

Seed ‘primeomics’: plants memorize their germination under stress

Ashish Kumar Srivastava^{1,2*} , Jisha Suresh Kumar^{1,†} and Penna Suprasanna^{1,#}

¹*Nuclear Agriculture and Biotechnology Division, Bhabha Atomic Research Centre, Mumbai, 400085, India*

²*Homi Bhabha National Institute, Mumbai, 400094, India*

ABSTRACT

Seed priming is a pre-germination treatment administered through various chemical, physical and biological agents, which induce mild stress during the early phases of germination. Priming facilitates synchronized seed germination, better seedling establishment, improved plant growth and enhanced yield, especially in stressful environments. In parallel, the phenomenon of ‘stress memory’ in which exposure to a sub-lethal stress leads to better responses to future or recurring lethal stresses has gained widespread attention in recent years. The versatility and realistic yield gains associated with seed priming and its connection with stress memory make a critical examination useful for the design of robust approaches for maximizing future yield gains. Herein, a literature review identified selenium, salicylic acid, poly-ethylene glycol, CaCl₂ and thiourea as the seed priming agents (SPRs) for which the most studies have been carried out. The average priming duration for SPRs generally ranged from 2 to 48 h, i.e. during phase I/II of germination. The major signalling events for regulating early seed germination, including the *DOG1* (delay of germination 1)–abscisic acid (ABA)–heme regulatory module, ABA–gibberellic acid antagonism and nucleus–organelle communication are detailed. We propose that both seed priming and stress memory invoke a ‘bet-hedging’ strategy in plants, wherein their growth under optimal conditions is compromised in exchange for better growth under stressful conditions. The molecular basis of stress memory is explained at the level of chromatin reorganization, alternative transcript splicing, metabolite accumulation and autophagy. This provides a useful framework to study similar mechanisms operating during seed priming. In addition, we highlight the potential for merging findings on seed priming with those of stress memory, with the dual benefit of advancing fundamental research and boosting crop productivity. Finally, a roadmap for future work, entailing identification of SPR-responsive varieties and the development of dual/multiple-benefit SPRs, is proposed for enhancing SPR-mediated agricultural productivity worldwide.

Key words: abscisic acid, chromatin, gibberellic acid, histones, retrograde signalling, seed germination, somatic stress-induced memory, transcriptional regulation

CONTENTS

I. Introduction	2
II. The use of sprs in crops	3
(1) Selenium	5
(2) Salicylic acid	5
(3) Polyethylene glycol	5
(4) CaCl ₂	6
(5) Thiourea	6
III. Molecular basis of seed priming in plants	6
IV. Roles of molecular signalling in the control of seed dormancy and germination	7
(1) DOG1–ABA–heme regulatory module	9
(2) ABA–GA antagonism	9

* Address for correspondence (Tel: 0091-22-25593870; E-mail: ashish@barc.gov.in; ashishbarc@gmail.com).

† Present address: Ludwig-Maximilians-University of Munich Faculty of Biology, Biocenter 82152 Planegg-Martinsried, Germany

Superannuated on 30-June-2020

(3) Nucleus–organelle communication	10
V. Stress memory and seed priming: two faces of the same coin	10
VI. Ways forward for implementing seed priming at a wider scale	13
VII. Conclusions	15
VIII. Acknowledgements	15
IX. References	15
X. Supporting information	21

I. INTRODUCTION

Plants face multiple environmental stresses throughout their lifespan that not only reduce their growth, but also negatively affect crop productivity. These stresses include both abiotic factors like drought, salt, temperature, nutrient deficiency, light, and ozone (O₃), as well as biotic agents including pathogens, pests and competition with weeds. Further, under field conditions, various stresses occur in combinations that magnify stress severity (Pandey *et al.*, 2017; Zandalinas, Fritschl & Mittler, 2020). According to the National Climate Assessment (NCA)-USDA, the highest losses in global crop production can be attributed to abiotic stresses (~50%), followed by weeds (~34%), insects (~18%) and pathogens (~16%) (<https://www.neefusa.org>). Among abiotic factors, drought and heat contribute to yield losses of 63–87 and 42%, respectively in maize (*Zea mays*); 57 and 31% in wheat (*Triticum aestivum*) and 53–92 and 50% in rice (*Oryza sativa*) in varied regions across the globe. Drought alone can reduce crop production by 45–69, 46–71 and 60% in chickpea (*Cicer arietinum*), soybean (*Glycine max*) and sunflower (*Helianthus annuus*), respectively (Fahad *et al.*, 2017). Soil salinity is similarly detrimental, significantly reducing the yield of various crops (Zorb, Geilfus & Dietz, 2019). In recent years, heavy metal-induced toxicity has achieved prominence, not only in reducing yield but also quality of crops like rice, mustard (*Brassica juncea*) and soybean (Muehe *et al.*, 2019; Rai *et al.*, 2019). A major challenge for plant scientists is to minimize stress-induced crop losses to meet global food supply for an increasing world population, which is projected to reach 9 billion by 2050 (<https://www.un.org>).

Currently, multiple strategies are used to enhance crop yield under stress conditions (Table 1). The most traditional and widely accepted approach is the development of improved cultivars using crop breeding (Moose & Mumm, 2008). However, this is time-consuming and dependent upon the availability of germplasm with desirable traits. Such cultivation of naturally stress-resistant plants has been suggested as a means to diversify agriculture (Zhang, Li & Zhu, 2018b). Complementing this approach is the use of transgenic technology/genome-editing, which involves the genetic manipulation of single/multiple genes. In recent years, various genes have been targeted to develop genetically modified crops (GMCs) with enhanced yield under field conditions. For example, a triple mutation in the *PLY1*, *PLY4* and *PLY6* abscisic acid (ABA) receptors resulted in an approximately 30% increase in seed yield in rice (Miao *et al.*, 2018). Similarly, the *OsGS3*, *OsGW2* and *OsGn1a* triple mutants of two elite rice varieties J809 and

L237 showed a 68 and 30% increase in yield per panicle, respectively (Zhou *et al.*, 2019). Recently, CRISPR-Cas9 (clustered regularly interspaced short palindromic repeats-CRISPR-associated protein 9) was used to introduce mutations in cis-regulatory elements of *OsTBI* (*TEOSINTE BRANCHEDI*) that positively regulated the expression of several pleiotropic traits such as culm strength, number of spikelets per panicle and tiller number (Cui *et al.*, 2020). In tomato (*Lycopersicon esculentum*) and rice, mutation in *LIN* (a MADS-box family member) alters inflorescence characteristics resulting in increased seed yield (Soyk *et al.*, 2017). Isopentenyl-transferase (IPT)-overexpressed cotton (*Gossypium hirsutum*) show enhanced drought tolerance and significant increase in seed cotton production by 27–44%, particularly when subjected to pre-flowering water-deficit stress conditions (Zhu *et al.*, 2018). In maize, ARGOS8 (AUXIN-REGULATED GENE INVOLVED IN ORGAN SIZE 8) variants under drought-stress conditions showed significant yield improvement of nearly 5 bushels per acre (4%) compared to wild-type plants (Shi *et al.*, 2017). Genetic technology has also been used in *de novo* domestication, leading to a significant increase in fruit size as well as fruit number in wild tomato (Zsögön *et al.*, 2018).

Taken together, transgenic technology in combination with CRISPR/Cas9-based genome editing tools is likely to accelerate the development of new crop varieties. However, regulatory restrictions (Halford, 2019; Mackelprang & Lemaux, 2020) mean that the multilocation field trials of transgenic crops are still limited (Table 1). Moreover, it remains difficult to convince farmers to change their preferred varieties because of likely variations in agronomic practices and consumer acceptance. An alternative is a chemical-based non-genetic approach wherein plant bioregulators (PBRs) are used as foliar sprays to enhance stress tolerance and crop yield (Srivastava *et al.*, 2016; Kerchev *et al.*, 2019). The foliar application of PBRs, while effective, remains labour intensive, especially in larger field areas and dense crop plantations (Table 1).

Seed priming represents a versatile approach for mitigating stress-induced damage in widely cultivated local crop varieties. In this approach, seeds are allowed to imbibe a chemical/biological priming agent and then cultivated using normal agronomic practices (Farooq *et al.*, 2019). Although, the priming treatment is given only for a short duration during initial seed germination, its effects can last for the entire life cycle of the plant. Most priming agents synchronize seed germination and enable plants to survive better under adverse environmental conditions. However, the signalling events operating during the initial phases of seed germination

Table 1. Advantages and disadvantages of approaches used for enhancing stress tolerance in crops

	Approach	Advantages	Disadvantages
Genetic	Traditional or marker-assisted crop breeding	Easy commercialization due to fewer regulatory restrictions. Can be accomplished with basic laboratory infrastructure.	Dependent on the availability of germplasm with desired trait. Time-consuming and labour intensive.
	Transgenic technology/ genome-editing	Can introduce single/multiple genes into plants from related or unrelated species. Regulatory gene(s) can be utilized to impart tolerance to multi-stress conditions. Inducible promoters can be used to express desired gene(s) only at specific time or developmental stage. Can accelerate the process of domestication of wild species.	Commercialization is low due to regulatory restrictions. Can cause metabolic imbalance or off-target effects. Requires skilled manpower and advanced laboratory infra-structure.
Non-genetic	Foliar application of plant bioregulators (PBRs)	Ease of use for locally cultivated varieties. Cost-effective	Increased chemical load to agricultural land. Difficult to implement at larger scales, especially for densely cultivated crops. Dependent upon crop/variety-specific dose-optimization studies.
	Seed priming	Ease of use for locally cultivated varieties. Cost-benefit ratio is high as treatment is applied only to seeds. Minimal ecological disturbance in the field.	Dependent upon crop/variety-specific dose-optimization studies.

and the molecular mechanisms associated with seed priming remain poorly understood. In addition, a deeper understanding of the molecular links between seed priming and stress memory could guide the design of improved strategies for enhancing crop productivity in a resource-efficient manner. To this end, the present review summarizes the available information on dose, priming duration and biological responses of diverse set of seed priming agents (SPRs). The major signalling events operating during the initial phases of seed germination and the molecular mechanisms associated with seed priming are discussed. In addition, molecular and genome-level changes are highlighted to integrate understanding of seed priming effects with studies on stress memory. Finally, a working model is proposed for the better implementation of SPR-based technology, for enhancing crop growth and productivity at a wider scale.

II. THE USE OF SPRs IN CROPS

Seed priming is a technique that has been in use for more than 100 years. Seeds are soaked in a SPR only for a short duration which does not extend to radicle protrusion. The primed seeds can then be either dried to their original water content for storage or can be sown directly into the field. In general, primed seeds display characteristics like improved vigour, synchronized germination and better crop establishment, which are all known to be positively related to the resource-use efficiency and yield of crops (Finch-Savage &

Bassel, 2016). A diverse range of SPRs are currently in use (Fig. 1). Considering their chemical nature and mode of action, SPRs can be classified as salts, hormones, physiological/non-physiological chemicals, nano-particles, physical treatments and biological agents. A multitude of effects at physiological, molecular, biochemical and metabolic levels together combine to improve the performance of SPR-treated plants. In brief, SPR treatments activate various enzymes like hydrolases, proteases, α -amylase and dehydrogenases, which facilitate endosperm weakening and stored reserve mobilization, to improve seed vigour. In addition, stress-responsive transcription factors, DNA-repair proteins and metabolites like sugar, antioxidants and osmolytes are also upregulated, together contributing to the stress-tolerant phenotype of SPR-treated plants (Farooq *et al.*, 2019). SPR treatment is also thought to create a priming memory in plants, imparting improved resilience against stress conditions (Savvides *et al.*, 2016). Together, this field of seed priming, collectively termed 'primeomics' (Balmer *et al.*, 2015), has opened up new research avenues for those interested in maximizing crop productivity.

We identified a total of 117 research articles published between 2015 and 2020 on 39 different type of SPRs (see online Supporting Information, Table S1 for a full list of these publications and the search string used. From each publication, we recorded the SPR used, the dose range, priming duration and biological response. For publications where responses to more than one SPRs were reported, we used either data from the one SPR with the largest response

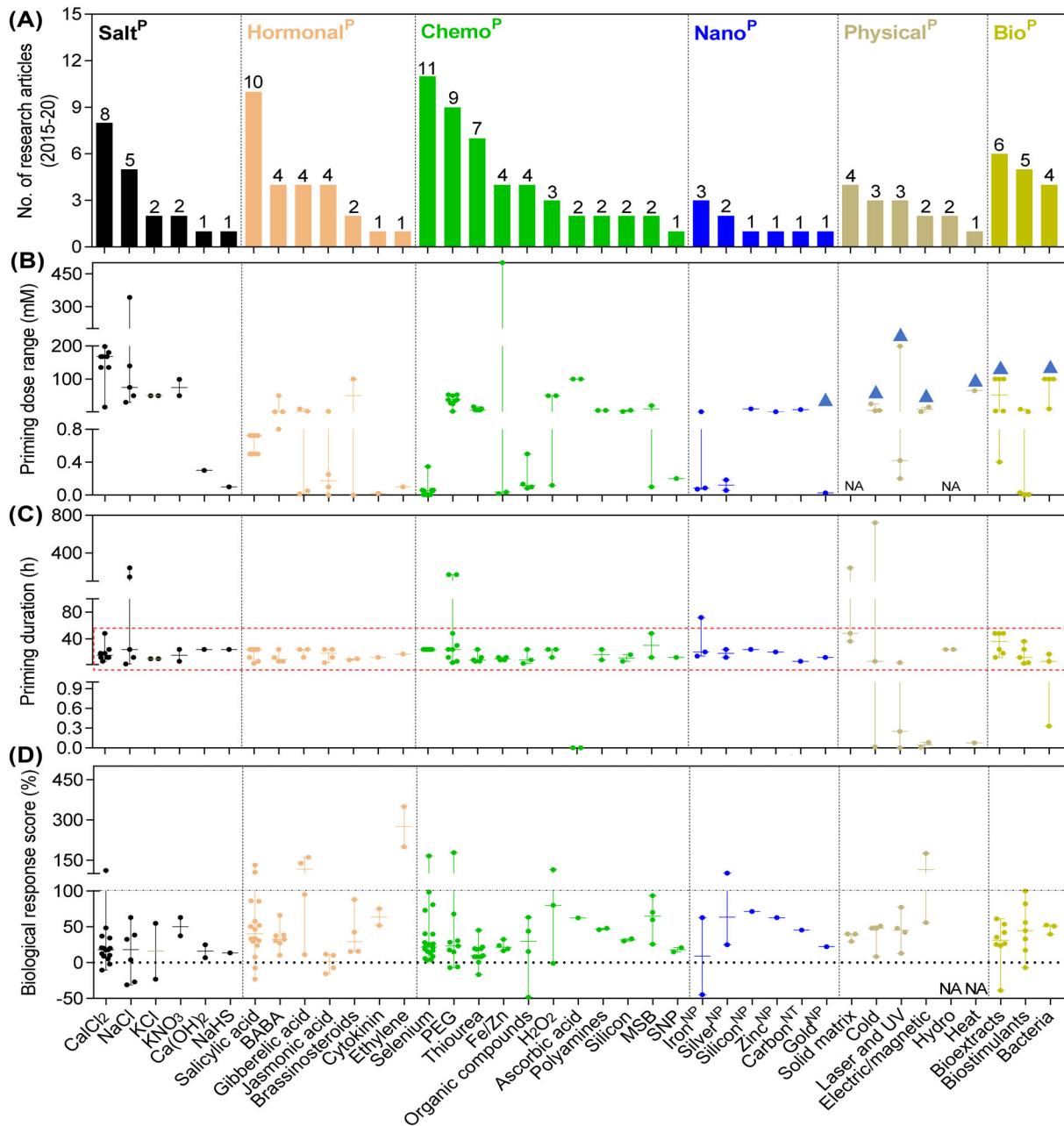


Fig. 1. Overview of seed priming agents (SPRs), their dose range and priming duration. On the basis of their chemical nature and mode of action, widely used SPRs are here classified either as salt (Salt^P), hormonal (Hormonal^P), chemical (Chemo^P), nanoparticle (Nano^P), physical (Physical^P) or biological (Bio^P) agents. Data were derived from a total of 117 research articles published between 2015 and 2020 on 39 different types of SPRs (see Table S1 for references and details of biological response scores). (A) Number of research articles, (B) dose range, (C) priming duration, and (D) biological response score for all SPRs. Blue triangles in B denote data points where different concentration units are applicable: for Gold^{NP} (parts per million), cold (°C), laser and UV (W/m²), electric (KV/m), magnetic (mT), heat (°C), bioextracts (%) and bacteria (1000 million colony forming units/ml). For solid matrix and hydro priming, concentration units are not applicable (NA). In C, the area between the red dotted lines indicates the priming duration for the majority of seed priming agents. BABA, β-amino butyric acid; PEG, poly-ethylene glycol; MSB, menadione sodium bisulfite; SNP, sodium nitroprusside; UV, ultraviolet. Superscript NP indicates nanoparticles; superscript NT indicates nanotubes.

or, where two SPRs had comparable seed germination/phenotypic responses, we used data from both (see Table S1). Where suitable information was reported, the biological response was calculated as the percentage change (primed *versus* non-primed) in six key plant growth and crop yield parameters: rate of seed germination (RG), plant biomass (PB), chlorophyll content (CC), enzymatic/non-enzymatic antioxidants (EA), osmolyte accumulation (OA) and seed yield/plant (SY). We then calculated the average biological response in response to SPR treatment for each study (Table S1).

On the basis of publication number, the SPRs for which the most studies are available are selenium (Se), salicylic acid (SA), poly-ethylene glycol (PEG), CaCl₂ and thiourea (TU) (Fig. 1A). The priming doses used for SPRs in the salt category appear relatively high compared with other SPRs (Fig. 1B). The priming duration most commonly used ranged from 2 to 48 h post-imbibition (Fig. 1C). On the basis of the biological response scores, the SPRs with the highest values (with a more than 100% change) were CaCl₂, SA, gibberellic acid (GA), ethylene, selenium, PEG, H₂O₂, magnetic and silver nanoparticles (Fig. 1D). The summary of previous studies in Fig. 1 could provide a framework for developing single or multiple SPR-based formulations for crops. A recent review has considered individual SPRs in detail, outlining their common and overlapping effects (Farooq *et al.*, 2019). Therefore, herein we focus on the stress-ameliorating potential of the five SPRs for which our review identified the most research has been conducted.

(1) Selenium

Se is an essential trace element for human and animals, but causes toxicity in excessive amounts. The United States Department of Agriculture (USDA) and the Agency for Toxic Substances and Disease Registry (ATSDR) set benchmark values of 55 and $\geq 900 \mu\text{g day}^{-1}$ as the recommended dietary allowance and toxic level respectively. Owing to its antioxidant properties, in animals Se has roles in reproduction, immune responses and thyroid hormone metabolism (Srivastava *et al.*, 2016). Whether Se has an essential role in plants is still unclear as they lack selenoproteins such as glutathione peroxidase (GPX). Chemically, Se is similar to sulphur, and thus is taken up by plants *via* sulphur transporters and is metabolized *via* the sulphur assimilatory pathway (Gupta & Gupta, 2016). Use of Se as a SPR (dose range: 0.0043–0.34 mM; priming duration: 24 h post-imbibition) has been investigated in rice. It shows an ameliorative potential in the presence of arsenic (As) [an ubiquitous environmental toxin and a recognized group-1 carcinogen (IARC, 2004)]: Se priming enhanced antioxidant potential, α -amylase activity, soluble sugar content and essential micronutrient uptake (Wang *et al.*, 2016a; Hussain *et al.*, 2016b; Moulick, Santra & Ghosh, 2018c). In addition, root-to-shoot and shoot-to-grain accumulation of As was reduced (Moulick, Santra & Ghosh, 2018a,b), suggesting that Se priming may represent

an effective approach for producing rice containing low levels of As.

