

Chapter 2

Drought Stress Memory and Drought Stress Tolerance in Plants: Biochemical and Molecular Basis

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2.1 Introduction

Global warming will not only affect air temperature but also influence the amount and distribution of precipitation possibly leading to more frequent drought spells in the future (Wang et al. 2014a). Drought is one of the major threats to plants, as water deficit affects the plant–water relations at all levels from molecular, cellular, and organ to the whole plant (Li et al. 2014a; Muscolo et al. 2015). Drought depresses plant growth and development, which results in the production of smaller organs, and hampered flower production and grain filling. Following drought, stomata close progressively with a parallel decline in net photosynthesis and water-use efficiency (Farooq et al. 2009a, b). Stomatal conductance is controlled not only by soil water condition, but by a complex interaction of intrinsic and extrinsic factors (Liu et al. 2006). Depending on the availability of soil moisture, activities of the enzymes of carbon assimilation and the enzymes involved in adenosine triphosphate synthesis are decreased (Farooq et al. 2009a, b). One of the major factors responsible for impaired plant growth and productivity under drought stress is the production of reactive oxygen species in organelles including chloroplasts, mitochondria, and peroxisomes (Farooq et al. 2009a, b; Wei et al. 2015). The overproduction of reactive oxygen species (ROS) results in the peroxidation of cellular membrane lipids and degradation of enzyme proteins and nucleic acids (Li et al. 2013).

A number of physiological and biochemical processes at molecular, tissue, organ, and whole-plant levels are involved in drought tolerance mechanism. For instance, the plant water loss is reduced by increasing stomatal resistance, and the water uptake is increased by developing large and deep root systems (Liu et al. 2006). Among plant growth substances, salicylic acid, melatonin and abscisic acid

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were reported to play an important role in drought tolerance. Scavenging of reactive oxygen species by enzymatic and nonenzymatic systems, cell membrane stability, and expression of stress proteins are also vital mechanisms of drought tolerance (Farooq et al. 2009a, b). Drought stress effects can be managed by production of most appropriate plant genotypes, seed priming, plant growth regulators, use of osmoprotectants, and some other strategies.

2.2 Priming, Stress Memory, and Drought Tolerance

The increased climatic variability and more frequent episodes of extreme conditions also result in plants being exposed to not only one single drought event but also multiple abiotic stresses at different periods. Although the abiotic stresses occurring at different stages result in a higher risk of injury, earlier stress events may prime the plant to protect it against later stresses. A large body of evidence has shown that a previous exposure to different types of stress can affect the subsequent responses and eventually prepare the plants to more quickly or actively respond to future stresses (Ramírez et al. 2015; Walter et al. 2011; Li et al. 2014a). The trigger for stress tolerance (the early moderate stress event) is referred to “priming.” Priming has been known as a potential way to enhance the stress tolerance of plant (Bruce et al. 2007), which is related to stress memory. Stress memory involves multiple modifications at physiological, proteomic, transcriptional levels and epigenetic mechanisms in plants (Kinoshita and Seki 2014), which can occur in any periods of the life cycle, including seed germination, vegetative growth, and reproductive growth (Ramírez et al. 2015; Munné-Bosch and Alegre 2013). Recently, many studies have focused on exploring the mechanisms of the priming effects and stress memory in the formation of drought tolerance in different plant species (Ramírez et al. 2015; Walter et al. 2011; Wang et al. 2014c, 2015; Shukla et al. 2015; Li et al. 2015b). In this chapter, we summarized recent advancements in physiological, biochemical and molecular and cellular research related to drought tolerance formation in plants. The mechanisms of drought stress memory and the possible priming-induced cross-tolerance to other abiotic stresses are discussed.

2.2.1 Seed Priming

Seed priming is different from plant priming, although both could result in increased stress tolerance. As stated above, priming is a process where a first exposure to a moderate stress enables plants to be more tolerant to subsequent stress events (Conrath 2011). Seed priming is pre-sowing partial hydration of seeds without allowing radicle emergence to improve germination rate and stress tolerance of germinating seeds, and even to improve the seedling establishment. A hypothetical model has been proposed to illustrating the cellular physiology of priming-induced

Table 2.1 Various seed priming methods adopted for developing drought tolerance in plants

