acid (BABA), and melatonin] and other techniques (e.g., plasma treatment) to equip plants with faster and more efficient responses against future stresses, in the absence of a primary stress, can also be considered as a *trans*-priming approach. Recently, in rice [93], cold plasma treatment, SA application, and a combined plasma/SA treatment applied on seeds enhanced seedling tolerance to salinity stress. Photosynthetic parameters, including chlorophyll pigment levels and photosynthetic gas exchange, were significantly improved by independent and combined priming

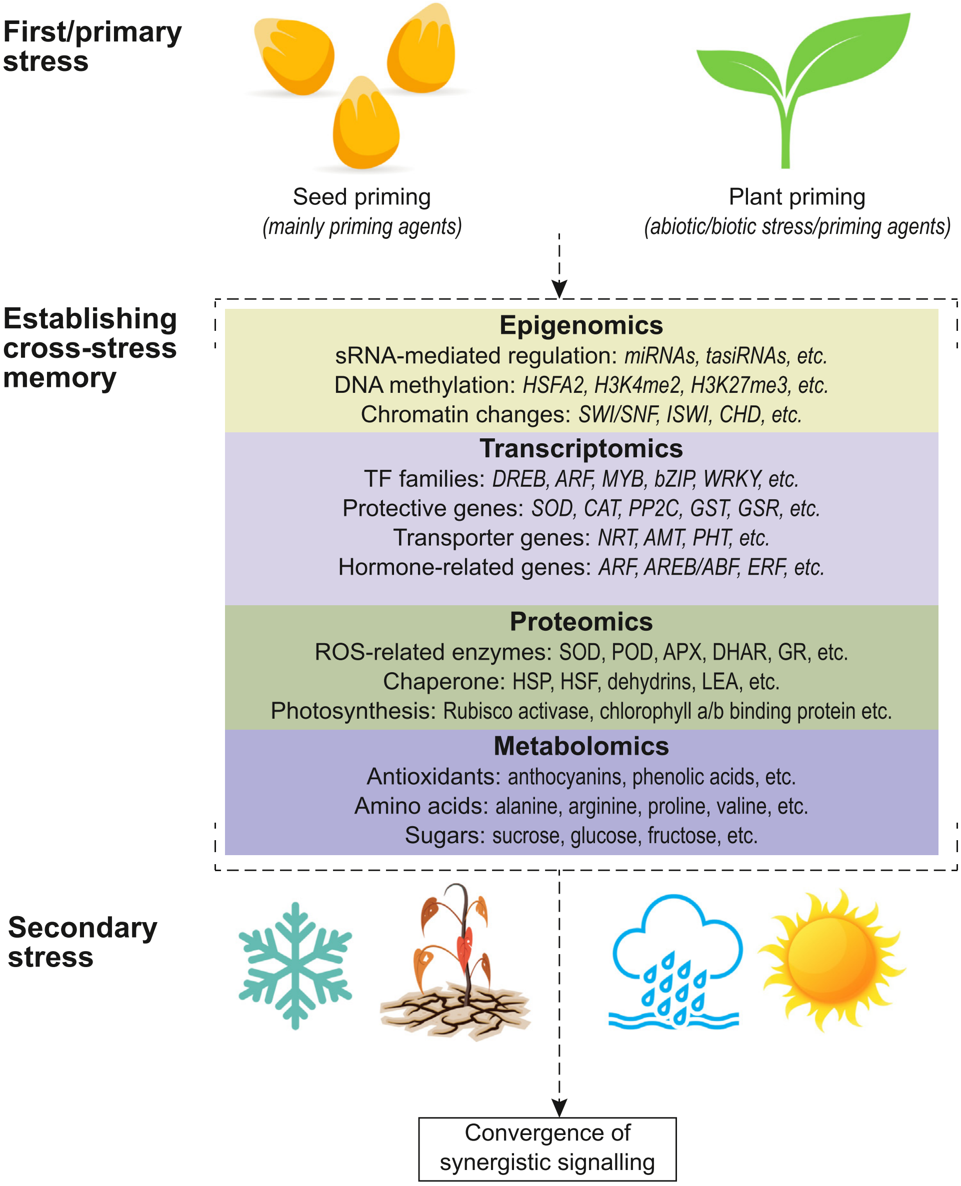

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Figure 2. Cross-stress priming and signalling networks. A schematic of the interactions between synergistic stress responses and signalling pathways in cross-stress memory. Secondary stresses shown at the bottom of the figure (L-R) may include (but not be limited to) frost/cold, drought, flooding/waterlogging, and heat. Artwork images from Adobe Stock (stock.adobe.com). Abbreviations: APX, ASCORBATE PEROXIDASE 2; AREB/ABF, ABA-responsive element 3; CAT, catalase; CHD, chromodomain helicase DNA-binding; DHAR, dehydroascorbate reductase; DREB, dehydration-responsive element binding protein 2; GR, glutathione reductase; HSF, heat shock transcription factor; ISWI, imitation SWITCH; LEA, late embryogenesis abundant; NRT, nitrate transporter; POD, peroxidase; PP2C, protein phosphatase 2C; SOD, superoxide dismutase; SWI/SNF, switch/sucrose nonfermentable; tasiRNA, trans-acting small interfering RNA; WRKY, WRKY-type transcription factor.

methods. Antioxidant enzyme activities (SOD, CAT, APX, and POD) were also significantly enhanced, thereby decreasing the oxidative damage to membranes. Therefore, the external application of priming agents (on seeds in particular) could provide an effective alternative to elicit cross-stress tolerance when field-scale abiotic stress priming for improved crop management is not practical.

Concluding remarks: where to now?

The biodiversity in crop species alone, grown across different regions of the world, provides a range of variation in the physiological, biochemical, and molecular mechanisms that counteract stress. The discovery that plants have 'cognitive abilities' to form and retain memories provides exciting new opportunities for scientists and plant breeders to diversify short-term and/or long-term stress memory capabilities to enable the intelligent design of multiple trait combinations that offer adaptive advantages. However, the application value of transforming lab-based or control environment-based knowledge to field-based breeding practices needs to be carefully assessed. Given that phenotypic or physiological stress plasticity transferred to the offspring without the modification of gene sequences (i.e., epigenetic-based transgenerational stress memory) can trigger the memory to be reset, in-field validation is crucial [37]. The recovery period of an initial stress, or the repetitive recovery periods of