(2) Salicylic acid

Salicylic acid (SA; o-hydroxy benzoic acid) is a plant hormone known for its ability to induce systemic resistance in response to plant pathogens. However, over a narrow dose range, it can also regulate growth processes by inducing low-level accumulation of reactive oxygen species (ROS), which serve as secondary messengers in plants (Dempsey & Klessig, 2017). The seed priming effects of SA (dose range: 0.5–0.725 mM; priming duration: 3–24 h post-imbibition) have been demonstrated in crops like maize and rice under chilling, cadmium and nutrient-deprived stress conditions (Table S1). At the biochemical level, SA priming leads to enhanced antioxidant capacity, α -amylase activity, soluble sugar content and respiration rate (Wang *et al.*, 2016a,b; Hussain *et al.*, 2016b). A synergistic compatibility with other SPRs, such as H₂O₂, has also been demonstrated. For instance, in maize, combined SA+H₂O₂ priming upregulated the expression of GA biosynthesis- (*ZmGA20ox1* and *ZmGA3ox2*), GA signalling- (*ZmGID1* and *ZmGID2*) and ABA catabolism-related (*ZmCYP707A2*) genes, leading to higher seed germination rate under chilling stress conditions (Li *et al.*, 2017). In rice, SA priming alters the global transcriptome by modulating the expression of various photosynthesis- and defence-related genes under submerged stress conditions. In addition, strong overlap between the SA- and Se-priming-induced transcriptome was reported (Hussain *et al.*, 2016c). It will be interesting to evaluate potential additive effects of combined treatment of SA and Se.

(3) Polyethylene glycol

Polyethylene glycol (PEG) reduces the water potential and hence can be used to induce dehydration stress in plants. PEG seed priming (dose range: 2.5–52.5 mM; priming duration: 4–168 h post-imbibition) can mediate enhanced growth and tolerance in crops like rice, wheat and sorghum (*Sorghum bicolor*) (Table S1). One possible mechanism to explain PEG-mediated priming is that it limits water uptake inside the seeds and hence slows the progress of germination-related processes. This may ensure minimal DNA/protein damage during the transition of seeds from a dehydrated to rehydrated state. However, at high doses, PEG can cause seeds to lose their germination ability. PEG-primed plants show robust antioxidant capacity and higher accumulation of compatible solutes compared to non-primed plants (Zhang *et al.*, 2015; Abid *et al.*, 2018; Boucelha, Djebbar & Abris-Belbachir, 2019). In *Brassica napus*, PEG priming upregulates the expression of genes like *LEA4-1*, *LEA4-5* and *ABI5* (Kubala *et al.*, 2015) and modifies structural features of seeds, such as the formation of microcracks and the induction of additional void spaces (Lechowska *et al.*, 2019). In wheat, long-lasting impacts of PEG seed

priming have been demonstrated: total grain production in primed plants was higher than in non-primed individuals (Abid *et al.*, 2018).

(4) CaCl_2

Seed priming potential of CaCl_2 (dose range: 15–198 mM; priming duration: 6–48 h post-imbibition) has been reported in wheat, rice and chickpea (Table S1). As for PEG, CaCl_2 increases the osmotic or solute potential of the germination solution and thus slows the rate of germination. In addition, Ca^{2+} has a well-known signalling-dependent effect on seed germination (Kudla, Batistic & Hashimoto, 2010). Both these factors make careful optimization of dose and duration essential for implementing CaCl_2 seed priming. In wheat, CaCl_2 -primed plants showed a significant improvement in growth, yield and cost–benefit ratio, especially under terminal drought (Farooq *et al.*, 2017b; Tabassum *et al.*, 2018) and salt (Tabassum *et al.*, 2017) stress conditions. These effects were associated with lower oxidative damage and improved plant–water balance in chickpea and bean (*Vicia faba*) plants under chilling (Farooq *et al.*, 2017a) and cadmium (Nouairi *et al.*, 2019) stress, respectively. CaCl_2 priming also supports the cultivation of zero-tillage wheat and can facilitate rice–wheat inter-cropping systems (Nawaz *et al.*, 2016).

(5) Thiourea

TU is a thiol-based ROS scavenger and anti-nitrification factor and its seed-priming potential (dose range: 6.5–16.5 mM; priming duration: 6–24 h post-imbibition) has been demonstrated in various crops including wheat, mungbean (*Vigna radiata*) and cluster bean (*Cyamopsis tetragonoloba*) (Table S1). Since, ROS are required for the survival of plants (Mittler, 2017), the dose and duration of TU exposure should be carefully considered. Using a supplementation approach, TU-mediated effects have been studied at multiple organizational levels. At the physiological level, TU improved source-to-sink relationships leading to increased crop yield. At the molecular level, it improved cellular energetics, co-ordinated calcium and ABA signalling, maintained water homeostasis, enhanced antioxidant defence, improved sulphur metabolism and microRNA (miRNA)–hormone balance (Srivastava *et al.*, 2014, 2016, 2017). In wheat, seed priming with TU leads to a uniform germination pattern with better seedling establishment (Chattha *et al.*, 2017). Seed priming with TU can also be combined with later foliar application to maximize yield benefits in plants like cluster bean (Meena *et al.*, 2016) and niger (*Guizotia abyssinica*) (Namrata *et al.*, 2018).

The priming potential of SPRs has been successfully demonstrated in major crops including rice, wheat and maize. Despite having their own specific effects, a common feature of SPRs is that their beneficial effects tend to be limited to a particular dose range. Hence, a precise crop/variety-level dose optimization is best practice for using SPRs in crop cultivation.

III. MOLECULAR BASIS OF SEED PRIMING IN PLANTS

Although, the molecular basis of seed priming has not been explored in detail, changes at the messenger RNA (mRNA) as well as protein levels have been investigated in response to selected SPRs. For instance, the targeted transcriptomic profiling of genes encoding antioxidants [*ANS* (anthocyanin synthase), *CAT* (catalase), *SOD* (superoxide dismutase), *APX* (ascorbate peroxidase) and *GR* (glutathione reductase)], osmolytes [*P5CS* (pyrroline-5-carboxylate synthase) and *PDH* (proline dehydrogenase)], an ion-transporter [*NHX* (sodium/hydrogen antiporter)], ABA biosynthetic enzymes [*NCED3* (9-cis-epoxycarotenoid dioxygenase 3)] and transcription factors [*TRAB-1* (transcription factor responsible for ABA regulation 1), *WRKY-71* (WRKY DNA-binding protein 71), *OsEm* (late embryogenic abundant protein)] have been performed in response to priming with spermine (Spm) and spermidine (Spd) in rice. Most of these genes were found to be upregulated even at the seedling stage, coinciding with greater accumulation of endogenous Spm and Spd under NaCl stress conditions (Paul & Roychoudhury, 2017). Similarly, increased expression of *OsNHX1* was observed in sodium selenite-primed rice seedlings, resulting in a higher K^+/Na^+ ratio under NaCl stress conditions (Subramanyam, Du Laing & Van Damme, 2019). In contrast to Spm/Spd, PEG-mediated amelioration of nano-Zinc oxide stress in rice was associated with reduced expression levels of genes encoding antioxidants (Salah *et al.*, 2015).

SPR treatment also can affect genes related to calcium signalling and hormone metabolism. Seed priming with calcium compounds [$\text{Ca}(\text{OH})_2$, $\text{Ca}(\text{NO}_3)_2$, and CaCl_2] and sodium hydro sulphide (NaHS) trigger expression of calcium signalling-related genes such as *CBL10* (calcineurin-B-like 10) in rice (Singh, Banerjee & Roychoudhury, 2019) and *CDPK* (Ca^{2+} -dependent protein kinase) in squash *Cucurbita pepo* (Valivand, Amooaghaie & Ahadi, 2019), respectively. Dual priming with SA+ H_2O_2 upregulated the expression of GA biosynthetic genes like $\zeta_{mGA20ox1}$ and $\zeta_{mGA3ox2}$, and downregulated the GA catabolism gene $\zeta_{mGA2ox1}$, while promoting expression of the ABA catabolism gene $\zeta_{mCYP707A2}$. In addition, the GA signalling mediators ζ_{mGID1} and ζ_{mGID2} were upregulated, together promoting seed germination in maize under chilling stress conditions (Li *et al.*, 2017). The activation of GA-biosynthetic genes together with increased production of active GA was observed under NaCl-priming mediated accelerated seed germination in tomato (Nakaune *et al.*, 2012). Additionally, DNA damage repair-related genes were upregulated in response to biopriming which improved seed germination and seedling establishment in *Medicago truncatula* (Forti *et al.*, 2020).

Seed priming has also been combined with triggering of plant immunity using biologically active compounds such as heat-stable metabolites isolated from root-associated *Bacillus* spp. This technology, termed seed defence biopriming (SDB), has been demonstrated to induce the expression of

resistance marker genes related to SA, ethylene, and jasmonic acid (JA) signalling, resulting in increased mortality of the insect pest *Spodoptera litura* in cucumber (*Cucumis sativus*) tissues (Song *et al.*, 2017). Whole-genome transcriptomic profiling was performed in 4-day-old rice seedlings under submergence stress with and without Se or SA priming. The pathway and gene ontology term enrichment analyses revealed that functional categories related to secondary metabolism, development, cell, transport, protein, and metal handling were over-represented after Se or SA priming (Hussain *et al.*, 2016a). Recently, the mechanism by which β -aminobutyric acid (BABA) mediates seed priming has been studied using an iTraQ (isobaric tags for relative and absolute quantitation)-based proteomics approach. This analysis of differentially expressed proteins indicated a more rapid activation of SA- and Ca^{2+} -dependent defence signalling. In addition, BABA priming also alters sugar metabolism to provide more substrates for the synthesis of secondary metabolites, which protected mango (*Mangifera indica*) fruit from pathogen attacks (Li *et al.*, 2019c).

It is thus clear that SPR treatments affect levels of hormones, signalling mediators, transcription factors and defence genes/proteins during the early stages of seed germination. Further, a more rapid and/or stronger activation of defence responses upon subsequent exposure to stress in plants derived from primed seed indicates the potential for future exploration of the presence of ‘stress-memory’-related molecular components arising in response to SPR treatment.

IV. ROLES OF MOLECULAR SIGNALLING IN THE CONTROL OF SEED DORMANCY AND GERMINATION

The most frequently used priming duration for various SPRs ranges from 2 to 48 h, and is applied at the onset of seed germination (Fig. 1C). During this time, the seed undergoes a series of complex molecular events which are essential for its transition from a quiescent to metabolically active state. The process of seed germination is triphasic, consisting of an initial rapid phase of water imbibition (phase I), followed by a plateau phase of stable water uptake (phase II) and concluding with a burst of water uptake, elongation of the embryonic axis and radical emergence (phase III). The period over which these phases take place is crop-specific and varies significantly among the model plant *A. thaliana* and crops like rice, wheat and maize (Fig. 2A).

In general, phase I is dominated by the activation of repair mechanisms to restore any dehydration-induced damage that took place during seed maturation. Such damaging events include the conversion of aspartyl residues of proteins to isoaspartyl, progressive loss of telomeric sequences, DNA strand breakage and loss of proper DNA confirmation (Weitbrecht, Muller & Leubner-Metzger, 2011). During repair, protein

isoaspartyl residues are reconverted to aspartyl by the action of isoaspartyl methyl transferase. In addition, various genes encoding for DNA ligases, formamidopyrimidine-DNA glycosylase, 8-oxoguanine DNA glycosylase/lyase and poly-ADP-ribose polymerases (PARPs) are upregulated to repair damaged DNA (Rajjou *et al.*, 2012).

Following this, seeds enter into phase II, wherein water uptake remains stable and the testa (seed coat) ruptures. During imbibition, ROS accumulate inside the seed, leading to carbonylation of storage proteins like cruciferin, and reserve mobilization (Ventura *et al.*, 2012). Thioredoxin (Trx), a regulatory disulphide protein, plays a major role in the reduction of protein disulphide bonds in starchy endosperms and embryos, thereby contributing towards their mobilization and the reductive activation of enzymes that support seed germination. This phase is also characterized by the synthesis of proteins using newly transcribed mRNAs and the synthesis of new mitochondria to enable the generation of sufficient energy to complete germination (Oracz & Stawska, 2016; Sano, Rajjou & North, 2020). Another characteristic feature of this phase is the increased biosynthesis of methionine, which not only supports the translation of new proteins, but also acts as a precursor for S-adenosyl methionine (SAM). SAM is a universal methyl group donor and supports major biosynthetic pathways to regulate seed germination (Rajjou *et al.*, 2012). Phases I and II are together referred to as seed germination *sensu stricto*, during which imbibed seeds maintain their desiccation tolerance and retain the ability to recapitulate their maturation processes, even under unfavourable conditions (Nonogaki, 2019a). Hence, phases I and II represent the best timing for implementing SPR treatments.

Phase III involves a rapid increase in water uptake, enabling cell elongation as well as DNA replication and cell division. Additionally, the endosperm specifically expresses cell wall remodelling proteins like endo- β -1,4-mannanase, endo- β -1,3-glucanase, expansins, xyloglucan endo transglycosylase, pectin methylesterase and polygalacturonase, which likely have roles in endosperm tissue weakening (Nonogaki, 2014). Endosperm weakening may facilitate radicle emergence – the culmination of successful seed germination.

These molecular changes occur in seeds as early as 1–2 h post-imbibition (HPI). In *A. thaliana*, more than 12000 mRNA transcripts are stored in dry seeds, and at 6 HPI the seed transcriptome is significantly different from that of dry seeds (Nakabayashi *et al.*, 2005). Similarly dynamic changes in the seed transcriptome have been demonstrated in rice (Howell *et al.*, 2009), wheat (Yu *et al.*, 2014) and maize (Jimenez-Lopez *et al.*, 2011). The stored mRNAs are responsible for maintaining seed germination ability in the presence of various transcriptional inhibitors (Rajjou *et al.*, 2004). The preferential oxidation of polysome-associated stored mRNAs has been shown to prevent the translation of seed germination inhibitory proteins. By contrast, monosome-bound mRNAs, which have features such as

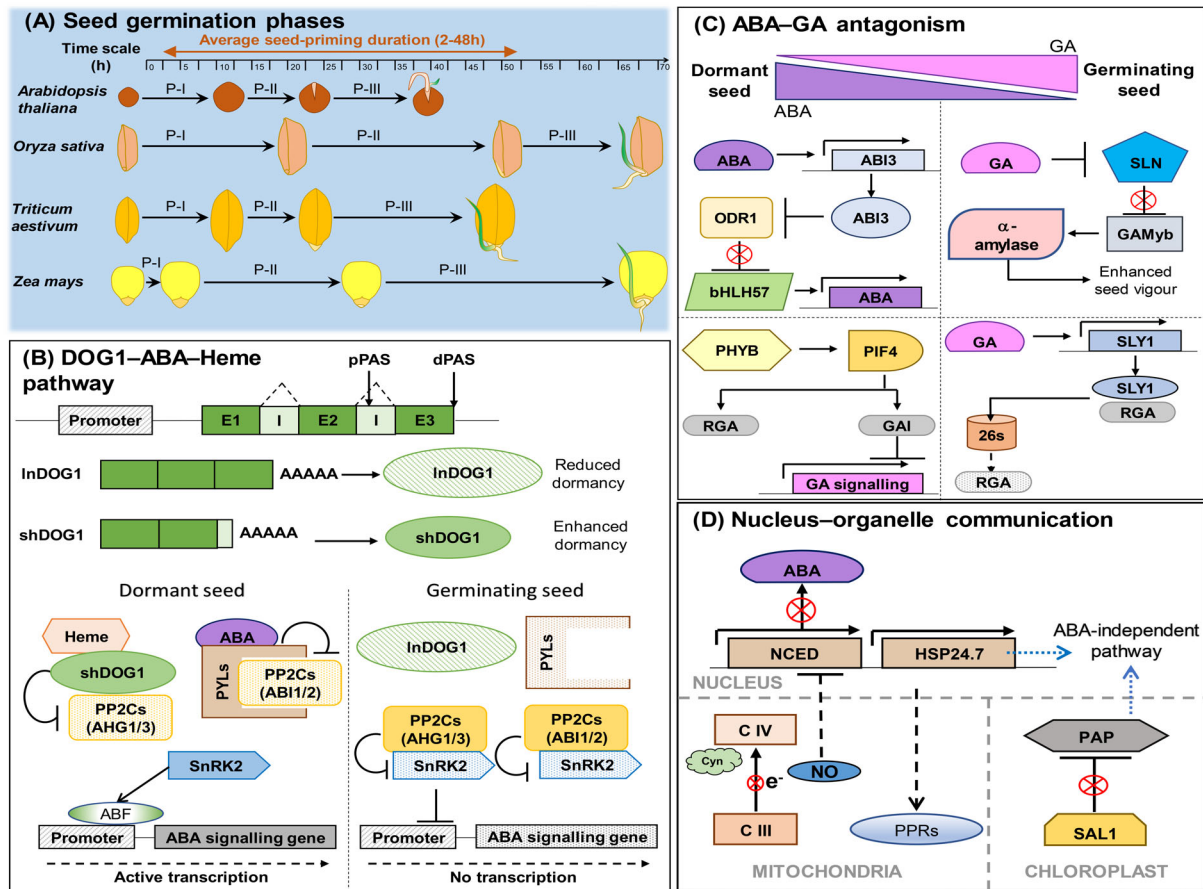


Fig. 2. Phases of seed germination phases and major signalling events controlling early seed germination/dormancy. (A) Illustration of triphasic seed germination. Germination begins with phase I (P-I) in which there is initial rapid water imbibition, followed by a plateau (phase II; P-II) of stable water uptake, and concluding with phase III (P-III) in which elongation of the embryonic axis and radical emergence occurs. (B) The delay of germination1 (DOG1)-abscisic acid (ABA)-heme pathway for regulating seed dormancy/germination. *DOG1* pre-mRNA undergoes alternative polyadenylation at proximal (pPAS) and distal (dPAS) sites to produce shorter (shDOG1; favours seed dormancy) and longer (InDOG1; favours seed germination) versions of *DOG1*, respectively. Heme-bound shDOG1 interacts with and suppresses protein phosphatase 2Cs (PP2Cs) like ABA hypersensitive germination 1/3 (AHG1/3). Additionally, canonical abscisic acid (ABA) signalling, with components like pyrabactin resistance like (PYL) ABA receptors and ABA insensitive 1/3 (ABI1/3) PP2Cs, is also activated. PP2C inhibition activates SNF1-related protein kinase 2 (SNRK2), which activates the transcription of ABA responsive genes through ABA binding factors (ABFs). As the seed germinates dPAS is preferred and InDOG1 is predominant. This form has less affinity for PP2Cs. PP2Cs suppress SNRK2s, reducing the expression of ABA responsive genes and thus support germination. (C) The role of ABA-giberellic acid (GA) antagonism in the regulation of seed germination. Higher levels of ABA and GA facilitate dormancy or germination, respectively. ABA favours the transcription and translation of ABA insensitive 3 (ABI3) which suppresses ODR1 [reversal of the RDO (reduced dormancy) phenotype] and thereby removes ODR1-mediated suppression of ABA biosynthesis. Simultaneously, GA signalling genes are repressed by DELLA proteins like GA-insensitive (GAI) activated by phytochrome interacting factor 4 (PIF4)-mediated phytochrome B (PHYB) photoreceptors. Another GA-suppressing DELLA protein is repressor of GA (RGA). RGA degradation by the 26 s proteasome is mediated by GA induced SLEEPY1 (SLY1) F-box containing proteins. GAs also mediate de-repression of the transcription factor GAMYB, thereby increasing α -amylase synthesis that enhances seed vigour by mobilizing stored starch. (D) The role of nucleus-organelle communication during seed germination. In mitochondria, blockage of electron transport (as seen under cyanide treatment) from Complex III (CIII) to Complex IV (CIV) leads to the generation of nitric oxide (NO) which acts as retrograde signal to suppress NCE1 transcription. Redox imbalances also induce heat shock proteins (HSP24.7) that impair cytochrome c oxidase (COX) maturation and promote germination in an ABA-independent pathway. The synthesis and transport of pentatricopeptide repeat-containing proteins (PPRs), which act as RNA-editing factors for various mitochondrial genes, represent an anterograde route for regulating seed germination. Another metabolite 3'-phosphoadenosine 5'-phosphate (PAP) acts as a chloroplast retrograde signal that is activated upon redox inactivation of SAL1 (a catabolic phosphatase for PAP). PAP represses seed germination in an ABA-independent manner.

shorter transcripts, low GC% (guanine–cytosine %) in UTRs (untranslated regions), weak secondary structure and a GAAGAAGAA motif in 5'UTRs, are relatively more stable. In *A. thaliana*, ~17% of monosome-associated mRNAs are translationally upregulated during early seed germination and encode for proteins responsive to water deprivation and cell cycle arrest (Bai *et al.*, 2020). Neo-synthesized mRNAs contribute to the energy demand and thereby, facilitate seed germination (Sano *et al.*, 2019). We provide an integrated view of major signalling events responsible for regulating seed dormancy and germination in Fig. 2B–D, and discuss these in the following sections.