Plant species	Priming methods	References
<i>Cicer arietinum</i>	Hydropriming	Kaur et al. (2002)
<i>Cicer arietinum</i>	Osmopriming with mannitol	Elkoca et al. (2007)
<i>Saccharum officinarum</i>	Halopriming with NaCl	Pandita et al. (2010)
<i>Oryza sativa</i>	Hydropriming, Osmopriming with KNO ₃	Basra et al. (2005)
<i>Oryza sativa</i>	Osmopriming with KCl and CaCl ₂	Farooq et al. (2010)
<i>Oryza sativa</i>	Osmopriming with PEG	Yuan-Yuan et al. (2010)
<i>Spinacea oleracea</i>	Osmopriming with PEG	Chen and Arora (2011)
<i>Spinacea oleracea</i>	Osmopriming	Chen et al. (2013)
<i>Lesquerella fendleri</i>	Osmopriming with PEG	Windauer et al. (2007)
<i>Zea mays</i> and <i>Spinacea oleracea</i>	Osmopriming with PEG	Chen et al. (2012)
<i>Zea mays</i>	Ascorbic Acid, Salicylic Acid, and Hydrogen Peroxide	Ahmad et al. (2015)
<i>Triticum aestivum</i>	Hydropriming	Meena et al. (2014)
<i>Triticum aestivum</i>	Chemical priming (KH ₂ PO ₄ , H ₂ O ₂ , NO)	Giri and Schillinger (2003)
<i>Bromus</i>	Osmopriming with PEG	Tavili et al. (2011)

stress tolerance, which involves two strategies (Chen and Arora 2012). First, seed priming sets in motion activities involved in seed germination, such as respiration, endosperm weakening and seed reserve (starch) degradation, which facilitate the transition of quiescent dry seeds into germinating state and increase the germination potential (Chen and Arora 2012; Li et al. 2013). Second, imposing abiotic stress to germinating seeds to stimulate stress responses (e.g., activation of ROS scavenging systems and accumulation of stress response proteins), hence inducing cross-tolerance (Chen and Arora 2012).

Various priming methods, including hydropriming, osmopriming, chemical priming, hormonal priming, biological priming, redox priming, and solid matrix priming, have been reported to improve seed germination under osmotic stress and promote the drought tolerance in seedlings (Jisha et al. 2012) (Table 2.1). Hydropriming significantly increases the root and shoot length compared with seedlings obtained from non-primed seeds in drought condition (Kaur et al. 2002). In addition, hydropriming has been used as an easy seed invigoration treatment for maize inbred lines under salinity and drought stress (Janmohammadi et al. 2008). Also, osmopriming with PEG can improve the germination of *Bromus* seeds under drought (Tavili et al. 2011). Comparing to hydropriming, priming with PEG has a better effect on seed germination and seedling growth under drought (Yuan-Yuan et al. 2010). In *Agropyron elongatum*, osmopriming with gibberellin (GA) and abscisic acid (ABA) increased CAT and SOD activities, and enhanced the drought tolerance, in relation to unprimed seeds (Eisvand et al. 2010). In addition, seed priming with triazoles affects turf grass growth and response to drought (Shahrokhi et al. 2011).

2.2.2 Plant Acclimation to Drought

Plant priming, which differs from seed priming, is a process that an earlier exposure to biotic stress enhances plants' tolerance to later abiotic or biotic insult (Chen and Arora 2012; Bruce et al. 2007). The similar process, with abiotic stress as the first exposure instead of biotic stress, is considered as acclimation or hardening (Chen et al. 2012; Bruce et al. 2007). However, in some studies, the earlier exposure to abiotic stress that favors the tolerance to later stress is also called plant priming (Li et al. 2014a, 2015b; Wang et al. 2014b, c). Plant priming induces stress memory, which is mediated by protein, transcription factors and the modifications in epigenetics, and this process is always accompanied by compromised plant growth (Chinnusamy and Zhu 2009; Chen and Arora 2012). The plants can acclimate to the drought event by modifications at morphological, metabolic, subcellular, proteomic and transcriptional levels, and even changes in microRNA expression.