cyclic stresses, are critical for establishing and reinforcing the correct stress memory because this is when the majority of information is integrated and shaped. When the consequence of stress memory is negative (often in stress-sensitive germplasm), then it would be more favourable to reset or erase such stress in the future generation(s). Further studies are still required to fully understand the underlying mechanisms of how to precisely elicit and reset stress memory. Importantly, research also needs to include a wider range of crop germplasm with different developmental speeds, stress tolerance levels, breeding strategies, and geographical spread. In addition, determination of the most efficient and effective priming stage(s) and the priming intensity is also critical. For example, HS priming during booting in bread wheat varieties induced the most pronounced beneficial impact on post-anthesis HS adaptation, compared with priming applied at stem elongation and anthesis [19]. Seed priming also shows potential for building transgenerational stress memory [17,93] but will require some consideration to ensure commercial viability. At present, growers and seed producers keep the highest-quality seed to maximise crop germination. Therefore, the trade-off between decreased seed quality due to parental stress and improved seedling vigour and/or stress tolerance in the offspring needs to be carefully managed. A better understanding of the mechanisms associated with the application of priming agents will create additional opportunities for more cost-effective priming mimics and seed production technologies (see Outstanding questions).

Outstanding questions

What epigenetic markers will enable the most efficient development of stress memory by plant breeders?

What stress-priming methods have the greatest positive impact on stress tolerance in different crops? When should they be applied (what developmental stage) and to what extent?

How can stress memory be reset or reactivated reliably when needed?

How will the balance between parental fitness and optimisation of stress tolerance in the offspring be managed for commercial seed production?

Through establishing a reference platform of stress memory genes (e.g., Type III genes with significant roles in reproduction), can we utilise high-throughput screening methods (e.g., single-cell microarrays) to efficiently detect inheritable/heritable imprints in different somatic and meiotic tissues?

What epigenetic pathways regulate WL memory? How is transcriptional memory involved in the WL recovery period?

Through the identification and validation of regulators involved in plant cross-stress tolerance, can we utilise genetic modification approaches to prioritise regulatory pathway(s) over what may conventionally take place, thereby eliminating current trade-offs that occur through plant development?

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Declaration of interests

None declared by authors.

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