(1) DOG1–ABA–heme regulatory module

In plants, dormancy restricts the progression of seeds into or through germination, even under favourable conditions (Chahtane, Kim & Lopez-Molina, 2017). Endosperm-derived ABA is essential to repress the growth of the embryo and hence is critical for maintaining seed dormancy. ‘Dry-after ripening’ is another process by which seeds lose dormancy and acquire the capacity to germinate. Similar to seed germination phases (Fig. 2A), dry-after ripening time is also variable across different plants and is maternally regulated (Piskurewicz *et al.*, 2016). Among the genes/regulatory network(s) known to regulate seed dormancy (Nonogaki, 2014, 2019a, b; Han & Yang, 2015), the DOG1–ABA–heme (DAH) module has been elucidated in great detail (Fig. 2B). Delay of germination 1 (DOG1) is a key seed dormancy inducer protein that interacts physically with clade A protein phosphatases 2C (PP2Cs) such as ABA hypersensitive germination1 (AHG1) and AHG3, through its N-terminal DSYLEW residue (positions 13–18), thus inhibiting their activity. Both AHG1 and AHG3 repress protein kinases such as SNF1-related protein kinase 2 (SnRK2), that are essential for the progression of ABA signalling. Hence, AHG1/3 and DOG1 can be considered as negative and positive regulators of ABA signalling, respectively. This is supported by studies on the *ahg1/3* double-mutant, which displays higher SnRK2 activity and delayed seed germination (Nishimura *et al.*, 2018).

In addition to the DOG1–PP2C pathway, canonical ABA signalling wherein ABA binds with pyrabactin resistance1/PYR1-like (PYR1/PYLs) receptors to inhibit PP2Cs like abscisic acid insensitive 1 (ABI1) and ABI2 to de-repress SnRK2s that target ABA binding factors (ABFs), is also operational in seeds. For example, PYL12 and PYL1 have been demonstrated to regulate seed dormancy in rice (Miao *et al.*, 2018). DOG1 also has the capacity to bind with the C-terminal of heme at His245 and His249. Heme binding is not essential for DOG1 to bind with AHG1/3, suggesting the existence of an AHG1/3-independent pathway by which the DOG1–heme complex regulates seed dormancy (Nishimura *et al.*, 2018). Although the exact mechanism is not clear, the DOG1–heme complex is proposed to enhance ABA sensitivity by stabilizing germination-suppressing transcription factors (Nonogaki, 2019b).

The post-transcriptional-level regulation of *DOG1* is also known. *DOG1* has both distal and proximal poly-A sites which are responsible for generating exon-3-harboured long-*DOG1* and exon-3-lacking short-*DOG1*, respectively. The genomic DNA corresponding to exon-3-*DOG1* also contains a promoter element for transcribing antisense-*DOG1* (as*DOG1*), which functions to fine-tune *DOG1* expression. Both long-*DOG1* and short-*DOG1* are of biological significance as they act as negative and positive regulators of seed dormancy, respectively (Cyrek *et al.*, 2016). The active transcription of long-*DOG1* also promotes H₂B-monoubiquitylation at the as*DOG1* promoter which act as repressive marks, thereby reducing as*DOG1* expression. The contrasting phenotypes of *A. thaliana* mutants *fy-2* (reduced dormancy) and *cpl1* (enhanced dormancy), which have lower and higher levels of as*DOG1*, respectively (Kowalczyk *et al.*, 2017), indicate that as*DOG1* acts as a secondary regulator of seed dormancy.

A chromatin remodeller PICKEL (PKL) has been shown to induce the deposition of H₃K₂₇me₃ repressive marks on the *DOG1* promoter element, inhibiting its transcription. The *pk1* mutant of *A. thaliana* exhibits enhanced seed dormancy (Tong *et al.*, 2020). Ethylene response factor 12 (ERF12) and topless (TPL) both repress *DOG1* expression by occupying its promoter, suggesting the presence of cross-talk between DOG1 and ethylene-dependent pathways (Li *et al.*, 2019d). Another transcription factor, Leucine zipper transcription factor 67 (bZip67) also interacts with the *DOG1* promoter and represses its expression, especially under low-temperature conditions (Bryant *et al.*, 2019). The pseudo-phosphatase reduced dormancy 5 (RDO5) directly interacts with DOG1, adding further complexity to the regulation of seed dormancy (Xiang *et al.*, 2016). Seed dormancy 4-like (AtSdr4L) has been shown to inhibit seed dormancy by promoting GA biosynthesis, although its exact function is unknown. The *dog1/atsdr4l* double-mutant showed enhanced seed dormancy, similar to that of the *atsdr4l* single-mutant, suggesting that AtSdr4L functions downstream of DOG1 (Cao *et al.*, 2020).

Given its multifaceted regulation, the DAH module has been proposed to act as a core hub to ensure seed germination only under favourable growth conditions.

(2) ABA–GA antagonism

The central and antagonistic relationships between ABA and GA, in terms of regulating seed dormancy (Fig. 2C) are well documented (Tuan *et al.*, 2018; Vishal & Kumar, 2018), and have been demonstrated in response to SA-mediated seed priming in maize (Li *et al.*, 2017). A higher level of GA (~10-fold more than ABA) is a major driving force behind the phase II to III transition during seed germination. The expression of major ABA biosynthetic genes including *ABA1* (ABA-deficient 1), *ABA2/3*, *NCED6* (9'-cis-epoxycarotenoid dioxygenase 6) and *NCED9* is downregulated post-imbibition; while genes related to ABA catabolism such as *CYP707A1* (ABA 8'-hydroxylases) and *CYP707A2* are upregulated. ABA insensitive 3 (ABI3), ABI4 and ABI5 represent important

ABA-responsive transcription factors that establish seed dormancy. *ABI3* represses the expression of *ODR1* (reversal of the *RDO* phenotype) which negatively affects the expression of *NCED6* and *NCED9* as well as ABA levels in freshly harvested seeds (Liu *et al.*, 2020).

In contrast to ABA, GA biosynthesis genes, including *GA3ox1* (gibberellin 3-oxidase 1) and *GA3ox2*, are upregulated immediately after imbibition. GA signalling regulators include gibberellin-insensitive dwarf 1 (*GID1*; a GA receptor), GA-insensitive (*GAI*), repressor of GA (*RGA*), repressor of GA-like 2 (*RGL2*), *SLEEPY1* (*SLY1*; a F-box-containing protein), *SNEEZY* and *SPINDLY* (*SPY*), which co-ordinate in a series of molecular and biophysical events ultimately leading to seed germination (Ravindran & Kumar, 2019). In *A. thaliana*, *GAI*, *RGA*, *RGL1*, *RGL2*, and *RGL3* represent the five major DELLA proteins. Of these, *RGL2* is the major DELLA factor which stimulates ABA biosynthesis by inducing *ABI5* (ABA-insensitive 5; a bZIP transcription factor) expression and stabilizing *ABI5* and hence, is a key negative regulator of GA functioning. GA-dependent degradation of DELLA protein, via the 26S proteasome mediated by *SLY1*, allows the transcription factor *GAMYB* to activate α -amylases during seed germination. The α -amylases catalyse the hydrolysis of starch to glucose and thus provide energy required for seed germination. Additionally, GA induces the expression of *EXPANSIN2* (*EXPA2*), which mediates cell elongation and cell-wall loosening, both vital components of testa rupture (Bassel, 2016). *NAC25*, a *RGL2* target protein, has been identified as an upstream component that regulates *EXPA2* expression (Sanchez-Montesino *et al.*, 2019). Like *RGL2*, *SPY* is another negative regulator involved in GA signalling. It encodes O-linked N-acetylglucosamine (O-GlcNAc) and regulates *RGA* activity through O-GlcNAc modification (Nelson & Steber, 2018). In addition, the GA pathway is integrated with light-induced signalling. Phytochrome B (*PhyB*) is a light-absorbing photoreceptor which transduces light signals to phytochrome-interacting factor 1 (*PIF1*); *PIF1* can then directly induce *RGA* and *GAI* transcription to repress GA signalling. *RVE1* (*Reveille1*) is another myeloblastosis (*Myb*)-like transcription factor that functions to reduce GA levels by directly repressing *GA3ox2* expression. In addition, *RVE1* can also abolish *RGL2*–*SLY1* interaction and hence, inhibit seed germination (Yang *et al.*, 2020a). Recently, *PIF1*–*RVE1* interaction has been demonstrated and genetic studies confirm that *RVE1* can promote the DNA-binding ability of *PIF1* to induce *ABI3* expression, thereby repressing seed germination (Yang *et al.*, 2020b).

Apart from *PIF1*, a few other candidates have also been characterized that are dual-targeted to both ABA and JA signalling pathways for regulating seed dormancy. For instance, *OsGLP2-1* (germin-like protein 2-1) responds antagonistically in response to ABA and GA supplementation in rice. *ABI5*-dependent enhanced expression of *OsGLP2-1* has been demonstrated to deepen seed dormancy (Wang *et al.*, 2020a). *COP9* signalosome (*CSN*) is a conserved heteromeric protein complex known to regulate the CULLIN-RING family of ubiquitin E3 ligases (*CRLs*),

including the SCF sub-family of E3s. The *csn* mutants *csn1-10* and *csn5a-1* exhibit defects in the timely degradation of *RGL2* and hence appear hyper-dormant. In addition, *CSN5A* can mediate the degradation of *ABI5*, which functions downstream to *RGL2* (Jin *et al.*, 2018). Taken together, ABA–JA co-regulators can function to fine-tune the timing of seed germination.

(3) Nucleus–organelle communication

The first evidence of organelle-dependent control of seed germination arose from the ancient practice of using cyanide (CN; a mitochondrial respiration inhibitor) to break seed dormancy (Hendricks & Taylorson, 1972). This paradoxical phenomenon of poisoning seeds to stimulate germination indicated that activation of the alternative respiration pathway is essential for seed germination (Yentur & Leopold, 1976). CN inhibits the activity of complex-IV (*COX*; cytochrome c oxidase); as a consequence, the electron flow from complex III to IV is disrupted. The premature termination of electron flow leads to the formation of NO, which functions as a mitochondrial retrograde signal to suppress the nuclear transcription of *NCED*, the rate-limiting enzyme of the ABA biosynthesis pathway (Nonogaki, 2019b). In cotton, redox imbalance within mitochondria has been shown to activate synthesis of the temperature-responsive heat-shock protein GhHSP24.7, which impairs *COX* maturation and enhances seed germination in an ABA-independent manner (Ma *et al.*, 2019). In addition, *COX* biogenesis in mitochondria is dependent upon anterograde signalling from the nucleus. This includes the active biosynthesis of pentatricopeptide repeat containing proteins (*PPRs*) that function as RNA editing factors (Nonogaki, 2019b). Another metabolite 3'-phosphoadenosine 5'-phosphate (*PAP*) acts as a chloroplast retrograde signal that is activated through the redox inactivation of *SAL1* (a catabolic phosphatase for *PAP*). The exogenous supplementation of *PAP* repressed seed germination in both the wild type and *abil-1* mutant in combination with either ABA or paclobutrazol (a GA biosynthesis inhibitor), but not by itself. This suggests that *PAP*-mediated retrograde signalling can bypass *ABI1* signalling to activate ABA-dependent gene expression and restore seed dormancy (Pornsiriwong *et al.*, 2017).

Taken together, the initial phases of seed germination, during which SPR treatments are applied, are under the co-ordinated regulation of multiple signalling mechanisms (Fig. 2B–D). Unfortunately, with the exception of ABA–GA antagonism, the modulation of such mechanisms by SPRs has not been explored in detail, even for the most commonly used SPRs, and this represents a significant issue that should be the focus of future research efforts.

V. STRESS MEMORY AND SEED PRIMING: TWO FACES OF THE SAME COIN

Plants face recurrent stresses throughout their life cycle. As an adaptive mechanism, plants retain 'memories' of

previously encountered stress that help them to confront impending stresses more rapidly and more efficiently. Such stress memories can be induced artificially through pre-exposure to low-dose stresses termed ‘priming cues’. The induced stress memory is called ‘acquired tolerance’ and it can be retained either in the short term (somatic memory), or may be transferred to succeeding generations (inter-generational memory), or in some cases, inherited across generations (trans-generational memory). Multiple mechanisms, including chromatin remodelling, alternative transcript splicing, metabolite accumulation and autophagy have been used to explain somatic memory in plants (Fig. 3). However, chromatin-dependent regulation is considered a key mechanism for regulating stress memories in plants (Baurle, 2018; Friedrich *et al.*, 2019; Baurle & Trindade, 2020).

The basic unit of chromatin is the nucleosome, composed of a 147-bp segment of DNA helix wrapped around a histone protein octamer (Luger *et al.*, 1997). Each nucleosome consists of two molecules each of the four histones, H2A, H2B, H3, and H4, linked by a strand of DNA with which the linker histone H1 may be associated (Kornberg, 1974). Apart from these canonical histones, plants also possess variant histones which have minor differences in their amino acid sequences. At the chromatin level, stress memory is conferred by different epigenetic modifications including post-translational histone modifications, changes in nucleosome occupancy, replacement of canonical histones with their variants and DNA methylation. These epigenetic modifications alter the overall accessibility of genes for transcription. While some histone marks such as H₃K₄me₃ and H₃K₄me₁ are characteristic of transcriptionally active genes, H₃K₂₇me₃ contributes towards transcriptional silencing of repressed genes while others like H₃K₉me₂ and H₃K₉me₃ are mainly concentrated in chromocentres and serve a constitutively repressive function (Ramirez-Prado *et al.*, 2018). Active (H₃K₄me₃) and repressive (H₃K₂₇me₃) histone marks function independently and are not mutually exclusive on memory-related target loci (Liu, Fromm & Avramova, 2014).

The deposition of active histone marks is known to be regulated in a stress-dependent manner. For instance, heat-stress priming activates a transcription factor HsfA2 (HEAT SHOCK FACTOR A2) which functions to deposit H₃K₄me on the promoters of heat-stress memory-related genes including *APX2* (ascorbate peroxidase 2) and *HSP21* (heat-shock protein 21). The unspliced transcripts of *APX2* and *HSP21* accumulate, even without increased levels of HsfA2, and contribute to acquired thermotolerance (Lamke *et al.*, 2016a). Similarly, JA priming induced MYC2 (a basic helix–loop–helix domain-containing transcription factor) functions resulting in deposition of H₃K₄me₃ on the promoters of ABA-dependent genes, and leading to enhanced dehydration tolerance in JA-primed plants (Liu & Avramova, 2016). The enhanced deposition of H₃K₄me₃ in the promoters of several stress-responsive loci was also demonstrated in cold-primed potato (*Solanum tuberosum*) plants (Zeng *et al.*, 2019). Besides methylation, cold-priming-dependent activation of *COR* (COLD RESPONSIVE) genes was associated with increased

histone acetylation and reduced nucleosome occupancy (Park *et al.*, 2018a). Among histone variants, H2A.Z deposition has been implicated in responses to temperature fluctuations in the ambient range (Kumar & Wigge, 2010). In *A. thaliana*, H2A.Z has been associated with both active as well as repressive chromatin states (Sura *et al.*, 2017); however, a direct role of H2A.Z in regulating stress-induced somatic memory has not been demonstrated.

The accessibility of genomic DNA for transcription is also affected by nucleosome occupancy, which reflects the fraction of cells from a population wherein a specific DNA fragment is occupied by a histone octamer. While most genomic DNA is occupied by nucleosomes, many functional regions including promoters, enhancers and terminators have low nucleosome occupancy, and some regions are nucleosome-free (Struhl & Segal, 2013). To address this, multiple types of chromatin remodelling ATPase complexes exist, which catalyse the disruption of DNA–histone contacts, leading to nucleosome sliding or eviction. According to conserved ATPase domains, chromatin-remodelling ATPases are divided into four major subfamilies including INO80/SWR1, CHD, ISWI (imitation switch) and SWI/SNF (switch/sucrose non-fermentable), although many additional types of chromatin remodellers exist in plants (Han *et al.*, 2015). In *A. thaliana*, one such remodeller is *FORGETTER1* (*FGT1*), with *fgt1* mutants displaying reduced levels of heat-induced gene expression during the memory phase. *FGT1* interacts with the SWI/SNF and ISWI sub-families and modulates the occupancy of nucleosomes in promoter regions of several heat-stress memory genes including *Hsa32*, which encodes a heat-stress-associated 32-kDa protein (Brzezinka *et al.*, 2016). *PICKLE* (*PKL*) is another chromatin remodeller identified from *A. thaliana* which enables plants to retain cold stress memory (Yang *et al.*, 2019). Thus, *FGT1* and *PKL1* represent connecting links for mediating heat and cold stress memory, respectively, at the chromatin level. In the absence of recurrent stress, the activation of stress-induced memory could impart a penalty on the plants. Hence, plants also possess mechanisms to erase active chromatin marks. For instance, in *A. thaliana*, a H3K4 demethylase *JUMONJI 17* (*JMJ17*) was shown to act as a negative regulator of dehydration stress tolerance (Huang *et al.*, 2019). However, the exact role of *JMJ17* in modulating dehydration stress-induced memory has not been investigated.