2.2.2.1 Stomatal Regulation and Drought Acclimation

Morphological changes are consequence of a wide spectrum of physiological and molecular programs evolved to acclimate to drought conditions (Valdes et al. 2013). The morphological acclimation strategy usually includes smaller leaf area to decrease the transpiration and larger root system to enhance the water uptake capacity, and both are related to water-use efficiency (WUE). Some studies reported that WUE increases at moderate drought when water consumption dropped while photosynthetic rate remained high, that is, moderate drought often results in higher WUE (Varga et al. 2015; Peuke et al. 2006). It has also been documented that water supplies well below the optimum level led to a reduction in WUE as a consequence of stress effects, while above-optimum water supplies would result in the opposite tendency (Varga et al. 2013). Most recently, Varga et al. (2015) suggested that WUE decreased in some cultivars even in response to water deficit stress during early growth stages, while it dropped significantly when water was withheld at heading or grain filling except in the case of early maturing cultivars in wheat.

Stomatal regulation is one of the key mechanisms allowing plants to optimize CO₂ assimilation versus evaporative water loss (Tombesi et al. 2015). The stomatal density (SD) has been closely related to WUE and drought tolerance (Hepworth et al. 2015). Modification of SD in response to drought is contingent on the severity of drought, which varies among plant species (Hamanishi et al. 2012). For instance, drought decreased the stomatal numbers in wheat (Quarrie and Jones 1977), *Squash cotyledons* (Sakurai et al. 1986), and *Phytolacca dioica* (Silva et al. 2009). However, increased stomatal density was observed in grass with moderate drought stress (Xu and Zhou 2008). Plants with lower SD have significantly reduced levels of transpiration, and were able to grow continuously under drought condition (Doheny-Adams et al. 2012). The plants with reduced SD were also found to have significantly higher WUE (Franks et al. 2015). With *Arabidopsis thaliana* plant lines which have stomatal

densities ranging from c. 50 to 250 % of normal levels, Hepworth et al. (2015) found that plants with less than half of their normal complement of stomata, and correspondingly reduced levels of transpiration, conserve soil moisture and are able to avoid drought stress but show little or no reduction in shoot nitrogen concentrations especially when water availability is restricted. By contrast, plants with over twice the normal density of stomata have a greater capacity for nitrogen uptake, except when water supply is limited (Hepworth et al. 2015). However, the stomatal development in response to drought is complicated and influenced by the expressions of many genes, such as *STOMAGEN*, *ERECTA (ER)*, *STOMATA DENSITY AND DISTRIBUTION 1 (SDD1)*, and *FAMA* (Hamanishi et al. 2012). More factors are probably involved in this process (Hamanishi et al. 2012); further exploration of these players in the stomatal development pathway would provide an increased insight into the long-term modulation of stomatal morphology in response to drought stress.

2.2.2.2 Metabolic Responses and Drought Tolerance

Plants reprogramming their metabolic pathways to acclimate to drought stress could result in changes in the upstream production and downstream utilization of metabolites (Baerenfaller et al. 2012; Suseela et al. 2015). Recent extensive and elegant metabolomics approaches have revealed that stressed plants invest in the production of important metabolites such as amino acids, organic acids, phenolic acids, polyamines, and lipids that partially mitigate stress by acting as osmoregulators, antioxidants, and defense compounds (Rivas-Ubach et al. 2012). Drought stress can also alter the content and composition of leaf proteins leading to changes in the proportion of structural and soluble proteins (Suseela et al. 2015). In oat (*Avena sativa* L.), the key processes involved in drought tolerance have been defined by metabolomic approach (Sanchez-Martin et al. 2015). During a time course of increasing water deficit, metabolites from leaf samples were profiled using direct infusion-electrospray mass spectroscopy (DI-ESI-MS) and high-performance liquid chromatography (HPLC) ESI-MS/MS and the data were analyzed using principal component analysis (PCA) and discriminant function analysis (DFA). The involvement of metabolite pathways was confirmed through targeted assays of key metabolites and physiological experiments in oat (Sanchez-Martin et al. 2015). This metabolomics experiment highlights a drought tolerance mechanism based on salicylate signaling pathways and the changes in carbon, antioxidant, and photooxidative metabolism. To identify the metabolic traits related to drought tolerance, a metabolomics and phenotypic study with four contrasting lentil accessions was carried out during germination and early growth stages (Muscolo et al. 2015). It was found that metabolic differences in the stress tolerance of the different genotypes were related to a reduction in the levels of tricarboxylic acid (TCA) cycle intermediates. In addition, ornithine and asparagine were identified as drought stress-specific metabolite indicators. In wheat, some metabolic parameters were also identified as good indicators of drought stress tolerance, such as the total protein content, glutamine synthetase (GS) enzyme activities, and the presence of GS isoforms.

Recently, the ^1H Nuclear magnetic resonance (NMR) spectroscopy is applied to monitor and quantify the degree of metabolic impact induced by drought, since NMR can bring high-throughput spectroscopic/structural information on a wide range of metabolites simultaneously with high analytical precision. The main advantage is that it can avoid biases against various classes of compounds (Silvente et al. 2012). The metabolic profiles in two soybean genotypes under short-term drought stress demonstrate critical differences in physiological responses between the genotypes. Metabolic changes in response to drought stress highlight the pools of metabolites that play key roles in the adjustment of metabolism and physiology of the soybean genotypes to response to drought stress (Silvente et al. 2012).

2.2.2.3 Photosynthetic Adaptation to Drought

The increased rate of photorespiration in plant that is observed during the onset of drought stress can be seen as an acclimation process to avoid an over-excitation of PSII under more severe drought conditions (Massacci et al. 2008). In cotton, photosynthetic electron transport is promoted during the onset of drought stress due to a higher efficiency of the open PSII reaction centers (Massacci et al. 2008). The additional energy is used to increase the rate of photorespiration while photosynthesis is kept constant or slightly decreases (Massacci et al. 2008). Chlorophyll fluorescence measurement has been proven as an efficient and reproducible tool for evaluating plant susceptibility index to drought (Su et al. 2015; Mishra et al. 2012). It can be used in selection of drought-tolerant cultivar and comparison of photosynthetic electron transport among cultivars with contrasting drought tolerance. The experiment with different wheat cultivars released in different years documented that the modern and intermediate cultivars had more sensitive stomata to water shortage, but the decreased activity of the PSII reaction center helped avoid damage from photo-inhibition in these cultivars (Guan et al. 2015).

Chlororespiration is a respiratory electron transport chain in the thylakoid membrane of chloroplasts, which interacts with photosynthetic electron transport, involving both the non-photochemical reduction and plastoquinones oxidation with the corresponding consumption of oxygen (Ibáñez et al. 2010). It was found that the chlororespiration and the cyclic electron pathways play important roles in the tolerance to drought, and the different adaptive mechanisms to drought stress were indicated in sun and shade plants. In addition, the nitrate nutrition-induced chloroplast downsizing also significantly affects the mesophyll conductance and photosynthesis of rice in response to drought stress (Li et al. 2012). Recently, the proteomic and enzymatic studies documented that the main regulatory mechanisms for high drought tolerance of apple plants include the maintaining of Calvin cycle function by increasing key enzymes and stabilization of photosynthetic electron transfer, thus enhance net photosynthesis rate (Zhou et al. 2015). In addition, the response of signal regulatory proteins and abiotic stress-responsive proteins to drought also helps plants to cope with drought stress.

2.2.2.4 Mitochondrial Acclimation to Drought

One of the important factors determining the effect of water stress on plant productivity is its impact on mitochondrial respiration in different organs. Although specific rates of respiration are typically lower than the rate of net photosynthesis, the respirations by roots and shoots play key roles in determining the carbon balance and productivity of plants (Atkin and Macherel 2009). Of the CO₂ fixed each day by net photosynthesis in well-watered plants, 30–70 % is released back into atmosphere by the respiration of plants (Atkin et al. 2006; Loveys et al. 2002), and 50–70 % of whole-plant respiration occurs in the leaves (Atkin et al. 2007). The maintenance of mitochondrial respiration can also play several positive roles in helping plants grow and survive, both in normal and water-stress conditions (Atkin and Macherel 2009). Atkin and Macherel (2009) summarized that mitochondria and chloroplasts are closely connected by metabolic and signaling networks, and that, in intact leaves, photosynthesis depends to a large extent on mitochondrial functions. This reliance on mitochondria has the potential to be further enhanced under water-stress conditions. The mitochondria show a high flexibility in electron transfer and energy dissipation, which is very important for optimizing the energy balance in plants under drought stress. Alternative oxidase (AOX) constitutes a non-energy conserving branch of the mitochondrial electron transport chain. AOX activity may be important to avoid reactive oxygen species (ROS) generation by the chain under water stress (Wang and Vanlerberghe 2013). A study compared leaf *AOX1a* transcript and AOX protein amounts in wild-type (WT) *Nicotiana tabacum* plants experiencing mild to severe drought, and found mild to moderate drought resulted in a progressive and modest increase in AOX amount, accompanied by a progressive increased expression of different ROS-scavenging components (Wang and Vanlerberghe 2013). Under these conditions, transgenic plants with suppressed AOX amount, due to an RNA interference construct, were not compromised in their ability to manage ROS load and prevent cellular damage. Under severe drought condition, plants lacking AOX suffered more cellular damage than did WT and, at the most severe stage, were found to down-regulate rather than upregulate the transcript level of several important ROS-scavenging components (Wang and Vanlerberghe 2013). In addition, WT plants could still recover rapidly after rewatering, but the recoverability of AOX knockdown plants was strongly compromised. However, a priority for future studies should be to clarify the ability of AOX affecting the functions of mitochondrion under drought stress.