The genome-wide reprogramming of active (H₃K₄me₃) and repressive (H₃K₂₇me₃) histone marks has also been demonstrated in response to salt-induced priming (Sani *et al.*, 2013). One of the best-characterized target loci responsible for salt stress-induced memory is Δ 1-pyrroline-5-carboxylate synthetase 1 (*P5CS1*), which encodes a rate-limiting enzyme for proline biosynthesis (Szabados & Savoure, 2010). Elevated levels of H₃K₄me₃ on *P5CS1* chromatin cause stronger induction of *P5CS1* gene expression during the memory phase (Feng *et al.*, 2016). Apart from *P5CS1*, *bZIP17* (basic-leucine zipper 17) and *HRD3A* (Hmg-CoA reductase degradation 3A), which are important in the unfolded protein response (UPR) and endoplasmic reticulum-associated degradation (ERAD),

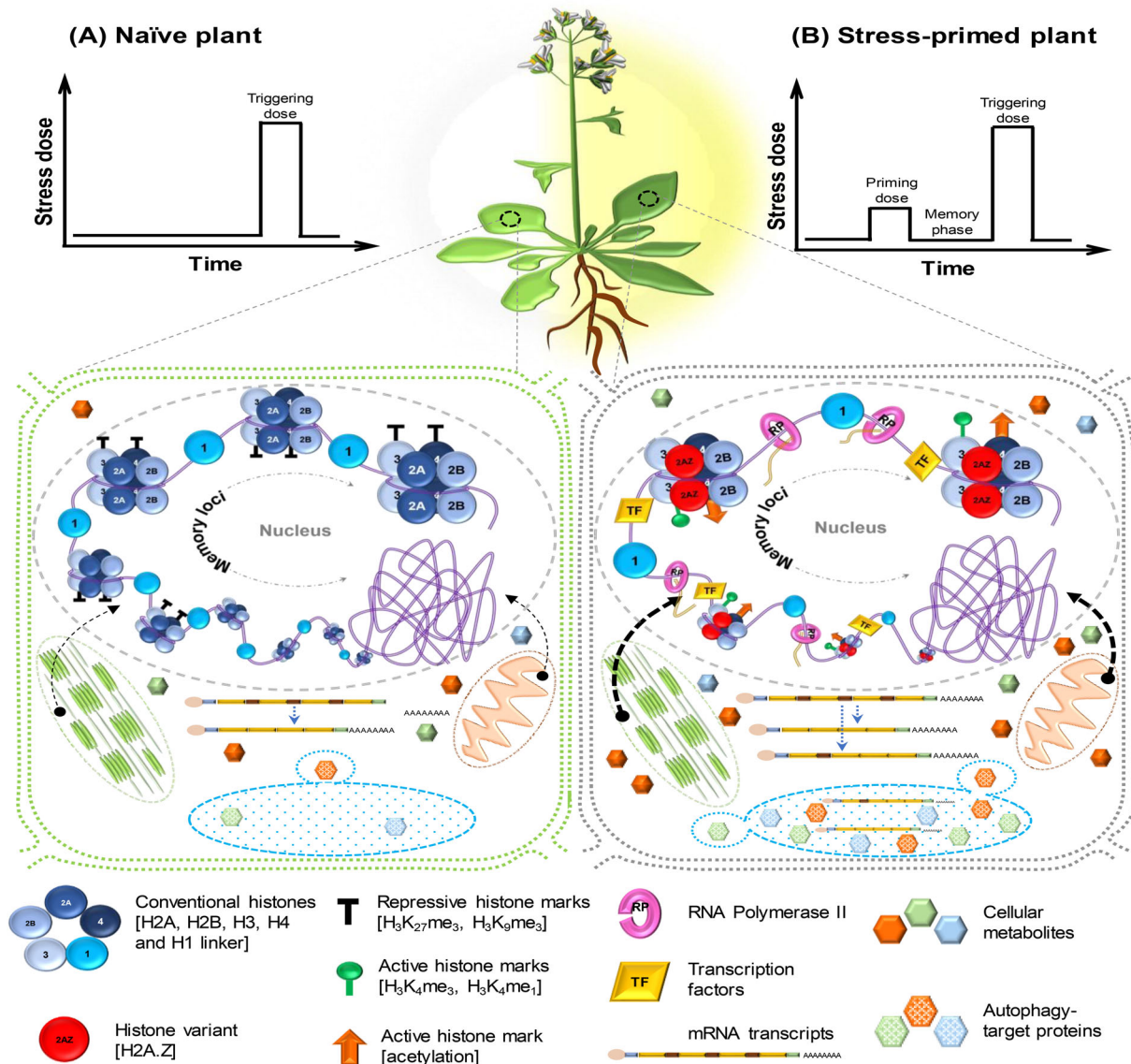


Fig. 3. Molecular mechanisms underlying stress memory in plants. Exposure to low-dose sub-lethal stress (priming dose) primes the plants to face recurring lethal stress (triggering dose) in a better manner than naïve or non-primed plants. At the molecular level, priming is known to induce various mechanisms including chromatin remodelling, alternative transcript splicing, metabolite accumulation and autophagy, which together regulate stress memory in plants. At the chromatin level, stress priming induces the deposition of active histone marks (H₃K₄me₃, H₃K₄me₁, and acetylation) at stress memory-dependent target loci. By contrast, more repressive marks (H₃K₂₇me₃ and H₃K₉me₃) are found in non-primed plants. The replacement of canonical histones with variants like H₂A.Z and low nucleosomal occupancy contribute to RNA polymerase II-dependent transcriptional activation in primed plants. In addition, a greater number of splice variants are formed which significantly increases the coding capacity of primed plants. The accumulation of various cellular metabolites, including sugar and lipids and autophagy-target proteins, along with better communication between chloroplast/mitochondria and nucleus further contribute to the ‘alert’ phenotype of primed plants.

respectively, also remain upregulated during the memory phase after low-dose salt exposure in *A. thaliana* (Tian *et al.*, 2019). These results clearly suggest that higher accumulation of proline, coupled with activation of the UPR and ERAD, enables primed plants to show better growth in response to future salt exposure. In *A. thaliana*, drought stress priming also induced accumulation of H₃K₄me₃ on

the promoters of major drought-responsive genes including *RD29B* (responsive to desiccation 29B) and *RAB18* (responsive to ABA 18). The transcription initiation form of RNA polymerase II (Ser5P; serine 5 phosphorylated Pol II) also persists at these loci, indicating that the stalled Pol II acts as ‘active marks’ while the transcriptional memory persists (Ding, Fromm & Avramova, 2012).

Chromatin-independent mechanisms also operate to regulate stress-induced somatic memory in plants. For instance, chloroplast-to-nucleus ROS signalling (Van Buer, Cvetkovic & Baier, 2016) and upregulated expression of the aquaporins *PIP1;4* and *PIP2;5* (plasma membrane intrinsic proteins) (Rahman *et al.*, 2020) have been demonstrated to be important under cold acclimation in *A. thaliana*. Heat-stress induced thermo-memory is also linked with alternative transcript splicing, which is considered a key mechanism for increasing the coding capacity of plant genomes (Srivastava *et al.*, 2018). In *A. thaliana*, global splicing rearrangement has been observed in response to heat (Ling *et al.*, 2018) as well as cold (Vyse *et al.*, 2020) stress priming. Intron splicing efficiency in *HsfA2*, which generates an alternative splice variant lacking a nuclear export signal, has been shown to be associated with the loss of heat-stress-induced memory in tomato (Hu *et al.*, 2020).

The stress-induced accumulation of cellular metabolites can also act as a ‘metabolic imprint’ that modulates plant responses during the memory phase (Schwachtje *et al.*, 2019). Priming with glucose, a fundamental signalling and metabolic molecule, induces the accumulation of Hikeshi-like protein 1 (HLP1); the latter facilitates the deposition of active H₃K₄me₃ on thermo-memory-related loci including *HSP70* and hence positively regulates acquired thermotolerance in *A. thaliana* (Sharma *et al.*, 2019). Enhanced production of branched-chain amino acids, raffinose family oligosaccharides, lipolysis products and tocopherols is also observed in thermo-primed plants (Serrano *et al.*, 2019). In response to cold-priming, raffinose accumulates significantly and regulates plant memory towards freezing stress (Zuther *et al.*, 2019). Apart from metabolite accumulation, salt-primed cells were shown to have a thicker cell wall with higher lignin content, suggesting that the adjustment of physical properties is important for regulating salt stress-induced memory in *A. thaliana* (Chun *et al.*, 2019). In coffee (*Coffea canephora*), prior exposure to drought is associated with higher activities of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo) and extensive metabolite re-programming, which enable the plant to face recurrent drought efficiently (Menezes-Silva *et al.*, 2017). In plants, the process of autophagy functions to degrade stress-induced proteins and other biomolecules during the recovery phase (Su *et al.*, 2020). Hence, autophagy could act as negative regulator of stress-induced memory, as substantiated by the improved thermo-memory in autophagy mutants of *A. thaliana* (Sedaghatmehr *et al.*, 2019). Apart from model plant *A. thaliana*, stress-induced memory has been reported in various crops including sugar cane (*Saccharum officinarum*) (Marcos *et al.*, 2018), maize (Virlovet *et al.*, 2018), rice (Li *et al.*, 2019a) and wheat (Wang *et al.*, 2020b) (Table S2).

The phenotypic effects observed in response to somatic stress memory overlaps with those of seed priming, despite the fact that SPR treatments are given only during the early hours of seed germination. A detailed comparison between seed priming and stress memory is provided in Table 2. Although, a diverse range of SPRs are in use (Fig. 1), unlike

stress memory, the mechanistic information about seed priming is still limited. While most SPRs are expected to have specific effects, a unified mechanism can be proposed wherein SPR treatment generates a mild (sub-lethal) stress inside the seed that prepares the emerged plant to face recurrent stresses more efficiently. This is supported by two observations: (1) primed seed show a synchronized germination pattern; and (2) during the early hours of post-priming, growth of seedlings from primed seed is slower than that of non-primed seed. It is thus likely that seed priming forces plants to begin germination under stress. During seed-to-seedling transition, the prevailing stress marks can be imprinted on the genome just as in stress-primed plants, leading to improved stress tolerance. It will be interesting to focus future work on understanding whether the mechanistic knowledge about stress memory (Fig. 3) provides a framework to understand the molecular basis of seed priming.

VI. WAYS FORWARD FOR IMPLEMENTING SEED PRIMING AT A WIDER SCALE

Despite the availability of SPRs with proven agronomic utility, the maximum potential of seed priming has still not been realized, especially at a global level. In Fig. 4, we plot the distribution of all articles that we identified on seed priming (Table S1) and somatic stress memory (Table S2), according to the study species and country of origin. Although we argue above that both seed priming and stress memory share a comparable phenotype (Table 2), research in these areas has not followed a common trajectory. SPR-based research is dominated by developing countries such as India, China and Pakistan on three major staple food crops: rice, wheat and maize (Fig. 4A). By contrast, most stress memory research has been carried out in Germany, China and the USA, using the model plant *Arabidopsis thaliana* (Fig. 4B). One possible reason for this difference could be that research in Asian countries, especially India and Pakistan, has focussed more on crop plants, so as to meet the food demands of a growing population. Interestingly, China is dominant in both fields. One objective of the present review was to enhance interactions between plant scientists studying SPRs and stress memory, to the advantage of both fields. On the one hand, for traditional studies of stress memory, the results of SPR studies may have translational relevance. On the other hand, a deeper understanding of the molecular basis of actions of SPRs will suggest potential cellular targets/signalling pathways/signalling networks to be applied to field stress scenarios. These could be targeted through Crispr/Cas9-assisted transgenic or molecular breeding approaches. Thus, a combined approach to studying stress memory and SPRs could enrich both fundamental and applied aspects of crop stress responses.

Differences in responses to SPR treatments are expected according to plant species or variety. We suggest that systematic screening should be performed to promote the cultivation

Table 2. Comparison between seed priming and somatic stress memory in plants

Seed priming	Stress memory
<p>Similarities</p> <p>Exposure to various agents at the time of seed germination makes plants more efficient in terms of responding to stress conditions.</p> <p>The growth of primed plants can be compromised under optimal growth conditions.</p> <p>Plants grown from primed seed show increased stress tolerance at the whole-plant level.</p> <p>Dissimilarities</p> <p>Nature of the priming treatment and subsequent stress need not be the same.</p> <p>Memory phase is long term, ranging from weeks to months.</p> <p>Performed during the initial stages of seed germination when most metabolic and defence pathways are inactive.</p> <p>Seed priming is applied only once.</p> <p>Molecular basis is largely unknown. Most studies are correlative.</p> <p>Majority of research performed on crops, including rice, wheat and maize.</p>	<p>Exposure to a sub-lethal stress prepares plants to face future or recurring lethal stress in a better manner.</p> <p>Priming cues in the form of mild stress can reduce growth in the absence of recurrent stress.</p> <p>Stress-induced memory is widespread and active in all tissues.</p> <p>Nature of priming cue and actual stress is the same; except in cases of cross-tolerance.</p> <p>Memory phase is short-term, ranging from hours to days.</p> <p>Performed at seedling or vegetative stages of plants when they have functional metabolism and an active defence system.</p> <p>Repeated exposure or stress-training is possible.</p> <p>The underlying molecular basis is well investigated and involves various mechanisms, including chromatin modification, transcriptional splicing and metabolite accumulation.</p> <p>Most stress memory research involves the model plant <i>Arabidopsis thaliana</i>.</p>

of local varieties that respond best to seed priming, so as to maximize the cost–benefit ratio for farmers. Additionally, the precise conditions for seed priming, such as ambient light levels, temperature, nutrient medium and whether samples are shaken, require optimization to ensure reproducible results. Development of dual/multiple SPR-based

formulations is another option to maximize yield benefits. In parallel, genome-wide association studies (GWASs) should be performed to identify the genetic basis of SPR-dependent actions. The ultimate objective will be to identify naturally occurring genotypes with an inherent capacity to produce reliable SPR-dependent phenotypes.

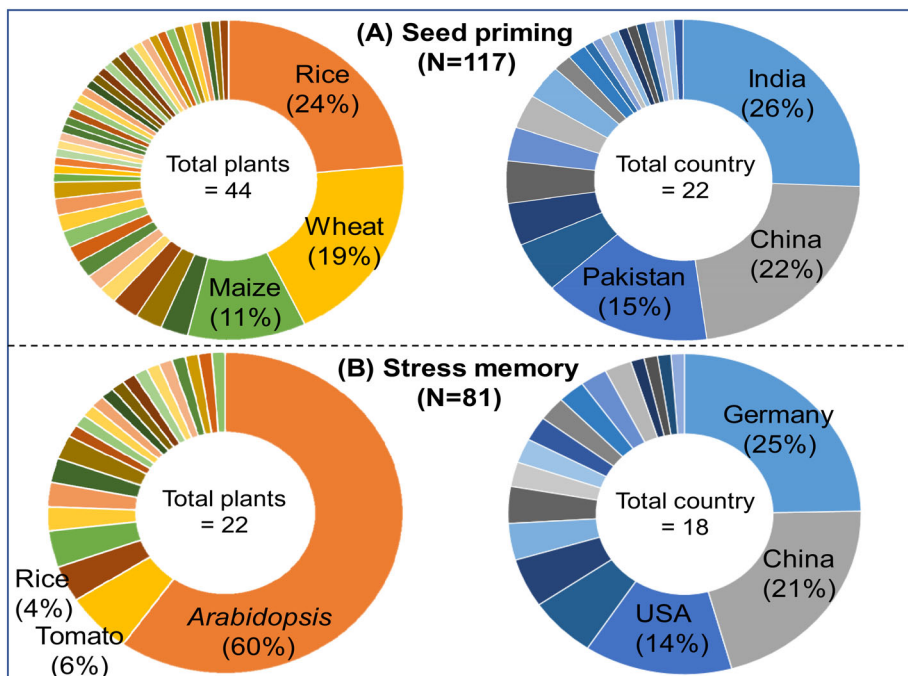


Fig. 4. World-wide status of seed-priming (A) and stress-memory-based (B) research, according to study species and country in which the research originated. See Tables S3 and S4 for the detailed data.

VII. CONCLUSIONS

(1) This review highlights the potential of seed priming strategies to enhance plant performance under stressful conditions. The five SPRs used most often in recent research (Se, SA, PEG, CaCl₂ and TU) were discussed.

(2) The average seed priming duration with SPRs ranged from 2 to 48 h, i.e. during phases I and II of seed germination. The major signalling events controlling these early phases of seed germination include DOG1–ABA–heme-based regulation, ABA–GA antagonism and nucleus–organelle communication.

(3) Since both seed priming and stress memory induce a ‘bet-hedging’ strategy in plants, they produce an overlapping phenotype, compromising plant growth under optimal conditions *in lieu* of better growth under stressful conditions. The molecular basis of stress memory is detailed at the level of chromatin reorganization, alternative transcript splicing, metabolite accumulation and autophagy. We argue that this could provide a framework to study similar mechanisms involved in seed priming.

(4) Integration of seed-priming and stress-memory-related research, identification of SPR-responsive varieties and development of dual/multiple benefit SPRs are proposed as a way forward for improving SPRs-mediated agriculture productivity worldwide.

VIII. ACKNOWLEDGEMENTS

A.K.S. and P.S. acknowledge financial support from the Department of Biotechnology (DBT) and Biotechnology and Biological Sciences Research Council (BBSRC) under the Newton-Bhabha Fund. A.K.S. would like to acknowledge Mrs. Pooja Negi for critical reading of the manuscript. The authors declare no competing financial interests.

IX. REFERENCES

References identified with an asterisk are used only in the supporting information.*

- ABDANI NASIRI, A., MORTAZAEINEZHAD, F. & TAHERI, R. (2018). Seed germination of medicinal sage is affected by gibberellic acid, magnetic field and laser irradiation. *Electromagnetic Biology and Medicine* **37**, 50–56.
- ABID, M., HAKEEM, A., SHAO, Y., LIU, Y., ZAHOR, R., FAN, Y., SUYU, J., ATA-UL-KARIM, S. T., TIAN, Z. & JIANG, D. (2018). Seed osmopriming invokes stress memory against post-germinative drought stress in wheat (*Triticum aestivum* L.). *Environmental and Experimental Botany* **145**, 12–20.
- *ACHARYA, P., JAYAPRAKASHA, G. K., CROSBY, K. M., JIFON, J. L. & PATIL, B. S. (2019). Green-synthesized nanoparticles enhanced seedling growth, yield, and quality of onion (*Allium cepa* L.). *ACS Sustainable Chemistry & Engineering* **7**, 14580–14590.
- *ACHARYA, P., JAYAPRAKASHA, G. K., CROSBY, K. M., JIFON, J. L. & PATIL, B. S. (2020). Nanoparticle-mediated seed priming improves germination, growth, yield, and quality of watermelons (*Citrullus lanatus*) at multi-locations in Texas. *Scientific Reports* **10**, 5037.
- *ALCANTARA, B. K., MACHEMER-NOONAN, K., JUNIOR, F. G. S. & AZEVEDO, R. A. (2015). Dry priming of maize seeds reduces aluminum stress. *PLoS One* **10**(12), e0145742.
- *ALCANTARA, B. K., RIZZI, V., GAZIOLA, S. A. & AZEVEDO, R. A. (2017). Soluble amino acid profile, mineral nutrient and carbohydrate content of maize kernels

harvested from plants submitted to ascorbic acid seed priming. *Anais da Academia Brasileira de Ciências* **89**, 695–704.

- *ALI, Q., DAUD, M. K., HAIDER, M. Z., ALI, S., RIZWAN, M., ASLAM, N., NOMAN, A., IQBAL, N., SHAHZAD, F., DEEBA, F. & ALI, I. (2017). Seed priming by sodium nitroprusside improves salt tolerance in wheat (*Triticum aestivum* L.) by enhancing physiological and biochemical parameters. *Plant Physiology and Biochemistry* **119**, 50–58.
- *ANUP, C. P., MELVIN, P., SHILPA, N., GANDHI, M. N., JADHAV, M., ALI, H. & KINI, K. R. (2015). Proteomic analysis of elicitation of downy mildew disease resistance in pearl millet by seed priming with β-aminobutyric acid and *Pseudomonas fluorescens*. *Journal of Proteome Research* **120**, 58–74.
- *ASTHIR, B., KAUR, R. & BAINS, N. S. (2015a). Variation of invertase activities in four wheat cultivars as influenced by thiourea and high temperature. *Acta Physiologiae Plantarum* **37**, 1712.
- *ASTHIR, B., THAPAR, R., BAINS, N. S. & FAROOQ, M. (2015b). Biochemical responses of thiourea in ameliorating high temperature stress by enhancing antioxidant defense system in wheat. *Russian Journal of Plant Physiology* **62**, 875–882.
- *BAENAS, N., VILLAÑO, D., GARCÍA-VIGUERA, C. & MORENO, D. A. (2016). Optimizing elicitation and seed priming to enrich broccoli and radish sprouts in glucosinolates. *Food Chemistry* **204**, 314–319.
- BAI, B., VAN DER HORST, S., CORDEWENER, J. H. G., AMERICA, T., HANSON, J. & BENTSINK, L. (2020). Seed-stored mRNAs that are specifically associated to monosomes are translationally regulated during germination. *Plant Physiology* **182**, 378–392.
- *BAJWA, A. A., FAROOQ, M. & NAWAZ, A. (2018). Seed priming with sorghum extracts and benzyl aminopurine improves the tolerance against salt stress in wheat (*Triticum aestivum* L.). *Physiology and Molecular Biology of Plants* **24**(2), 239–249.
- *BALI, S., KAUR, P., JAMWAL, V. L., GANDHI, S. G., SHARMA, A., OHRI, P., BHARDWAJ, R., ALI, M. A. & AHMAD, P. (2020). Seed priming with jasmonic acid counteracts root knot nematode infection in tomato by modulating the activity and expression of antioxidative enzymes. *Biomolecules* **10**(1), 98.
- BALMER, A., PASTOR, V., GAMIR, J., FLORES, V. & MAUCH-MANI, B. (2015). The ‘prime-ome’: towards a holistic approach to priming. *Trends in Plant Science* **20**(7), 443–452.
- BASSEL, G. W. (2016). To grow or not to grow? *Trends in Plant Science* **21**(6), 498–505.
- BAURLE, I. (2018). Can’t remember to forget you: chromatin-based priming of somatic stress responses. *Seminars in Cell and Developmental Biology* **83**, 133–139.
- BAURLE, I. & TRINDADE, I. (2020). Chromatin regulation of somatic abiotic stress memory. *Journal of Experimental Botany* **71**(17), 5269–5279.
- *BHANDAWAT, A., JAYASWALL, K., SHARMA, H. & ROY, J. (2020). Sound as a stimulus in associative learning for heat stress in Arabidopsis. *Communicative & Integrative Biology* **13**(1), 1–5.
- *BISWAS, S., BISWAS, A. K. & DE, B. (2018). Metabolomics analysis of *Cajanus cajan* L. seedlings unravelled amelioration of stress induced responses to salinity after halopriming of seeds. *Plant Signaling & Behavior* **13**(7), 1489670.
- *BOLT, S., ZUTHER, E., ZINTL, S., HINCHA, D. K. & SCHMÜLLING, T. (2017). ERF105 is a transcription factor gene of *Arabidopsis thaliana* required for freezing tolerance and cold acclimation. *Plant, Cell & Environment* **40**(1), 108–120.
- *BOSE, A. K., MOSER, B., RIGLING, A., LEHMANN, M. M., MILCU, A., PETER, M., RELLSTAB, C., WOHLGEMUTH, T. & GESSLER, A. (2020). Memory of environmental conditions across generations affects the acclimation potential of scots pine. *Plant, Cell & Environment* **43**(5), 1288–1299.
- BOUCELHA, L., DJEBBAR, R. & ABOUSS-BELBACHIR, O. (2019). *Vigna unguiculata* seed priming is related to redox status of plumule, radicle and cotyledons. *Functional Plant Biology* **46**(6), 584–594.
- *BOUKARI, N., JELALI, N., RENAUD, J. B., YOUSSEF, R. B., ABDELLY, C. & HANNOUFA, A. (2019). Salicylic acid seed priming improves tolerance to salinity, iron deficiency and their combined effect in two ecotypes of Alfalfa. *Environmental and Experimental Botany* **167**, 103820.
- BRYANT, F. M., HUGHES, D., HASSANI-PAK, K. & EASTMOND, P. J. (2019). Basic LEUCINE ZIPPER TRANSCRIPTION FACTOR67 transactivates DELAY OF GERMINATION1 to establish primary seed dormancy in *Arabidopsis*. *Plant Cell* **31**(6), 1276–1288.
- *BRZEZINKA, K., ALTMANN, S. & BÄURLE, I. (2019). Brushy1/Tonsoku/Mgoun3 is required for heat stress memory. *Plant, Cell & Environment* **42**(3), 771–781.
- BRZEZINKA, K., ALTMANN, S., CZESNICK, H., NICOLAS, P., GORKA, M., BENKE, E., KABELITZ, T., JAHNE, F., GRAF, A., KAPPEL, C. & BAURLE, I. (2016). *Arabidopsis* FORGETTER1 mediates stress-induced chromatin memory through nucleosome remodeling. *eLife* **5**, 17061.
- *BUSZEWICZ, D., ARCHACKI, R., PALUSIŃSKI, A., KOTLIŃSKI, M., FOGTMAN, A., IWANICKA-NOWICKA, R., SOSNOWSKA, K., KUCIŃSKI, J., PUPEL, P., OŁĘDZKI, J. & DADLEZ, M. (2016). HD2C histone deacetylase and a SWI/SNF chromatin remodelling complex interact and both are involved in mediating the heat stress response in *Arabidopsis*. *Plant, Cell & Environment* **39**(10), 2108–2122.
- CAO, H., HAN, Y., LI, J., DING, M., LI, Y., LI, X., CHEN, F., SOPPE, W. J. & LIU, Y. (2020). *Arabidopsis thaliana* SEED DORMANCY 4-LIKE regulates dormancy and germination by mediating the gibberellin pathway. *Journal of Experimental Botany* **71**(3), 919–933.