2.2.2.5 Proteomic Acclimation to Drought

High-throughput methods have facilitated the identifying key regulatory processes, genes, and proteins that provide a theoretical basis for breeding drought-tolerant plant varieties. Proteomics has proven to be a good tool to explore biochemical pathways and the complex response mechanism of plants to drought stress (Zhou et al. 2015). The proteomic study with a drought-tolerant apple (*Malus domestica* Borkh) cultivar suggested that the main regulatory mechanisms for high WUE under

moderate drought stress included the maintaining of Calvin cycle function by increasing the activity of key enzymes, stabilizing photosynthetic electron transfer, and keeping reactive oxygen species at normal level by regulating the photosynthetic electron transfer chain, photorespiration and ROS scavenging capability, thus preventing photoinhibition, reducing ROS production, and enhancing net photosynthesis rate. In addition, studies have indicated that some of the signal regulatory proteins and abiotic stress-responsive proteins also help plants to cope with drought stress (Zhou et al. 2015). Our recent finding showed that prior mild drought priming contributed to the homeostasis of oxidative metabolism and relatively better photosynthesis, and modification of oxidative stress defense, C metabolism and photosynthesis related proteins, hence to less grain yield loss caused by later spring low temperature stress (Fig. 2.1) (Li et al. 2014c).

Drought-inducible proteins are divided into two main groups: abiotic stress tolerance proteins including chaperones, detoxification enzymes, and mRNA-binding proteins; and regulatory proteins such as protein kinases, protein phosphatases, or other signal-related proteins (Ashoub et al. 2013). Different plant organs (e.g., root, stem, and leaf) contain different drought-inducible proteins and show distinct responses to drought (Hao et al. 2015). Differentially expressed proteins (DEPs) in roots, intermediate sections between roots and leaves (ISRL), and leaves in wheat showed significant changes in expression in response to drought stress and recovery. Numerous DEPs associated with cell defense and detoxifications were significantly regulated in roots and ISRLs, while in leaves, DEPs related to photosynthesis showed significant changes in expression. Expression of six Heat shock proteins (HSPs) potentially related to drought tolerance was significantly upregulated under drought conditions, and these proteins were involved in a complex protein–protein interaction network (Hao et al. 2015). Also, in wheat, proteomic analysis showed an increased abundance of proteins related to defense and oxidative stress responses such as GLPs, GST, and SOD, and those related to protein processing such as small HSPs in roots of both genotypes in response to drought stress (Faghani et al. 2014). In common bean, the majority of identified proteins in response to drought stress are classified into functional categories that include energy metabolism, photosynthesis, ATP interconversion, protein synthesis and proteolysis, stress and defense related proteins (Zadraznik

Fig. 2.1 Global presentation on response of winter wheat to the combination of freeze and water stress (drought and waterlogging). The numbers in parentheses indicate the protein spots in Table 2.2. The up- and downregulation of pathways in different stress treatments as compared with the CC were indicated by red and blue triangles, respectively. *APX* ascorbate peroxidase, *AsA* Ascorbic acid, *ATPase* ATP synthase, *CAT* catalase, *CYS* cysteine, *CYSase* cysteine synthase, *Cyt b₆f* cytochrome, *DHA* dehydroascorbate, *DHAR* monodehydroascorbate reductase, *Fd* ferredoxin, *FNR* ferredoxin-NADP⁺ reductase, *Glc-6-P* Glucose-6-phosphate, *GPX* glutathione peroxidase, *GR* glutathione reductase, *GSH* glutathione, *GSSG* oxidized glutathione, *G-3-PD* glyceraldehyde-3-phosphate dehydrogenase, *MDA* monodehydroascorbate, *MDH* malate dehydrogenase, *PC* plastocyanin, *PEP* phosphoenolpyruvate, *PEPC* phosphoenolpyruvate carboxylase, *P-GY* 3-phosphoglycerate, *PQ* plastoquinone, *P₆₈₀* and *P₇₀₀* PSII and PSI reaction center pigments, *Q_A* and *Q_B*, PSII primary and secondary plastoquinone electron acceptors, *RB* Ribulose biphosphate, *RET* respiratory electron transport, *R-1, 5* *BCA* ribulose-1,5-bisphosphate carboxylase activase, *SAM* S-adenosyl-L-methionine, *SAMase* S-adenosyl-L-methionine synthesis, *SOD* superoxide dismutase, *Suc* sucrose, *Triose-P* Triosephosphate, *UDP-Glc* Uridine diphosphate glucose, ¹O₂ singlet oxygen

et al. 2013). In addition to providing new information on the response to water deprivation, the proteomic study offers opportunities to pursue the breeding of wheat with enhanced drought tolerance using identified candidate genetic markers (Hajheidari et al. 2007). The proteomic studies also provide the basic insight needed to further investigate the molecular regulatory mechanism of drought tolerance.

2.2.2.6 Transcriptional Acclimation to Drought

Technological innovations over the past decades have made it possible to measure changes in gene expression (transcript levels) on genome-wide scales (Zhang et al. 2014; Udvardi et al. 2007; Urano et al. 2010). This enables an unprecedented overview of the global molecular changes occurring under drought stress. There are many published reports on transcriptomic variation induced by drought treatments in a variety of plant species (Zhang et al. 2014). In *Medicago*, the plants were subjected to a progressive drought stress over 14 days by withholding of water followed by rewatering to expose the plant to mild, moderate, and severe drought stress before rehydration. Transcriptome analysis of roots and shoots from control, mildly, moderately and severely stressed, and rewatered plants, identified many thousands of genes that were altered in expression in response to drought. Many genes with expression tightly coupled to the plant water potential (i.e., drought intensity), including eight NACs, eight MYBs, six AP2/EREBPs, six bZIPs, five HDs, four bHLHs, and other TFs, were identified suggesting their involvement in *Medicago* drought adaptation responses (Zhang et al. 2014). In chickpea, an oligonucleotide microarray was used for analyzing the transcriptomic profiles of unigenes in leaf and root under drought stress (Wang et al. 2012a), revealing that 4815 differentially expressed unigenes were either ≥ 2 -fold up- or ≤ 0.5 -fold downregulated in at least one of the five time points during drought stress. 2623 and 3969 unigenes were time-dependent differentially expressed in root and leaf, respectively. In this study, 110 pathways in two tissues were found to respond to drought stress. Compared to the control, 88 and 52 unigenes were expressed only in drought-stressed root and leaf, respectively, while nine unigenes were expressed in both the tissues (Wang et al. 2012a). Transcriptome analyses using transgenic Arabidopsis and soybean plants showed that the downstream genes of GmDREB1B;1 included numerous soybean-specific stress-inducible genes that encode an ABA receptor family protein, GmPYL21, and translation-related genes, such as ribosomal proteins, indicating that soybean DREB1/CBF-type transcription factors function in drought stress-responsive gene expression (Kidokoro et al. 2015). Recently, many genes and transcription factors were identified as key players for conferring ABA sensitivity and drought tolerance. In wheat, it was reported that an R2R3 MYB transcription factor, TaPIMP1, mediates drought stresses through regulation of defense- and stress-related genes (Zhang et al. 2012). In *Arabidopsis thaliana*, overexpression of *FTL1/DDF1*, an AP2 transcription factor, enhances tolerance to drought stresses (Kang et al. 2011). In rice, OsbZIP23 is documented as a major player of the bZIP family in rice for conferring ABA-dependent drought and salinity tolerance and has high potential usefulness in genetic improvement of stress tolerance (Xiang et al. 2008).