- *CAO, Q., LI, G., CUI, Z., YANG, F., JIANG, X., DIALLO, L. & KONG, F. (2019). Seed priming with melatonin improves the seed germination of waxy maize under chilling stress via promoting the antioxidant system and starch metabolism. *Scientific Reports* **9**(1), 1–12.
- *CARVALHO, A., REIS, S., PAVIA, I. & LIMA-BRITO, J. E. (2019). Influence of seed priming with iron and/or zinc in the nucleolar activity and protein content of bread wheat. *Protoplasma* **256**(3), 763–775.
- CHAHTANE, H., KIM, W. & LOPEZ-MOLINA, L. (2017). Primary seed dormancy: a temporally multilayered riddle waiting to be unlocked. *Journal of Experimental Botany* **68**(4), 857–869.
- CHATTHA, M. B., KHAN, I., MAHMOOD, A., CHATTHA, M. U., ANJUM, S. A., ASHRAF, U., ZAIN, M. & BILAL, U. (2017). Seed priming with thiourea improves the performance of late sown wheat. *Journal of Agricultural Research* **55**(1), 29–39.
- *CHOMONTOWSKI, C. & PODLASKI, S. (2020). Impact of sugar beet seed priming using the SMP method on the properties of the pericarp. *BMC Plant Biology* **20**(1), 32.
- CHUN, H. J., BAEK, D., CHO, H. M., JUNG, H. S., JEONG, M. S., JUNG, W. H., CHOI, C. W., LEE, S. H., JIN, B. J., PARK, M. S., KIM, H. J., CHUNG, W. S., LEE, S. Y., BOHNERT, H. J., BRESSAN, R. A., et al. (2019). Metabolic adjustment of *Arabidopsis* root suspension cells during adaptation to salt stress and mitotic stress memory. *Plant and Cell Physiology* **60**(3), 612–625.
- *CONG, W., MIAO, Y., XU, L., ZHANG, Y., YUAN, C., WANG, J., ZHUANG, T., LIN, X., JIANG, L., WANG, N. & MA, J. (2019). Transgenerational memory of gene expression changes induced by heavy metal stress in rice (*Oryza sativa* L.). *BMC Plant Biology* **19**(1), 282.
- CUI, Y., HU, X., LIANG, G., FENG, A., WANG, F., RUAN, S., DONG, G., SHEN, L., ZHANG, B., CHEN, D., ZHU, L., HU, J., LIN, Y., GUO, L., MATSUOKA, M. & QIAN, Q. (2020). Production of novel beneficial alleles of a rice yield-related QTL by CRISPR/Cas9. *Plant Biotechnology Journal* **18**(10), 1987–1989.
- CYREK, M., FEDAK, H., CIESIELSKI, A., GUO, Y., SLIWA, A., BRZEZNIAK, L., KRZYCZMONIK, K., PIETRAS, Z., KACZANOWSKI, S., LIU, F. & SWIEZEWSKI, S. (2016). Seed dormancy in *Arabidopsis* is controlled by alternative polyadenylation of DOG1. *Plant Physiology* **170**(2), 947–955.
- *DE FREITAS GUEDES, F. A., NOBRES, P., FERREIRA, D. C. R., MENEZES-SILVA, P. E., RIBEIRO-ALVES, M., CORREA, R. L., DAMATTA, F. M. & ALVES-FERREIRA, M. (2018). Transcriptional memory contributes to drought tolerance in coffee (*Coffea canephora*) plants. *Environmental and Experimental Botany* **147**, 220–233.
- DEMPSEY, D. A. & KLESSIG, D. F. (2017). How does the multifaceted plant hormone salicylic acid combat disease in plants and are similar mechanisms utilized in humans? *BMC Biology* **15**(1), 23.
- DING, Y., FROMM, M. & AVRAMOVA, Z. (2012). Multiple exposures to drought 'train' transcriptional responses in *Arabidopsis*. *Nature Communications* **3**, 740.
- *DU, B., LUO, H., HE, L., ZHANG, L., LIU, Y., MO, Z., PAN, S., TIAN, H., DUAN, M. & TANG, X. (2019). Rice seed priming with sodium selenate: effects on germination, seedling growth, and biochemical attributes. *Scientific Reports* **9**(1), 4311.
- *ELLOUZI, H., SGHAYAR, S. & ABDELLY, C. (2017). H₂O₂ seed priming improves tolerance to salinity; drought and their combined effect more than mannitol in *Calaké maritima* when compared to *Eutrema salsguineum*. *Journal of Plant Physiology* **210**, 38–50.
- *ESPANANY, A., FALLAH, S. & TADAYYON, A. (2016). Seed priming improves seed germination and reduces oxidative stress in black cumin (*Nigella sativa*) in presence of cadmium. *Industrial Crops and Products* **79**, 195–204.
- FAHAD, S., BAJWA, A. A., NAZIR, U., ANJUM, S. A., FAROOQ, A., ZOHAI, A., SADI, S., NASIM, W., ADKINS, S., SAUD, S., IHSAN, M. Z., ALHARBY, H., WU, C., WANG, D. & HUANG, J. (2017). Crop production under drought and heat stress: plant responses and management options. *Frontiers in Plant Science* **8**, 1147.
- *FAN, J., XU, J., ZHANG, W., AMEE, M., LIU, D. & CHEN, L. (2019). Salt-induced damage is alleviated by short-term pre-cold treatment in bermudagrass (*Cynodon dactylon*). *Plants (Basel)* **8**(9), 347.
- *FANG, S., GAO, K., HU, W., SNIDER, J. L., WANG, S., CHEN, B. & ZHOU, Z. (2018). Chemical priming of seed alters cotton floral bud differentiation by inducing changes in hormones, metabolites and gene expression. *Plant Physiology and Biochemistry* **130**, 633–640.
- FAROOQ, M., HUSSAIN, M., NAWAZ, A., LEE, D. J., ALGHAMDI, S. S. & SIDDIQUE, K. H. M. (2017a). Seed priming improves chilling tolerance in chickpea by modulating germination metabolism, trehalose accumulation and carbon assimilation. *Plant Physiology and Biochemistry* **111**, 274–283.
- FAROOQ, M., USMAN, M., NADEEM, F., UR REHMAN, H., WAHID, A., BASRA, S. M. & SIDDIQUE, K. H. (2019). Seed priming in field crops: potential benefits, adoption and challenges. *Crop and Pasture Science* **70**(9), 731–771.
- FAROOQ, S., HUSSAIN, M., JABRAN, K., HASSAN, W., RIZWAN, M. S. & YASIR, T. A. (2017b). Osmopriming with CaCl₂ improves wheat (*Triticum aestivum* L.) production under water-limited environments. *Environmental Science and Pollution Research* **24**(15), 13638–13649.
- *FEGHENABI, F., HADI, H., KHODAVERDILOO, H. & VAN GENUCHTEN, M. T. (2020). Seed priming alleviated salinity stress during germination and emergence of wheat (*Triticum aestivum* L.). *Agricultural Water Management* **231**, 106022.
- FENG, X. J., LI, J. R., QI, S. L., LIN, Q. F., JIN, J. B. & HUA, X. J. (2016). Light affects salt stress-induced transcriptional memory of P5CS1 in *Arabidopsis*. *Proceedings of the National Academy of Sciences of the United States of America* **113**(51), E8335–E8343.
- FINCH-SAVAGE, W. E. & BASSEL, G. W. (2016). Seed vigour and crop establishment: extending performance beyond adaptation. *Journal of Experimental Botany* **67**(3), 567–591.
- *FIRTZLAFF, V., OBERLÄNDER, J., GEISELHARDT, S., HILKER, M. & KUNZE, R. (2016). Pre-exposure of *Arabidopsis* to the abiotic or biotic environmental stimuli “chilling” or “insect eggs” exhibits different transcriptomic responses to herbivory. *Scientific Reports* **6**(1), 1–13.
- *FORESTAN, C., FARINATI, S., ZAMBELLI, F., PAVESI, G., ROSSI, V. & VAROTTO, S. (2020). Epigenetic signatures of stress adaptation and flowering regulation in response to extended drought and recovery in *Zea mays*. *Plant, Cell & Environment* **43**(1), 55–75.
- FORTI, C., SHANKAR, A., SINGH, A., BALESTRAZZI, A., PRASAD, V. & MACOVEI, A. (2020). Hydropriming and biopriming improve *Medicago truncatula* seed germination and upregulate dna repair and antioxidant genes. *Genes* **11**(3), 242.
- *FRAGKOSTEFANAKIS, S., SIMM, S., EL-SHERSHABY, A., HU, Y., BUBLAK, D., MESIHOVIC, A., DARM, K., MISHRA, S. K., TSCHERSCH, B., THERES, K. & SCHARF, C. (2019). The repressor and co-activator Hs1B1 regulates the major heat stress transcription factors in tomato. *Plant, Cell & Environment* **42**(3), 874–890.
- FRIEDRICH, T., FAIVRE, L., BAURLE, I. & SCHUBERT, D. (2019). Chromatin-based mechanisms of temperature memory in plants. *Plant, Cell & Environment* **42**(3), 762–770.
- *GANGULY, D. R., CRISP, P. A., EICHTEN, S. R. & POGSON, B. J. (2018). Maintenance of pre-existing DNA methylation states through recurring excess-light stress. *Plant, Cell & Environment* **41**(7), 1657–1672.
- *GANGULY, D. R., STONE, B. A., BOWERMAN, A. F., EICHTEN, S. R. & POGSON, B. J. (2019). Excess light priming in *Arabidopsis thaliana* genotypes with altered DNA methylomes. *G3: Genes, Genomes, Genetics* **9**(11), 3611–3621.
- *GEORGI, E., KUGLER, K., PFEIFER, M., VANZO, E., BLOCK, K., DOMAGALSKA, M. A., JUD, W., ABDELGAWAD, H., ASARD, H., REINHARDT, R. & HANSEL, A. (2019). The systems architecture of molecular memory in poplar after abiotic stress. *Plant Cell* **31**(2), 346–367.
- *GERNA, D., ROACH, T., ARC, E., STÖGGL, W., LIMONTA, M., VACCINO, P. & KRANNER, I. (2018). Redox poise and metabolite changes in bread wheat seeds are advanced by priming with hot steam. *BioChemical Journal* **475**(23), 3725–3743.
- *GHEZAL, N., RINEZ, I., SBAL, H., SAAD, I., FAROOQ, M., RINEZ, A., ZRIBI, I. & HAOUALA, R. (2016). Improvement of *Pisum sativum* salt stress tolerance by bio-priming their seeds using *Typha angustifolia* leaves aqueous extract. *South African Journal of Botany* **105**, 240–250.
- *GHOLAMI, M., MOKHTARIAN, F. & BANINASAB, B. (2015). Seed halopriming improves the germination performance of black seed (*Nigella sativa*) under salinity stress conditions. *Journal of Crop Science and Biotechnology* **18**(1), 21–26.
- *GUERRA, T., SCHILLING, S., HAKE, K., GORZOLKA, K., SYLVESTER, F. P., CONRADS, B., WESTERMANN, B. & ROMEIS, T. (2020). Calcium-dependent protein kinase 5 links calcium signaling with N-hydroxy-l-pipecolic acid and SARD 1-dependent immune memory in systemic acquired resistance. *New Phytologist* **225**(1), 310–325.
- *GUHA, T., RAVIKUMAR, K. V. G., MUKHERJEE, A., MUKHERJEE, A. & KUNDU, R. (2018). Nanopriming with zero valent iron (nZVI) enhances germination and growth in aromatic rice cultivar (*Oryza sativa* cv. Gobindabhog L.). *Plant Physiology and Biochemistry* **127**, 403–413.
- *GULLY, K., CELTON, J. M., DEGRAVE, A., PELLETIER, S., BRISSET, M. N. & BUCHER, E. (2019). Biotic stress-induced priming and de-priming of transcriptional memory in *Arabidopsis* and apple. *Epigenomes* **3**(1), 3.
- GUPTA, M. & GUPTA, S. (2016). An overview of selenium uptake, metabolism, and toxicity in plants. *Frontiers in Plant Science* **7**, 2074.
- *HACISALIHOGU, G., KANTANKA, S., MILLER, N., GUSTIN, J. L. & SETTLES, A. M. (2018). Modulation of early maize seedling performance via priming under sub-optimal temperatures. *PLoS One* **13**(11), e0206861.
- HALFORD, N. G. (2019). Legislation governing genetically modified and genome-edited crops in Europe: the need for change. *Journal of the Science of Food and Agriculture* **99**(1), 8–12.
- *HAMEED, A., HAMEED, A., FAROOQ, T., NOREEN, R., JAVED, S., BATOOL, S., AHMAD, A., GULZAR, T. & AHMAD, M. (2019). Evaluation of structurally different benzimidazole as priming agents, plant defence activators and growth enhancers in wheat. *BMC Chemistry* **13**(1), 29.
- HAN, C. & YANG, P. (2015). Studies on the molecular mechanisms of seed germination. *Proteomics* **15**(10), 1671–1679.
- *HAN, N., FAN, S., ZHANG, T., SUN, H., ZHU, Y., GONG, H. & GUO, J. (2020). SIHY5 is a necessary regulator of the cold acclimation response in tomato. *Plant Growth Regulation* **91**, 1–12.
- *HAN, S. H., PARK, Y. J. & PARK, C. M. (2019). Light priming of thermotolerance development in plants. *Plant Signaling & Behavior* **14**(1), 1554469.
- HAN, S. K., WU, M. F., CUI, S. & WAGNER, D. (2015). Roles and activities of chromatin remodeling ATPases in plants. *The Plant Journal* **83**(1), 62–77.