Table 2.2 A list of studies on the roles of miRNAs in plant tolerance to environmental stresses

miRNAs	Plant species	Environmental stress	References
169	<i>Solanum lycopersicum</i>	Drought	Zhang et al. (2011)
169	<i>Arabidopsis</i>	Drought	Li et al. (2008)
319	<i>Agrostis capillaris</i>	Salinity and drought	Zhou et al. (2013)
394	<i>Arabidopsis</i>	Drought	Ni et al. 2012)
395	<i>Arabidopsis</i>	Salinity and drought	Kim et al. (2010b)
396	<i>Arabidopsis</i>	Salinity and drought	Gao et al. (2010)
398	<i>Arabidopsis</i>	Salinity and drought	Zhou et al. (2007)
402	<i>Arabidopsis</i>	Salinity, drought, and cold	Kim et al. (2010a)
168 and 528	<i>Zea mays</i>	Drought	Wei et al. (2009)

2.2.2.7 microRNAs Involved in Drought Tolerance

MicroRNAs (miRNAs) are an extensive class of endogenous, small RNA molecules that sit at the heart of regulating gene expression in multiple developmental and signaling pathways (Zhang 2015). Recent studies have shown that drought induces aberrant expression of many miRNAs, thus suggesting that miRNAs may be a new target for genetically improving plant tolerance to drought stresses (Table 2.2). miRNA expression response to drought stress is genotype-dependent. For instance, the expression of miR168 and miR396 was induced in *Arabidopsis* (Liu et al. 2008) and tobacco (Frazier et al. 2011), but was inhibited in rice by drought treatment (Zhou et al. 2010). However, some species-specific miRNAs are found in response to drought. In switchgrass, 17 drought-specific miRNAs were identified, of which four were conserved and 13 were switchgrass-specific miRNAs (Xie et al. 2014). In addition, novel species-specific miRNAs (hvu-miRX33, hvu-miRX34, and hvu-miRNA35) were found in barley induced by drought stress (Hackenberg et al. 2015). To identify genome-wide drought-responsive miRNAs in root and leaf, four small RNA libraries from both control and drought treated leaf and root samples were constructed and the small RNA populations were thoroughly sequenced (Eldem et al. 2012). The authors reported that drought significantly induced the aberrant expression of 263 and 368 miRNAs in leaf and root tissues, respectively. In cotton, it was also found that the expression changes of miRNAs are dose- and tissue-dependent under drought stress (Wang et al. 2013a).

Among these drought-responsive miRNAs, miR169 is one of the largest miRNA families that is conserved in all plant species (Zhang 2015). In *Arabidopsis*, miR169 can be inhibited by drought stress, and the drought-repressed miR169 expression was through an ABA-dependent pathway (Li et al. 2008). The target of miR169, nuclear factor Y (NF-Y) subunit A 5 (NFYA5), was strongly induced by drought stress when miR169 was inhibited (Li et al. 2008). Constitutive overexpression of miR169 in transgenic tomato significantly enhanced plant tolerance to drought stress after 7 days of drought treatment (Zhang et al. 2011). Under drought stress, non-transgenic wild-type tomato plants showed clear dehydration symptoms, while the transgenic plants that overexpressed miR169 grew very well. Thus, miR169 should be a promising target for improving plant tolerance to drought stress.

2.2.2.8 Hormonal Regulation

Absciscic Acid

It has long been recognized that the production of abscisic acid (ABA) in drying roots and its transport to the leaves play a key role in regulating plant water status during drought (Zhang and Davies 1990). In addition, ABA was found to be a dominant player in mediating the adaptation of the plant to other abiotic stresses, including drought and low temperature, by improving oxygen scavenging efficiency, increasing sugar accumulation and upregulating the expression of key enzymes (Jiang and Zhang 2001; Liu et al. 2013). In wheat, the involvement of ABA in drought (Ali et al. 1998) and low temperature stress (Lalk and Dörfling 1985) adaptation has been reported. Exogenous application of abscisic acid (ABA) significantly increased the tolerance of wheat seedlings suffering from 5 days of 15 % polyethylene glycol (PEG)-stimulated drought stress, as exemplified by increased shoot lengths and shoot and root dry weights, and decreased contents of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) (Wei et al. 2015). Under drought stress, ABA significantly increased contents of Glutathione (GSH) and ascorbate (ASA) in both leaves and roots. ABA temporally regulated the transcript levels of genes encoding ASA–GSH cycle enzymes. Moreover, these genes exhibited differential expression patterns between the root and leaf organs of ABA-treated wheat seedlings during drought stress. In wheat, the exogenous ABA application during grain filling stage decreased seed weight and slightly reduced seed set and seed number per spike; however, the seedlings from seeds of ABA-treated plants performed better under temperature stress, which is related to higher endogenous ABA level, and increased activities of the antioxidant enzymes (Li et al. 2014b), which can be expected to enhance drought tolerance as well (Fig. 2.2).