- *HASSINI, I., BAENAS, N., MORENO, D. A., CARVAJAL, M., BOUGHANMI, N. & MARTINEZ BALLESTA, M. D. C. (2017a). Effects of seed priming, salinity and methyl jasmonate treatment on bioactive composition of *Brassica oleracea* var. *capitata* (white and red varieties) sprouts. *Journal of the Science of Food and Agriculture* **97**(8), 2291–2299.
- *HASSINI, I., MARTINEZ-BALLESTA, M. C., BOUGHANMI, N., MORENO, D. A. & CARVAJAL, M. (2017b). Improvement of broccoli sprouts (*Brassica oleracea* L. var. *italica*) growth and quality by KCl seed priming and methyl jasmonate under salinity stress. *Scientia Horticulturae* **226**, 141–151.
- HENDRICKS, S. & TAYLORSON, R. (1972). Promotion of seed germination by nitrates and cyanides. *Nature* **237**(5351), 169–170.
- HOWELL, K. A., NARSAI, R., CARROLL, A., IVANOVA, A., LOHSE, M., USADEL, B., MILLAR, A. H. & WHELAN, J. (2009). Mapping metabolic and transcript temporal switches during germination in rice highlights specific transcription factors and the role of RNA instability in the germination process. *Plant Physiology* **149**(2), 961–980.
- *HU, T., JIN, Y., LI, H., AMOMBO, E. & FU, J. (2016). Stress memory induced transcriptional and metabolic changes of perennial ryegrass (*Lolium perenne*) in response to salt stress. *Physiologia Plantarum* **156**(1), 54–69.
- *HU, T., LIU, S. Q., AMOMBO, E. & FU, J. M. (2015). Stress memory induced rearrangements of HSP transcription, photosystem II photochemistry and metabolism of tall fescue (*Festuca arundinacea* Schreb.) in response to high-temperature stress. *Frontiers in Plant Science* **6**, 403.
- HU, Y., MESIHOVIC, A., JIMENEZ-GOMEZ, J. M., ROTH, S., GEBHARDT, P., BUBLAK, D., BOVY, A., SCHARF, K. D., SCHLEIFF, E. & FRAGKOSTEFANAKIS, S. (2020). Natural variation in HsIA2 pre-mRNA splicing is associated with changes in thermotolerance during tomato domestication. *New Phytologist* **225**(3), 1297–1310.
- *HUAN, Q., MAO, Z., CHONG, K. & ZHANG, J. (2018). Global analysis of H3K4me3/H3K27me3 in *Brachypodium distachyon* reveals VRN 3 as critical epigenetic regulation point in vernalization and provides insights into epigenetic memory. *New Phytologist* **219**(4), 1373–1387.
- HUANG, S., ZHANG, A., JIN, J. B., ZHAO, B., WANG, T. J., WU, Y., WANG, S., LIU, Y., WANG, J., GUO, P., AHMAD, R., LIU, B. & XU, Z. Y. (2019). *Arabidopsis* histone H3K4 demethylase JM17 functions in dehydration stress response. *New Phytologist* **223**(3), 1372–1387.
- *HUANG, Y., MO, Y., CHEN, P., YUAN, X., MENG, F., ZHU, S. & LIU, Z. (2016). Identification of SET domain-containing proteins in *Gossypium raimondii* and their response to high temperature stress. *Scientific Reports* **6**, 32729.
- IARC WORKING GROUP ON THE EVALUATION OF CARCINOGENIC RISKS TO HUMANS, WORLD HEALTH ORGANIZATION AND INTERNATIONAL AGENCY FOR RESEARCH ON CANCER (2004). *Some Drinking-water Disinfectants and Contaminants, Including Arsenic 84*. France: IARC.
- *HUSSAIN, A., RIZWAN, M., ALI, Q. & ALI, S. (2019). Seed priming with silicon nanoparticles improved the biomass and yield while reduced the oxidative stress and cadmium concentration in wheat grains. *Environmental Science and Pollution Research* **26**(8), 7579–7588.
- *HUSSAIN, S., KHAN, F., CAO, W., WU, L. & GENG, M. (2016a). Seed priming alters the production and detoxification of reactive oxygen intermediates in rice seedlings grown under sub-optimal temperature and nutrient supply. *Frontiers in Plant Science* **7**, 439.
- HUSSAIN, S., KHAN, F., HUSSAIN, H. A. & NIE, L. (2016b). Physiological and biochemical mechanisms of seed priming-induced chilling tolerance in rice cultivars. *Frontiers in Plant Science* **7**, 116.
- HUSSAIN, S., YIN, H., PENG, S., KHAN, F. A., KHAN, F., SAMEULLAH, M., HUSSAIN, H. A., HUANG, J., CUI, K. & NIE, L. (2016c). Comparative transcriptional profiling of primed and non-primed rice seedlings under submergence stress. *Frontiers in Plant Science* **7**, 1125.
- *JHANJI, S. & DHINGRA, M. (2020). Ameliorative effect of thiourea priming on germination characteristics of mungbean (*Vigna radiata* L.) under water and salinity stress. *Legume Research* **43**(3), 353–358.
- *JIMÉNEZ-ÁRIAS, D., PÉREZ, J. A., LUIS, J. C., MARTÍN-RODRÍGUEZ, V., VALDÉS-GONZÁLEZ, F. & BORGES, A. A. (2015). Treating seeds in menadione sodium bisulphite primes salt tolerance in *Arabidopsis* by inducing an earlier plant adaptation. *Environmental and Experimental Botany* **109**, 23–30.
- JIMENEZ-LOPEZ, S., MANCERA-MARTINEZ, E., DONAYRE-TORRES, A., RANGEL, C., URIBE, L., MARCH, S., JIMENEZ-SANCHEZ, G. & SANCHEZ DE JIMENEZ, E. (2011). Expression profile of maize (*Zea mays* L.) embryonic axes during germination: translational regulation of ribosomal protein mRNAs. *Plant and Cell Physiology* **52**(10), 1719–1733.
- JIN, D., WU, M., LI, B., BUCKER, B., KEIL, P., ZHANG, S., LI, J., KANG, D., LIU, J., DONG, J., DENG, X. W., IRISH, V. & WEI, N. (2018). The COP9 signalosome regulates seed germination by facilitating protein degradation of RGL2 and ABI5. *PLoS Genetics* **14**(2), e1007237.
- *JISHA, K. C. & PUTHUR, J. T. (2016a). Seed priming with BABA (β -amino butyric acid): a cost-effective method of abiotic stress tolerance in *Vigna radiata* (L.) Wilczek. *Protoplasma* **253**(2), 277–289.
- *JISHA, K. C. & PUTHUR, J. T. (2016b). Seed priming with beta-amino butyric acid improves abiotic stress tolerance in rice seedlings. *Rice Science* **23**(5), 242–254.
- *JOSHI, A., KAUR, S., DHARAMVIR, K., NAYYAR, H. & VERMA, G. (2018). Multi-walled carbon nanotubes applied through seed-priming influence early germination, root hair, growth and yield of bread wheat (*Triticum aestivum* L.). *Journal of the Science of Food and Agriculture* **98**(8), 3148–3160.
- *JUNG, H., LEE, H. N., MARSHALL, R. S., LOMAX, A. W., YOON, M. J., KIM, J., KIM, J. H., VIERSTRA, R. D. & CHUNG, T. (2020). *Arabidopsis* cargo receptor NBR1 mediates selective autophagy of defective proteins. *Journal of Experimental Botany* **71**(1), 73–89.
- *KARALIJA, E. & SELOVIĆ, A. (2018). The effect of hydro and proline seed priming on growth, proline and sugar content, and antioxidant activity of maize under cadmium stress. *Environmental Science and Pollution Research* **25**(33), 33370–33380.
- *KASOTE, D. M., LEE, J. H., JAYAPRAKASHA, G. K. & PATIL, B. S. (2019). Seed priming with iron oxide nanoparticles modulate antioxidant potential and defense-linked hormones in watermelon seedlings. *ACS Sustainable Chemistry & Engineering* **7**(5), 5142–5151.
- *KAUR, H., SIRHINDI, G., BHARDWAJ, R., ALYEMENI, M. N., SIDDIQUE, K. H. & AHMAD, P. (2018). 28-homobrassinolide regulates antioxidant enzyme activities and gene expression in response to salt- and temperature-induced oxidative stress in *Brassica juncea*. *Scientific Reports* **8**(1), 1–13.
- *KAYA, C., ASHRAF, M. & SÖNMEZ, O. (2015). Promotive effect of exogenously applied thiourea on key physiological parameters and oxidative defense mechanism in salt-stressed *Zea mays* L. plants. *Turkish Journal of Botany* **39**(5), 786–795.
- KERCHEV, P., VAN DER MEER, T., SUJEETH, N., VERLEE, A., STEVENS, C. V., VAN BREUSEGEM, F. & GECHEV, T. (2019). Molecular priming as an approach to induce tolerance against abiotic and oxidative stresses in crop plants. *Biotechnology Advances* **40**, 107503.
- *KHALIQ, A., ASLAM, F., MATLOOB, A., HUSSAIN, S., GENG, M., WAHID, A. & UR REHMAN, H. (2015). Seed priming with selenium: consequences for emergence, seedling growth, and biochemical attributes of rice. *Biological Trace Element Research* **166**(2), 236–244.
- *KISHIMOTO, I., ARIGA, I., ITABASHI, Y. & MIKAMI, K. (2019). Heat-stress memory is responsible for acquired thermotolerance in *Bangia fuscopurpurea*. *Journal of Phycolgy* **55**(5), 971–975.
- *KLEINMANN, J. A., SCHATLOWSKI, N., HECKMANN, D. & SCHUBERT, D. (2017). BLISTER regulates polycomb-target genes, represses stress-regulated genes and promotes stress responses in *Arabidopsis thaliana*. *Frontiers in Plant Science* **8**, 1530.
- *KOŁODZIEJCZYK, I., DZITKO, K., SZEWCZYK, R. & POSMYK, M. M. (2016). Exogenous melatonin improves corn (*Zea mays* L.) embryo proteome in seeds subjected to chilling stress. *Journal of Plant Physiology* **193**, 47–56.
- KORNBERG, R. D. (1974). Chromatin structure: a repeating unit of histones and DNA. *Science* **184**(4139), 868–871.
- KOWALCZYK, J., PALUSINSKA, M., WROBLEWSKA-SWINIARSKA, A., PIETRAS, Z., SZEWC, L., DOLATA, J., JARMOŁOWSKI, A. & SWIEZEWSKI, S. (2017). Alternative polyadenylation of the sense transcript controls antisense transcription of DELAY OF GERMINATION 1 in *Arabidopsis*. *Molecular Plant* **10**(10), 1349–1352.
- KUBALA, S., GARNCZARSKA, M., WOJTYLA, L., CLIPPE, A., KOSMALA, A., ZMIENKO, A., LUTTS, S. & QUINET, M. (2015). Deciphering priming-induced improvement of rapeseed (*Brassica napus* L.) germination through an integrated transcriptomic and proteomic approach. *Plant Science* **231**, 94–113.
- KUDLA, J., BATISTIC, O. & HASHIMOTO, K. (2010). Calcium signals: the lead currency of plant information processing. *Plant Cell* **22**(3), 541–563.
- KUMAR, S. V. & WIGGE, P. A. (2010). H2A.Z-containing nucleosomes mediate the thermosensory response in *Arabidopsis*. *Cell* **140**(1), 136–147.
- *LAMELAS, L., VALLEDOR, L., ESCANDÓN, M., PINTO, G., CAÑAL, M. J. & MEJÓN, M. (2020). Integrative analysis of the nuclear proteome in *Pinus radiata* reveals thermopriming coupled to epigenetic regulation. *Journal of Experimental Botany* **71**(6), 2040–2057.
- LAMKE, J., BRZEZINKA, K., ALTMANN, S. & BAURLE, I. (2016a). A hit-and-run heat shock factor governs sustained histone methylation and transcriptional stress memory. *The EMBO Journal* **35**(2), 162–175.
- *LAMKE, J., BRZEZINKA, K. & BÄURLE, I. (2016b). HSF2A2 orchestrates transcriptional dynamics after heat stress in *Arabidopsis thaliana*. *Transcription* **7**(4), 111–114.
- *LAN, W., WANG, W., YU, Z., QIN, Y., LUAN, J. & LI, X. (2016). Enhanced germination of barley (*Hordeum vulgare* L.) using chitoooligosaccharide as an elicitor in seed priming to improve malt quality. *Biotechnology Letters* **38**(11), 1935–1940.
- *LAURA, B., SILVIA, P., FRANCESCA, F., BENEDETTA, S. & CARLA, C. (2018). Epigenetic control of defense genes following MeJA-induced priming in rice (*O. sativa*). *Journal of Plant Physiology* **228**, 166–177.
- LECHOWSKA, K., KUBALA, S., WOJTYLA, L., NOWACZYK, G., QUINET, M., LUTTS, S. & GARNCZARSKA, M. (2019). New insight on water status in germinating *Brassica napus* seeds in relation to priming-improved germination. *International Journal of Molecular Sciences* **20**(3), 540.
- *LEMMENS, E., DELEU, L. J., DE BRIER, N., DE MAN, W. L., DE PROFT, M., PRINSEN, E. & DELCOUR, J. A. (2019). The impact of hydro-priming and osmo-priming on seedling characteristics, plant hormone concentrations, activity of

- selected hydrolytic enzymes, and Cell Wall and Phytate hydrolysis in sprouted wheat (*Triticum aestivum* L.). *ACS Omega* **4**(26), 22089–22100.
- *LEUENDORF, J. E., FRANK, M. & SCHMÜLLING, T. (2020). Acclimation, priming and memory in the response of *Arabidopsis thaliana* seedlings to cold stress. *Scientific Reports* **10**(1), 689.
- LI, P., YANG, H., WANG, L., LIU, H., HUO, H., ZHANG, C., LIU, A., ZHU, A., HU, J., LIN, Y. & LIU, L. (2019a). Physiological and transcriptome analyses reveal short-term responses and formation of memory under drought stress in rice. *Frontiers in Genetics* **10**, 55.
- *LI, B., LIU, Y., FU, J. D., ZHOU, Y. B., ZHENG, W. J., LAN, J. H., JIN, L. G., CHEN, M., MA, Y. Z., XU, Z. S. & MIN, D. H. (2019b). Genome-wide characterization and expression analysis of soybean TGA transcription factors identified a novel TGA gene involved in drought and salt tolerance. *Frontiers in Plant Science* **10**, 549.
- *LI, H., LI, H., LV, Y., WANG, Y., WANG, Z., XIN, C., LIU, S., ZHU, X., SONG, F. & LI, X. (2020a). Salt priming protects photosynthetic electron transport against low-temperature-induced damage in wheat. *Sensors* **20**(1), 62.
- LI, T., FAN, P., YUN, Z., JIANG, G., ZHANG, Z. & JIANG, Y. (2019c). β -aminobutyric acid priming acquisition and defense response of mango fruit to *Colletotrichum gloeosporioides* infection based on quantitative proteomics. *Cells* **8**(9), 1029.
- LI, X., CHEN, T., LI, Y., WANG, Z., CAO, H., CHEN, F., LI, Y., SOPPE, W. J. J., LI, W. & LIU, Y. (2019d). ETR1/RDO3 regulates seed dormancy by relieving the inhibitory effect of the ERF12-TPL complex on DELAY OF GERMINATION1 expression. *Plant Cell* **31**(4), 832–847.
- *LI, Y., BROOKS, M., YEOH-WANG, J., MCCOY, R. M., ROCK, T. M., PASQUINO, A., MOON, C. I., PATRICK, R. M., TANURDZIC, M., RUFFEL, S. & WIDHALM, J. R. (2020b). SDG8-mediated histone methylation and RNA processing function in the response to nitrate signaling. *Plant Physiology* **182**(1), 215–227.
- *LI, Z., GAO, Y., ZHANG, Y., LIN, C., GONG, D., GUAN, Y. & HU, J. (2018). Reactive oxygen species and gibberellin acid mutual induction to regulate tobacco seed germination. *Frontiers in Plant Science* **9**, 1279.
- LI, Z., XU, J., GAO, Y., WANG, C., GUO, G., LUO, Y., HUANG, Y., HU, W., SHETIWI, M. S. & GUAN, Y. (2017). The synergistic priming effect of exogenous salicylic acid and H₂O₂ on chilling tolerance enhancement during maize (*Zea mays* L.) seed germination. *Frontiers in Plant Science* **8**, 1153.
- LING, Y., SERRANO, N., GAO, G., ATIA, M., MOKHTAR, M., WOO, Y. H., BAZIN, J., VELUCHAMY, A., BENHAMED, M., CRESPI, M., GEHRING, C., REDDY, A. S. N. & MAHFOUZ, M. M. (2018). Thermopriming triggers splicing memory in *Arabidopsis*. *Journal of Experimental Botany* **69**(10), 2659–2675.
- LIU, F., ZHANG, H., DING, L., SOPPE, W. & XIANG, Y. (2020). REVERSAL OF RDO5 1, a homolog of rice seed dormancy 4, interacts with bHLH57 and controls ABA biosynthesis and seed dormancy in *Arabidopsis*. *Plant Cell* **32**(6), 1933–1948.
- *LIU, H. C., LÄMKE, J., LIN, S. Y., HUNG, M. J., LIU, K. M., CHARNG, Y. Y. & BÄURLE, I. (2018). Distinct heat shock factors and chromatin modifications mediate the organ-autonomous transcriptional memory of heat stress. *The Plant Journal* **95**(3), 401–413.
- *LIU, J., FENG, L., GU, X., DENG, X., QIU, Q., LI, Q., ZHANG, Y., WANG, M., DENG, Y., WANG, E. & HE, Y. (2019). An H3K27me3 demethylase-HSFA2 regulatory loop orchestrates transgenerational thermomemory in *Arabidopsis*. *Cell Research* **29**(5), 379–390.
- LIU, N. & AVRAMOVA, Z. (2016). Molecular mechanism of the priming by jasmonic acid of specific dehydration stress response genes in *Arabidopsis*. *Epigenetics & Chromatin* **9**, 8.
- LIU, N., FROMM, M. & AVRAMOVA, Z. (2014). H3K27me3 and H3K4me3 chromatin environment at super-induced dehydration stress memory genes of *Arabidopsis thaliana*. *Molecular Plant* **7**(3), 502–513.
- *LIU, N., STASWICK, P. E. & AVRAMOVA, Z. (2016). Memory responses of jasmonic acid-associated *Arabidopsis* genes to a repeated dehydration stress. *Plant, Cell & Environment* **39**(11), 2515–2529.
- *LIU, X., CHALLABATHULA, D., QUAN, W. & BARTELS, D. (2019a). Transcriptional and metabolic changes in the desiccation tolerant plant *Craterostigma plantagineum* during recurrent exposures to dehydration. *Planta* **249**(4), 1017–1035.
- *LIU, X., CHEN, Z., GAO, Y., LIU, Q., ZHOU, W., ZHAO, T., JIANG, W., CUI, X., CUI, J. & WANG, Q. (2019b). Combinative effects of *Azospirillum brasilense* inoculation and chemical priming on germination behavior and seedling growth in aged grass seeds. *PLoS One* **14**(5), e0210453.
- LUGER, K., MADER, A. W., RICHMOND, R. K., SARGENT, D. F. & RICHMOND, T. J. (1997). Crystal structure of the nucleosome core particle at 2.8 Å resolution. *Nature* **389**(6648), 251–260.
- *LV, Y., ZHANG, S., WANG, J. & HU, Y. (2016). Quantitative proteomic analysis of wheat seeds during artificial ageing and priming using the isobaric tandem mass tag labeling. *PLoS One* **11**(9), e0162851.
- *MA, H. Y., ZHAO, D. D., NING, Q. R., WEI, J. P., LI, Y., WANG, M. M., LIU, X. L., JIANG, C. J. & LIANG, Z. W. (2018). A multi-year beneficial effect of seed priming with gibberellic acid-3 (GA3) on plant growth and production in a perennial grass, *Lymus chinensis*. *Scientific Reports* **8**(1), 1–9.
- MA, W., GUAN, X., LI, J., PAN, R., WANG, L., LIU, F., MA, H., ZHU, S., HU, J., RUAN, Y. L., CHEN, X. & ZHANG, T. (2019). Mitochondrial small heat shock protein mediates seed germination via thermal sensing. *Proceedings of the National Academy of Sciences of the United States of America* **116**(10), 4716–4721.
- MACKELPRANG, R. & LEMAUX, P. G. (2020). Genetic engineering and editing of plants: an analysis of new and persisting questions. *Annual Review of Plant Biology* **71**, 659–687.
- *MADSEN, M. D., SVEJCAR, L., RADKE, J. & HULET, A. (2018). Inducing rapid seed germination of native cool season grasses with solid matrix priming and seed extrusion technology. *PLoS One* **13**(10), e0204330.
- *MAHAKHAM, W., SARMAH, A. K., MAENSIRI, S. & THEERAKULPISUT, P. (2017). Nanopriming technology for enhancing germination and starch metabolism of aged rice seeds using phytosynthesized silver nanoparticles. *Scientific Reports* **7**(1), 1–21.
- *MAHESH, H. M., MURALI, M., PAL, M. A. C., MELVIN, P. & SHARADA, M. S. (2017). Salicylic acid seed priming instigates defense mechanism by inducing PR-Proteins in *Solanum melongena* L. upon infection with *Verticillium dahliae* Kleb. *Plant Physiology and Biochemistry* **117**, 12–23.
- *MAŁKOWSKI, E., SITKO, K., SZOPIŃSKI, M., GIEROŃ, Ż., POGRZEBA, M., KALAJI, H. M. & ZIELEŃNIK-RUSINOWSKA, P. (2020). Hormesis in plants: the role of oxidative stress, auxins and photosynthesis in corn treated with Cd or Pb. *International Journal of Molecular Sciences* **21**(6), 2099.
- MARCOS, F. C., SILVEIRA, N. M., MOKOCHINSKI, J. B., SAWAYA, A., MARCHIORI, P. E. R., MACHADO, E. C., SOUZA, G. M., LANDELL, M. G. A. & RIBEIRO, R. V. (2018). Drought tolerance of sugarcane is improved by previous exposure to water deficit. *Journal of Plant Physiology* **223**, 9–18.
- *MASONDO, N. A., KULKARNI, M. G., FINNIE, J. F. & VAN STADEN, J. (2018). Influence of biostimulants-seed-priming on *Ceratothera triloba* germination and seedling growth under low temperatures, low osmotic potential and salinity stress. *Ecotoxicology and Environmental Safety* **147**, 43–48.
- *MASSARO, M., DE PAOLI, E., TOMASI, N., MORGANTE, M., PINTON, R. & ZANIN, L. (2019). Transgenerational response to nitrogen deprivation in *Arabidopsis thaliana*. *International Journal of Molecular Sciences* **20**(22), 5587.
- *MCLOUGHLIN, F., KIM, M., MARSHALL, R. S., VIERSTRA, R. D. & VIERLING, E. (2019). HSP101 interacts with the proteasome and promotes the clearance of ubiquitinated protein aggregates. *Plant Physiology* **180**(4), 1829–1847.
- MEENA, V., KAUSHIK, M., KUMAR, R., SINGH, M., MEENA, B., MEENA, B., MEENA, R. K., KUMAR, U. & KUMAR, S. (2016). Influence of growth regulators on nutrient concentrations, nutrient uptake and quality parameters of cluster bean varieties. *Legume Research* **39**(5), 797–801.
- *MENDANHA, T., ROSENQVIST, E., HYLDGAARD, B. & OTTOSEN, C. O. (2018). Heat priming effects on anthesis heat stress in wheat cultivars (*Triticum aestivum* L.) with contrasting tolerance to heat stress. *Plant Physiology and Biochemistry* **132**, 213–221.
- MENEZES-SILVA, P. E., SANGIARD, L., AVILA, R. T., MORAIS, L. E., MARTINS, S. C. V., NOBRES, P., PATREZE, C. M., FERREIRA, M. A., ARAUJO, W. L., FERNIE, A. R. & DAMATTA, F. M. (2017). Photosynthetic and metabolic acclimation to repeated drought events play key roles in drought tolerance in coffee. *Journal of Experimental Botany* **68**(15), 4309–4322.
- MIAO, C., XIAO, L., HUA, K., ZOU, C., ZHAO, Y., BRESSAN, R. A. & ZHU, J. K. (2018). Mutations in a subfamily of abscisic acid receptor genes promote rice growth and productivity. *Proceedings of the National Academy of Sciences of the United States of America* **115**(23), 6058–6063.
- MITTLER, R. (2017). ROS are good. *Trends in Plant Science* **22**(1), 11–19.
- MOOSE, S. P. & MUMM, R. H. (2008). Molecular plant breeding as the foundation for 21st century crop improvement. *Plant Physiology* **147**(3), 969–977.
- *MOSHYNETS, O. V., BABENKO, L. M., ROGALSKY, S. P., IUNGIN, O. S., FOSTER, J., KOSAKIVSKA, I. V., POTTTERS, G. & SPIERS, A. J. (2019). Priming winter wheat seeds with the bacterial quorum sensing signal N-hexanoyl-L-homoserine lactone (C6-HSL) shows potential to improve plant growth and seed yield. *PLoS One* **14**(2), e0209460.
- *MOSTEK, A., BÖRNER, A. & WEIDNER, S. (2016). Comparative proteomic analysis of β -aminobutyric acid-mediated alleviation of salt stress in barley. *Plant Physiology and Biochemistry* **99**, 150–161.
- *MOULICK, D., GHOSH, D. & SANTRA, S. C. (2016). Evaluation of effectiveness of seed priming with selenium in rice during germination under arsenic stress. *Plant Physiology and Biochemistry* **109**, 571–578.
- MOULICK, D., SANTRA, S. C. & GHOSH, D. (2018a). Effect of selenium induced seed priming on arsenic accumulation in rice plant and subsequent transmission in human food chain. *Ecotoxicology and Environmental Safety* **152**, 67–77.
- MOULICK, D., SANTRA, S. C. & GHOSH, D. (2018b). Rice seed priming with Se: a novel approach to mitigate As induced adverse consequences on growth, yield and As load in brown rice. *Journal of Hazardous Materials* **355**, 187–196.
- MOULICK, D., SANTRA, S. C. & GHOSH, D. (2018c). Seed priming with Se mitigates As-induced phytotoxicity in rice seedlings by enhancing essential micronutrient uptake and translocation and reducing As translocation. *Environmental Science and Pollution Research* **25**(27), 26978–26991.

- *MOULICK, D., SANTRA, S. C. & GHOSH, D. (2017). Seed priming with Se alleviate As induced phytotoxicity during germination and seedling growth by restricting As translocation in rice (*Oryza sativa* L cv IET-4094). *Ecotoxicology and Environmental Safety* **145**, 449–456.
- MUEHE, E. M., WANG, T., KERL, C. F., PLANER-FRIEDRICH, B. & FENDORF, S. (2019). Rice production threatened by coupled stresses of climate and soil arsenic. *Nature Communications* **10**(1), 4985.
- *MURGIA, I., GIACOMETTI, S., BALESTRAZZI, A., PAPARELLA, S., PAGLIANO, C. & MORANDINI, P. A. (2015). Analysis of the transgenerational iron deficiency stress memory in *Arabidopsis thaliana* plants. *Frontiers in Plant Science* **6**, 745.
- NAKABAYASHI, K., OKAMOTO, M., KOSHIBA, T., KAMIYA, Y. & NAMBARA, E. (2005). Genome-wide profiling of stored mRNA in *Arabidopsis thaliana* seed germination: epigenetic and genetic regulation of transcription in seed. *The Plant Journal* **41**(5), 697–709.
- NAKAUNE, M., HANADA, A., YIN, Y.-G., MATSUKURA, C., YAMAGUCHI, S. & EZURA, H. (2012). Molecular and physiological dissection of enhanced seed germination using short-term low-concentration salt seed priming in tomato. *Plant Physiology and Biochemistry* **52**, 28–37.
- NAMRATA, P., CHANDRAKAR, T., PRADHAN, A., SHARMA, G., NISHA, C. & IRFAN, S. (2018). Response of thiourea application on dehydrogenase activity in soil, yield and oil content of niger [*Guizotia abyssinica* (L) Cass.] under rainfed conditions of Bastar plateau zone. *International Journal of Current Microbiology and Applied Sciences* **7**(8), 3890–3897.
- NAWAZ, A., FAROOQ, M., AHMAD, R., BASRA, S. M. A. & LAL, R. (2016). Seed priming improves stand establishment and productivity of no till wheat grown after direct seeded aerobic and transplanted flooded rice. *The European Journal of Agronomy* **76**, 130–137.
- *NAWAZ, F., NAEEM, M., AKRAM, A., ASHRAF, M. Y., AHMAD, K. S., ZULFIQAR, B., SARDAR, H., SHABIR, R. N., MAJEED, S., SHEHZAD, M. A. & ANWAR, I. (2017). Seed priming with KNO₃ mediates biochemical processes to inhibit lead toxicity in maize (*Zea mays* L.). *Journal of the Science of Food and Agriculture* **97**(14), 4780–4789.
- *NEJATZADEH-BARANDOZI, F. (2018). Data on seed priming and seedling growth of Barli 21 tobacco varieties under polyethylene glycol and salinity stress conditions. *Data in Brief* **20**, 454–458.
- NELSON, S. K. & STEBER, C. M. (2018). Gibberellin hormone signal perception: down-regulating DELLA repressors of plant growth and development. In *Annual Plant Reviews Online* (eds P. HEDDEN, and S. G. THOMAS), pp. 153–187. Wiley-Blackwell, Hoboken, NJ.
- NISHIMURA, N., TSUCHIYA, W., MORESCO, J. J., HAYASHI, Y., SATOH, K., KAIWA, N., IRISA, T., KINOSHITA, T., SCHROEDER, J. I., YATES, J. R. 3RD, HIRAYAMA, T. & YAMAZAKI, T. (2018). Control of seed dormancy and germination by DOG1-AHG1 PP2C phosphatase complex via binding to heme. *Nature Communications* **9**(1), 2132.
- *NOMAN, A., ALI, Q., MAQSOOD, J., IQBAL, N., JAVED, M. T., RASOOL, N. & NASEEM, J. (2018). Deciphering physio-biochemical, yield, and nutritional quality attributes of water-stressed radish (*Raphanus sativus* L.) plants grown from Zn-Lys primed seeds. *Chemosphere* **195**, 175–189.
- NONOGAKI, H. (2014). Seed dormancy and germination-emerging mechanisms and new hypotheses. *Frontiers in Plant Science* **5**, 233.
- NONOGAKI, H. (2019a). Seed germination and dormancy: the classic story, new puzzles, and evolution. *Journal of Integrative Plant Biology* **61**(5), 541–563.
- NONOGAKI, H. (2019b). The long-standing paradox of seed dormancy unfolded? *Trends in Plant Science* **24**(11), 989–998.
- NOUAIRI, I., JALALI, K., ZRIBI, F., BARHOUMI, F., ZRIBI, K. & MHADHBI, H. (2019). Seed priming with calcium chloride improves the photosynthesis performance of faba bean plants subjected to cadmium stress. *Photosynthetica* **57**(2), 438–445.
- ORACZ, K. & STAWSKA, M. (2016). Cellular recycling of proteins in seed dormancy alleviation and germination. *Frontiers in Plant Science* **7**, 1128.
- PANDEY, P., IRULAPPAN, V., BAGAVATHIANNAN, M. V. & SENTHIL-KUMAR, M. (2017). Impact of combined abiotic and biotic stresses on plant growth and avenues for crop improvement by exploiting physio-morphological traits. *Frontiers in Plant Science* **8**, 537.
- *PANUCCIO, M. R., CHAABANI, S., ROULA, R. & MUSCOLO, A. (2018). Bio-priming mitigates detrimental effects of salinity on maize improving antioxidant defense and preserving photosynthetic efficiency. *Plant Physiology and Biochemistry* **132**, 465–474.
- PARK, J., LIM, C. J., SHEN, M., PARK, H. J., CHA, J. Y., INIESTO, E., RUBIO, V., MENGISTE, T., ZHU, J. K., BRESSAN, R. A., LEE, S. Y., LEE, B. H., JIN, J. B., PARDO, J. M., KIM, W. Y. & YUN, D. J. (2018a). Epigenetic switch from repressive to permissive chromatin in response to cold stress. *Proceedings of the National Academy of Sciences of the United States of America* **115**(23), E5400–E5409.
- *PARK, S., GILMOUR, S. J., GRUMET, R. & THOMAS, M. F. (2018b). CBF-dependent and CBF-independent regulatory pathways contribute to the differences in freezing tolerance and cold-regulated gene expression of two *Arabidopsis* ecotypes locally adapted to sites in Sweden and Italy. *PLoS One* **13**(12), e0207723.
- *PARVEEN, A., LIU, W., HUSSAIN, S., ASGHAR, J., PERVEEN, S. & XIONG, Y. (2019). Silicon priming regulates morpho-physiological growth and oxidative metabolism in maize under drought stress. *Plants (Basel)* **8**(10), 431.
- PAUL, S. & ROYCHOUDHURY, A. (2017). Seed priming with spermine and spermidine regulates the expression of diverse groups of abiotic stress-responsive genes during salinity stress in the seedlings of indica rice varieties. *Plant Gene* **11**, 124–132.
- *PENG, L., WANG, L., ZHANG, Y., DONG, A., SHEN, W. H. & HUANG, Y. (2018). Structural analysis of the *Arabidopsis* AL2-PAL and PRC1 complex provides mechanistic insight into active-to-repressive chromatin state switch. *Journal of Molecular Biology* **430**(21), 4245–4259.
- *PINTÓ-MARIJUAN, M., COTADO, A., FLETA-SORIANO, E. & MUNNÉ-BOSCH, S. (2017). Drought stress memory in the photosynthetic mechanisms of an invasive CAM species, *Aptenia cordifolia*. *Photosynthesis Research* **131**(3), 241–253.
- PISKUREWICZ, U., IWASAKI, M., SUSAKI, D., MEGIES, C., KINOSHITA, T. & LOPEZ-MOLINA, L. (2016). Dormancy-specific imprinting underlies maternal inheritance of seed dormancy in *Arabidopsis thaliana*. *eLife* **5**, e19573.
- PORNIRIWONG, W., ESTAVILLO, G. M., CHAN, K. X., TEE, E. E., GANGULY, D., CRISP, P. A., PHUA, S. Y., ZHAO, C., QIU, J. & PARK, J. (2017). A chloroplast retrograde signal, 3'-phosphoadenosine 5'-phosphate, acts as a secondary messenger in abscisic acid signaling in stomatal closure and germination. *eLife* **6**, e23361.
- *POTOK, M. E., WANG, Y., XU, L., ZHONG, Z., LIU, W., FENG, S., NARANBAATAR, B., RAYATPISHEH, S., WANG, Z., WOHLISCHLEGEL, J. A. & AUSIN, I. (2019). *Arabidopsis* SWR1-associated protein methyl-CpG-binding domain 9 is required for histone H2A. Z deposition. *Nature Communications* **10**(1), 1–14.
- *PREROSTOVA, S., DOBREV, P. I., KRAMNA, B., GAUDINOVA, A., KNIRSCH, V., SPICHAL, L., ZATLOUKAL, M. & VANKOVA, R. (2020). Heat acclimation and inhibition of cytokinin degradation positively affect heat stress tolerance of *Arabidopsis*. *Frontiers in Plant Science* **11**, 87.
- RAHMAN, A., KAWAMURA, Y., MAESHIMA, M., RAHMAN, A. & UEMURA, M. (2020). Plasma membrane aquaporins PIPs act in concert to regulate cold acclimation and freezing tolerance responses in *Arabidopsis thaliana*. *Plant and Cell Physiology* **61**, 787–802.
- RAI, P. K., LEE, S. S., ZHANG, M., TSANG, Y. F. & KIM, K. H. (2019). Heavy metals in food crops: health risks, fate, mechanisms, and management. *Environment International* **125**, 365–385.
- RAJJOU, L., DUVAL, M., GALLARDO, K., CATUSSE, J., BALLY, J., JOB, C. & JOB, D. (2012). Seed germination and vigor. *Annual Review of Plant Biology* **63**, 507–533.
- RAJJOU, L., GALLARDO, K., DEBEAUJON, I., VANDEKERCKHOVE, J., JOB, C. & JOB, D. (2004). The effect of alpha-amanitin on the *Arabidopsis* seed proteome highlights the distinct roles of stored and neosynthesized mRNAs during germination. *Plant Physiology* **134**(4), 1598–1613.
- RAMIREZ-PRADO, J. S., PIQUEREZ, S. J. M., BENDAHMANE, A., HIRT, H., RAYNAUD, C. & BENHAMED, M. (2018). Modify the histone to win the battle: chromatin dynamics in plant-pathogen interactions. *Frontiers in Plant Science* **9**, 355.
- *RASHEED, R., ASHRAF, M. A., KAMRAN, S., IQBAL, M. & HUSSAIN, I. (2018). Menadione sodium bisulphite mediated growth, secondary metabolism, nutrient uptake and oxidative defense in okra (*Abelmoschus esculentus* Moench) under cadmium stress. *Journal of Hazardous Materials* **360**, 604–614.
- RAVINDRAN, P. & KUMAR, P. P. (2019). Regulation of seed germination: the involvement of multiple forces exerted via gibberellic acid signaling. *Molecular Plant* **12**(10), 1416–1417.
- *REHMAN, A., FAROOQ, M., NAVEED, M., NAWAZ, A. & SHAHZAD, B. (2018). Seed priming of Zn with endophytic bacteria improves the productivity and grain biofortification of bread wheat. *The European Journal of Agronomy* **94**, 98–107.
- *REHMAN, H., IQBAL, H., BASRA, S. M., AFZAL, I., FAROOQ, M., WAKEEL, A. & NING, W. A. N. G. (2015a). Seed priming improves early seedling vigor, growth and productivity of spring maize. *Journal of Integrative Agriculture* **14**(9), 1745–1754.
- *REHMAN, H., KAMRAN, M., BASRA, S. M. A., AFZAL, I. & FAROOQ, M. (2015b). Influence of seed priming on performance and water productivity of direct seeded rice in alternating wetting and drying. *Rice Science* **22**(4), 189–196.
- *REIS, S., PAVIA, I., CARVALHO, A., MOUTINHO-PEREIRA, J., CORREIA, C. & LIMA-BRITO, J. (2018). Seed priming with iron and zinc in bread wheat: effects in germination, mitosis and grain yield. *Protoplasma* **255**(4), 1179–1194.
- *RI, P., CHOE, S. & JANG, Y. (2019). Study on laser pre-sowing treatment of rice seeds by free-falling transport method. *Information Processing in Agriculture* **6**(4), 515–521.
- *RIZWAN, M., ALI, S., ALI, B., ADREES, M., ARSHAD, M., HUSSAIN, A., UR REHMAN, M. Z. & WARIS, A. A. (2019). Zinc and iron oxide nanoparticles improved the plant growth and reduced the oxidative stress and cadmium concentration in wheat. *Chemosphere* **214**, 269–277.
- SALAH, S. M., YAJING, G., DONGDONG, C., JIE, L., AAMIR, N., QIJUAN, H., WEIMIN, H., MINGYU, N. & JIN, H. (2015). Seed priming with polyethylene glycol regulating the physiological and molecular mechanism in rice (*Oryza sativa* L.) under nano-ZnO stress. *Scientific Reports* **5**, 14278.
- *SAMOTA, M. K., SASI, M., AWANA, M., YADAV, O. P., AMITHA MITHRA, S. V., TYAGI, A., KUMAR, S. & SINGH, A. (2017). Elicitor-induced biochemical and molecular manifestations to improve drought tolerance in rice (*Oryza sativa* L.) through seed-priming. *Frontiers in Plant Science* **8**, 934.

- SANCHEZ-MONTESINO, R., BOUZA-MORCILLO, L., MARQUEZ, J., GHITA, M., DURAN-NEBREDA, S., GOMEZ, L., HOLDSWORTH, M. J., BASSEL, G. & ONATE-SANCHEZ, L. (2019). A regulatory module controlling GA-mediated endosperm cell expansion is critical for seed germination in *Arabidopsis*. *Molecular Plant* **12**(1), 71–85.
- SANI, E., HERZYK, P., PERRELLA, G., COLOT, V. & AMTMANN, A. (2013). Hyperosmotic priming of *Arabidopsis* seedlings establishes a long-term somatic memory accompanied by specific changes of the epigenome. *Genome Biology* **14**(6), R59.
- SANO, N., RAJJOU, L. & NORTH, H. M. (2020). Lost in translation: physiological roles of stored mRNAs in seed germination. *Plants (Basel)* **9**(3), 347.
- SANO, N., TAKEBAYASHI, Y., TO, A., MHIRI, C., RAJJOU, L. C., NAKAGAMI, H. & KANEKATSU, M. (2019). Shotgun proteomic analysis highlights the roles of long-lived mRNAs and de novo transcribed mRNAs in rice seeds upon imbibition. *Plant and Cell Physiology* **60**(11), 2584–2596.
- SAVVIDES, A., ALI, S., TESTER, M. & FOTOPOULOS, V. (2016). Chemical priming of plants against multiple abiotic stresses: mission possible? *Trends in Plant Science* **21**(4), 329–340.
- SCHWACHTJE, J., WHITCOMB, S. J., FIRMINO, A. A. P., ZUTHER, E., HINCHA, D. K. & KOPKA, J. (2019). Induced, imprinted and primed metabolic responses of plants to changing environments: do plants store and process information by metabolic imprinting and metabolic priming? *Frontiers in Plant Science* **10**, 106.
- *SEDAGHATMEHR, M., MUELLER-ROEBER, B. & BALAZADEH, S. (2016). The plastid metalloprotease FtsH6 and small heat shock protein HSP21 jointly regulate thermomemory in *Arabidopsis*. *Nature Communications* **7**(1), 1–14.
- SEDAGHATMEHR, M., THIRUMALAIKUMAR, V. P., KAMRANFAR, I., MARMAGNE, A., MASCLAUX-DAUBRESSE, C. & BALAZADEH, S. (2019). A regulatory role of autophagy for resetting the memory of heat stress in plants. *Plant, Cell & Environment* **42**(3), 1054–1064.
- *SEN, A. & PUTHUR, J. T. (2020). Influence of different seed priming techniques on oxidative and antioxidative responses during the germination of *Oryza sativa* varieties. *Physiology and Molecular Biology of Plants* **26**, 551–565.
- SERRANO, N., LING, Y., BAHIEDIN, A. & MAHFOUZ, M. M. (2019). Thermopriming reprograms metabolic homeostasis to confer heat tolerance. *Scientific Reports* **9**(1), 181.
- SHARMA, M., BANDAY, Z. Z., SHUKLA, B. N. & LAXMI, A. (2019). Glucose-regulated HLP1 acts as a key molecule in governing thermomemory. *Plant Physiology* **180**(2), 1081–1100.
- *SHETEIWY, M., SHEN, H., XU, J., GUAN, Y., SONG, W. & HU, J. (2017). Seed polyamines metabolism induced by seed priming with spermidine and 5-aminolevulinic acid for chilling tolerance improvement in rice (*Oryza sativa* L.) seedlings. *Environmental and Experimental Botany* **137**, 58–72.
- *SHETEIWY, M. S., AN, J., YIN, M., JIA, X., GUAN, Y., HE, F. & HU, J. (2019). Cold plasma treatment and exogenous salicylic acid priming enhances salinity tolerance of *Oryza sativa* seedlings. *Protoplasma* **256**(1), 79–99.
- *SHETEIWY, M. S., FU, Y., HU, Q., NAWAZ, A., GUAN, Y., LI, Z., HUANG, Y. & HU, J. (2016). Seed priming with polyethylene glycol induces antioxidative defense and metabolic regulation of rice under nano-ZnO stress. *Environmental Science and Pollution Research* **23**(19), 19989–20002.
- *SHETEIWY, M. S., GONG, D., GAO, Y., PAN, R., HU, J. & GUAN, Y. (2018). Priming with methyl jasmonate alleviates polyethylene glycol-induced osmotic stress in rice seeds by regulating the seed metabolic profile. *Environmental and Experimental Botany* **153**, 236–248.
- SHI, J., GAO, H., WANG, H., LAFFITTE, H. R., ARCHIBALD, R. L., YANG, M., HAKIMI, S. M., MO, H. & HABBEN, J. E. (2017). ARGOS 8 variants generated by CRISPR-Cas9 improve maize grain yield under field drought stress conditions. *Plant Biotechnology Journal* **15**(2), 207–216.
- SINGH, A., BANERJEE, A. & ROYCHOUDHURY, A. (2019). Seed priming with calcium compounds abrogate fluoride-induced oxidative stress by upregulating defence pathways in an indica rice variety. *Protoplasma* **257**, 767–782.
- *SINGH, A., GUPTA, R. & PANDEY, R. (2016). Rice seed priming with picomolar rutin enhances rhizospheric *Bacillus subtilis* CIM colonization and plant growth. *PLoS One* **11**(1), e0146013.
- *SINGH, N. B., SINGH, D. & SINGH, A. (2015). Biological seed priming mitigates the effects of water stress in sunflower seedlings. *Physiology and Molecular Biology of Plants* **21**(2), 207–214.
- *SINGH, P., CHATTERJEE, A., BHATIA, V. & PRAKASH, S. (2018). Application of laser biospeckle analysis for assessment of seed priming treatments. *Computers and Electronics in Agriculture* **169**, 105212.
- *SNEIDERIS, L. C., GAVASSI, M. A., CAMPOS, M. L., D'AMICO-DAMIAO, V. & CARVALHO, R. F. (2015). Effects of hormonal priming on seed germination of pigeon pea under cadmium stress. *Anais da Academia Brasileira de Ciências* **87**(3), 1847–1852.
- *SOLIMAN, M., ELKELISH, A., SOUAD, T., ALHAITHLOUL, H. & FAROOQ, M. (2020). Brassinosteroid seed priming with nitrogen supplementation improves salt tolerance in soybean. *Physiology and Molecular Biology of Plants* **26**(3), 501–511.
- SONG, G. C., CHOI, H. K., KIM, Y. S., CHOI, J. S. & RYU, C.-M. (2017). Seed defense biopriming with bacterial cyclodipeptides triggers immunity in cucumber and pepper. *Scientific Reports* **7**(1), 1–15.
- *SOUZA, M. O., PELACANI, C. R., WILLEMS, L. A., CASTRO, R. D., HILHORST, H. W. & LIGTERINK, W. (2016). Effect of osmopriming on germination and initial growth of *Physalis angulata* L. under salt stress and on expression of associated genes. *Anais da Academia Brasileira de Ciências* **88**, 503–516.
- SOYK, S., LEMMON, Z. H., OVED, M., FISHER, J., LIBERATORE, K. L., PARK, S. J., GOREN, A., JIANG, K., RAMOS, A., VAN DER KNAAP, E., VAN ECK, J., ZAMIR, D., ESHED, Y. & LIPPMAN, Z. B. (2017). Bypassing negative epistasis on yield in tomato imposed by a domestication gene. *Cell* **169**(6), 1142–1155 e12.
- SRIVASTAVA, A. K., LU, Y., ZINTA, G., LANG, Z. & ZHU, J. K. (2018). UTR-dependent control of gene expression in plants. *Trends in Plant Science* **23**(3), 248–259.
- SRIVASTAVA, A. K., PASALA, R., MINHAS, P. S. & SUPRASANNA, P. (2016). Plant bioregulators for sustainable agriculture: integrating redox signaling as a possible unifying mechanism. *Advances in Agronomy* **137**, 237–278.
- SRIVASTAVA, A. K., SABLOK, G., HACKENBERG, M., DESHPANDE, U. & SUPRASANNA, P. (2017). Thiourea priming enhances salt tolerance through co-ordinated regulation of microRNAs and hormones in *Brassica juncea*. *Scientific Reports* **7**, 45490.
- SRIVASTAVA, A. K., SRIVASTAVA, S., MISHRA, S., D'SOUZA, S. F. & SUPRASANNA, P. (2014). Identification of redox-regulated components of arsenate (as(V)) tolerance through thiourea supplementation in rice. *Metallomics* **6**(9), 1718–1730.
- STRUHL, K. & SEGAL, E. (2013). Determinants of nucleosome positioning. *Nature Structural & Molecular Biology* **20**(3), 267–273.
- SU, T., LI, X., YANG, M., SHAO, Q., ZHAO, Y., MA, C. & WANG, P. (2020). Autophagy: an intracellular degradation pathway regulating plant survival and stress response. *Frontiers in Plant Science* **11**, 164.
- SUBRAMANYAM, K., DU LAING, G. & VAN DAMME, E. J. (2019). Sodium selenate treatment using a combination of seed priming and foliar spray alleviates salinity stress in rice. *Frontiers in Plant Science* **10**, 116.
- *SUN, M., JIANG, F., ZHOU, R., WEN, J., CUI, S., WANG, W. & WU, Z. (2019). Respiratory burst oxidase homologue-dependent H2O2 is essential during heat stress memory in heat sensitive tomato. *Scientia Horticulturae* **258**, 108777.
- SURA, W., KABZA, M., KARLOWSKI, W. M., BIELUSZKOWSKI, T., KUS-SLOWINSKA, M., PAWELOSZEK, L., SADOWSKI, J. & ZIOLKOWSKI, P. A. (2017). Dual role of the histone variant H2A.Z in transcriptional regulation of stress-response genes. *Plant Cell* **29**(4), 791–807.
- SZABADOS, L. & SAVOURE, A. (2010). Proline: a multifunctional amino acid. *Trends in Plant Science* **15**(2), 89–97.
- *SZAKER, H. M., DARKÓ, É., MEDZHIRADSKY, A. R., JANDA, T., LIU, H. C., CHARNG, Y. Y. & CSORBA, T. (2019). miR824/AGAMOUS-LIKE16 module integrates recurring environmental heat stress changes to fine-tune post-stress development. *Frontiers in Plant Science* **10**, 1454.
- TABASSUM, T., FAROOQ, M., AHMAD, R., ZOHAI, A. & WAHID, A. (2017). Seed priming and transgenerational drought memory improves tolerance against salt stress in bread wheat. *Plant Physiology and Biochemistry* **118**, 362–369.
- TABASSUM, T., FAROOQ, M., AHMAD, R., ZOHAI, A. & SHAHID, M. (2018). Terminal drought and seed priming improves drought tolerance in wheat. *Physiology and Molecular Biology of Plants* **24**(5), 845–856.
- *THAKUR, A., SHARMA, K. D., SIDDIQUE, K. H. & NAYYAR, H. (2020). Cold priming the chickpea seeds imparts reproductive cold tolerance by reprogramming the turnover of carbohydrates, osmo-protectants and redox components in leaves. *Scientia Horticulturae* **261**, 108929.
- *THOMAS, D. T. & PUTHUR, J. T. (2019). Amplification of abiotic stress tolerance potential in rice seedlings with a low dose of UV-B seed priming. *Functional Plant Biology* **46**(5), 455–466.
- TIAN, L., ZHANG, Y., KANG, E., MA, H., ZHAO, H., YUAN, M., ZHU, L. & FU, Y. (2019). Basic-leucine zipper 17 and Hmg-CoA reductase degradation 3A are involved in salt acclimation memory in *Arabidopsis*. *Journal of Integrative Plant Biology* **61**(10), 1062–1084.
- *TOMBESI, S., FRIONI, T., PONI, S. & PALLIOTTI, A. (2018). Effect of water stress “memory” on plant behavior during subsequent drought stress. *Environmental and Experimental Botany* **150**, 106–114.
- TONG, M., LEE, K., EZER, D., CORTIJO, S., JUNG, J., CHAROENSANAWAN, V., BOX, M. S., JAEGER, K. E., TAKAHASHI, N., MAS, P., WIGGE, P. A. & SEO, P. J. (2020). The evening complex establishes repressive chromatin domains via H2A.Z deposition. *Plant Physiology* **182**(1), 612–625.
- *TORRES, E. S. & DEAL, R. B. (2019). The histone variant H2A.Z and chromatin remodeler BRAHMA act coordinately and antagonistically to regulate transcription and nucleosome dynamics in *Arabidopsis*. *The Plant Journal* **99**(1), 144–162.
- TUAN, P. A., KUMAR, R., REHAL, P. K., TOORA, P. K. & AYLEE, B. T. (2018). Molecular mechanisms underlying abscisic acid/gibberellin balance in the control of seed dormancy and germination in cereals. *Frontiers in Plant Science* **9**, 668.
- VALIVAND, M., AMOOGHAIE, R. & AHADI, A. (2019). Seed priming with H2S and Ca2+ trigger signal memory that induces cross-adaptation against nickel stress in zucchini seedlings. *Plant Physiology and Biochemistry* **143**, 286–298.
- VAN BUER, J., CVETKOVIC, J. & BAIER, M. (2016). Cold regulation of plastid ascorbate peroxidases serves as a priming hub controlling ROS signaling in *Arabidopsis thaliana*. *BMC Plant Biology* **16**(1), 163.
- *VAN BUER, J., PRESCHER, A. & BAIER, M. (2019). Cold-priming of chloroplast ROS signalling is developmentally regulated and is locally controlled at the thylakoid membrane. *Scientific Reports* **9**(1), 1–14.

- *VAN DOOREN, T. J., SILVEIRA, A. B., GILBAULT, E., JIMÉNEZ-GÓMEZ, J. M., MARTIN, A., BACH, L., TSNÉ, S., QUADRANA, L., LOUDET, O. & COLOT, V. (2020). Mild drought in the vegetative stage induces phenotypic, gene expression, and DNA methylation plasticity in *Arabidopsis* but no transgenerational effects. *Journal of Experimental Botany* **71**, 3588–3602.
- VENTURA, L., DONA, M., MACOVEI, A., CARBONERA, D., BUTTAFAVA, A., MONDONI, A., ROSSI, G. & BALESTRAZZI, A. (2012). Understanding the molecular pathways associated with seed vigor. *Plant Physiology and Biochemistry* **60**, 196–206.
- VIRLOUVET, L., AVENSON, T. J., DU, Q., ZHANG, C., LIU, N., FROMM, M., AVRAMOVA, Z. & RUSSO, S. E. (2018). Dehydration stress memory: gene networks linked to physiological responses during repeated stresses of *Zea mays*. *Frontiers in Plant Science* **9**, 1058.
- VISHAL, B. & KUMAR, P. P. (2018). Regulation of seed germination and abiotic stresses by gibberellins and abscisic acid. *Frontiers in Plant Science* **9**, 838.
- VYSE, K., FAIVRE, L., ROMICH, M., PAGTER, M., SCHUBERT, D., HINCHA, D. K. & ZUTHER, E. (2020). Transcriptional and post-transcriptional regulation and transcriptional memory of chromatin regulators in response to low temperature. *Frontiers in Plant Science* **11**, 39.
- WANG, H., ZHANG, Y., XIAO, N., ZHANG, G., WANG, F., CHEN, X. & FANG, R. (2020a). Rice GERMIN-LIKE PROTEIN 2-1 functions in seed dormancy under the control of abscisic acid and gibberellic acid signaling pathways. *Plant Physiology* **183**(3), 1157–1170.
- WANG, W., CHEN, Q., HUSSAIN, S., MEI, J., DONG, H., PENG, S., HUANG, J., CUI, K. & NIE, L. (2016a). Pre-sowing seed treatments in direct-seeded early rice: consequences for emergence, seedling growth and associated metabolic events under chilling stress. *Scientific Reports* **6**, 19637.
- WANG, W., PENG, S., CHEN, Q., MEI, J., DONG, H. & NIE, L. (2016b). Effects of pre-sowing seed treatments on establishment of dry direct-seeded early rice under chilling stress. *AoB Plants* **8**, plw074.
- WANG, W., WANG, X., ZHANG, J., HUANG, M., CAI, J., ZHOU, Q., DAI, T. & JIANG, D. (2020b). Salicylic acid and cold priming induce late-spring freezing tolerance by maintaining cellular redox homeostasis and protecting photosynthetic apparatus in wheat. *Plant Growth Regulation* **90**(1), 109–121.
- WEITBRECHT, K., MÜLLER, K. & LEUBNER-METZGER, G. (2011). First off the mark: early seed germination. *Journal of Experimental Botany* **62**(10), 3289–3309.
- *WIBOWO, A., BECKER, C., MARCONI, G., DURR, J., PRICE, J., HAGMANN, J., PAPAREDDY, R., PUTRA, H., KAGEYAMA, J., BECKER, J. & WEIGEL, D. (2016). Hyperosmotic stress memory in *Arabidopsis* is mediated by distinct epigenetically labile sites in the genome and is restricted in the male germline by DNA glycosylase activity. *eLife* **5**, 13546.
- *WU, L., HUO, W., YAO, D. & LI, M. (2019). Effects of solid matrix priming (SMP) and salt stress on broccoli and cauliflower seed germination and early seedling growth. *Scientia Horticulturae* **255**, 161–168.
- XIANG, Y., SONG, B., NEE, G., KRAMER, K., FINKEMEIER, I. & SOPPE, W. J. (2016). Sequence polymorphisms at the REDUCED DORMANCY5 pseudophosphatase underlie natural variation in *Arabidopsis* dormancy. *Plant Physiology* **171**(4), 2659–2670.
- *XIONG, J. L., LI, J., WANG, H. C., ZHANG, C. L. & NAEEM, M. S. (2018). Fullerol improves seed germination, biomass accumulation, photosynthesis and antioxidant system in *Brassica napus* L. under water stress. *Plant Physiology and Biochemistry* **129**, 130–140.
- YANG, L., JIANG, Z., LIU, S. & LIN, R. (2020a). Interplay between REVEILLE1 and RGA-LIKE2 regulates seed dormancy and germination in *Arabidopsis*. *New Phytologist* **225**(4), 1593–1605.
- YANG, L., JIANG, Z., JING, Y. & LIN, R. (2020b). PIF1 and RVE1 form a transcriptional feedback loop to control light-mediated seed germination in *Arabidopsis*. *Journal of Integrative Plant Biology* **62**, 1372–1384.
- YANG, R., HONG, Y., REN, Z., TANG, K., ZHANG, H., ZHU, J. K. & ZHAO, C. (2019). A role for PICKLE in the regulation of cold and salt stress tolerance in *Arabidopsis*. *Frontiers in Plant Science* **10**, 900.
- YENTUR, S. & LEOPOLD, A. C. (1976). Respiratory transition during seed germination. *Plant Physiology* **57**(2), 274–276.
- YU, Y., GUO, G., LV, D., HU, Y., LI, J., LI, X. & YAN, Y. (2014). Transcriptome analysis during seed germination of elite Chinese bread wheat cultivar Jimai 20. *BMC Plant Biology* **14**, 20.
- ZANDALINAS, S. I., FRITSCHI, F. B. & MITTLER, R. (2020). Signal transduction networks during stress combination. *Journal of Experimental Botany* **71**(5), 1734–1741.
- *ZANGANEH, R., JAMEI, R. & RAHMANI, F. (2018). Impacts of seed priming with salicylic acid and sodium hydrosulfide on possible metabolic pathway of two amino acids in maize plant under lead stress. *Molecular Biology Research Communications* **7**(2), 83.
- ZENG, Z., ZHANG, W., MARAND, A. P., ZHU, B., BUELL, C. R. & JIANG, J. (2019). Cold stress induces enhanced chromatin accessibility and bivalent histone modifications H3K4me3 and H3K27me3 of active genes in potato. *Genome Biology* **20**(1), 123.
- *ZHANG, C., PENG, X., GUO, X., TANG, G., SUN, F., LIU, S. & XI, Y. (2018a). Transcriptional and physiological data reveal the dehydration memory behavior in switchgrass (*Panicum virgatum* L.). *Biotechnology for Biofuels* **11**(1), 91.
- ZHANG, F., YU, J., JOHNSTON, C. R., WANG, Y., ZHU, K., LU, F., ZHANG, Z. & ZOU, J. (2015). Seed priming with polyethylene glycol induces physiological changes in sorghum (*Sorghum bicolor* L. Moench) seedlings under suboptimal soil moisture environments. *PLoS One* **10**(10), e0140620.
- ZHANG, H., LI, Y. & ZHU, J. K. (2018b). Developing naturally stress-resistant crops for a sustainable agriculture. *Nature Plants* **4**(12), 989–996.
- *ZHANG, X., MÉNARD, R., LI, Y., CORUZZI, G. M., HEITZ, T., SHEN, W. H. & BERR, A. (2020). *Arabidopsis* SDG8 potentiates the sustainable transcriptional induction of the pathogenesis-related genes PR1 and PR2 during plant defense response. *Frontiers in Plant Science* **11**, 277.
- *ZHANG, X., WANG, X., ZHUANG, L., GAO, Y. & HUANG, B. (2019). Abscisic acid mediation of drought priming-enhanced heat tolerance in tall fescue (*Festuca arundinacea*) and *Arabidopsis*. *Physiologia Plantarum* **167**(4), 488–501.
- *ZHAO, Y., HU, M., GAO, Z., CHEN, X. & HUANG, D. (2018). Biological mechanisms of a novel hydro-electro hybrid priming recovers potential vigor of onion seeds. *Environmental and Experimental Botany* **150**, 260–271.
- ZHOU, J., XIN, X., HE, Y., CHEN, H., LI, Q., TANG, X., ZHONG, Z., DENG, K., ZHENG, X., ARHER, S. A., CAI, G., QI, Y. & ZHANG, Y. (2019). Multiplex QTL editing of grain-related genes improves yield in elite rice varieties. *Plant Cell Reports* **38**(4), 475–485.
- *ZHOU, R., YU, X., LI, X., DOS SANTOS, T. M., ROSENQVIST, E. & OTTOSEN, C. O. (2020). Combined high light and heat stress induced complex response in tomato with better leaf cooling after heat priming. *Plant Physiology and Biochemistry* **151**, 1–9.
- ZHU, X., SUN, L., KUPPU, S., HU, R., MISHRA, N., SMITH, J., ESMAEILI, N., HERATH, M., GORE, M. A. & PAYTON, P. (2018). The yield difference between wild-type cotton and transgenic cotton that expresses IPT depends on when water-deficit stress is applied. *Scientific Reports* **8**(1), 1–11.
- ZORB, C., GELFUS, C. M. & DIETZ, K. J. (2019). Salinity and crop yield. *Plant Biology (Stuttgart, Germany)* **21**(Suppl 1), 31–38.
- ZSÖGÖN, A., ČERMÁK, T., NAVES, E. R., NOTINI, M. M., EDEL, K. H., WEINL, S., FRESCHI, L., VOYTAS, D. F., KUDLA, J. & PERES, L. E. P. (2018). De novo domestication of wild tomato using genome editing. *Nature Biotechnology* **36**(12), 1211–1216.
- ZUTHER, E., SCHAARSCHMIDT, S., FISCHER, A., ERBAN, A., PAGTER, M., MUBEEN, U., GIAVALISCO, P., KOPKA, J., SPRENGER, H. & HINCHA, D. K. (2019). Molecular signatures associated with increased freezing tolerance due to low temperature memory in *Arabidopsis*. *Plant, Cell & Environment* **42**(3), 854–873.

X. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Research articles published between 2015 and 2020 reporting the use of seed priming agents.

Table S2. Research publications on stress memory in *Arabidopsis thaliana* and a variety of crops.

Table S3. Distribution of research on seed priming published between 2015 and 2020 according to plant species and country in which the research originated.

Table S4. Distribution of research on somatic stress memory published between 2015 and 2020 according to plant species and country in which the research originated.

(Received 20 May 2020; revised 6 April 2021; accepted 9 April 2021)