Partial root-zone drying (PRD) is a water-saving irrigation strategy, which involves irrigating only part of the root zone, leaving the other part to dry to a pre-determined level before the next irrigation (Wang et al. 2012b; Plauborg et al. 2010; Liu et al. 2005a, 2006). PRD allows the induction of the ABA-based root-to-shoot chemical signaling system to regulate growth and water use and thereby increase WUE (Jacobsen et al. 2009; Liu et al. 2005b; Plauborg et al. 2010). Our results indicated that at mild soil water deficits, stomatal conductance of potato was controlled by root-originated ABA (Topbjerg et al. 2015; Sun et al. 2014, 2015; Liu et al. 2015; Kaminski et al. 2015). As a consequence of photosynthesis rate being less sensitive than stomatal conductance to soil water deficit, photosynthetic water-use efficiency was improved under mild soil water deficits (Liu et al. 2005b). ABA-based drought stress chemical signaling plays a key role in regulating crop vegetative and reproductive development and crop drought adaptation (reviewed by Liu et al. 2005b). Increased concentrations of ABA in the root induced by soil drying may maintain root growth and increase root hydraulic conductivity; both lead to an increase in water uptake and thereby postpone the development of water deficit in the shoot (Liu et al. 2005a). Root ABA is also transported in the xylem to the shoot and is perceived at the acting sites, where it causes stomatal closure and reduced

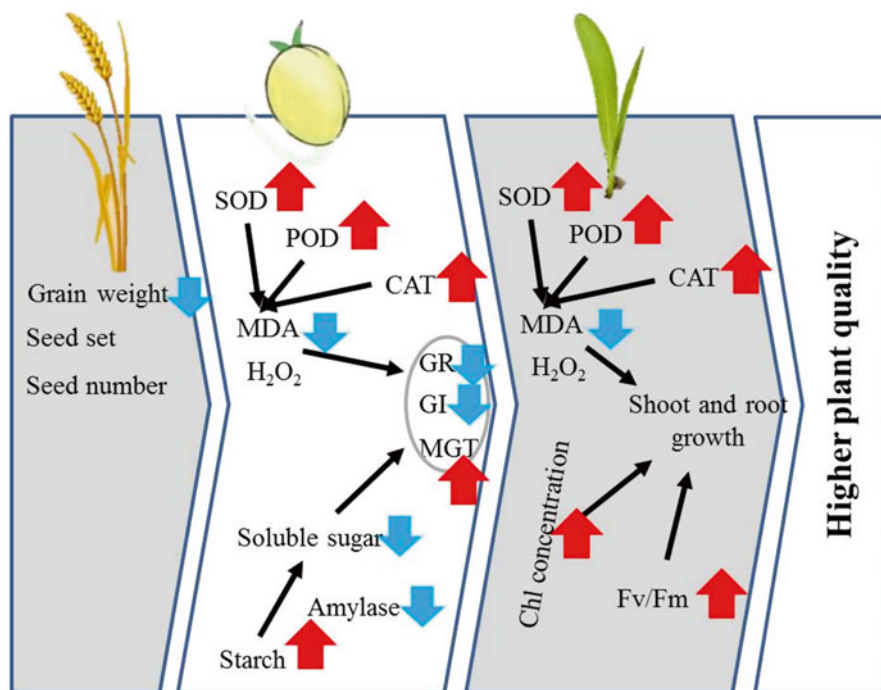


Fig. 2.2 Schematic representation of temperature and water stress tolerance in offspring induced by ABA during grain filling stage in wheat

leaf expansion, thereby preventing dehydration of leaf tissues and enhancing the chance for survival under prolonged drought (Liu et al. 2005a). ABA-based chemical signaling can be amplified by several factors, particularly increased pH in the xylem/apoplast, which retains anionic ABA (Liu et al. 2004, 2005a). Such an increase in xylem pH detected in field-grown maize might have been brought about by reduced nitrate uptake by plants during soil drying (Wang et al. 2012c, d). However, more attention should be paid to the network of ABA signaling of plants in response to drought stress.

Salicylic Acid

An early accumulation of salicylic acid (SA) affects stomatal opening, photorespiration, and antioxidant defenses before any detectable change in the relative water content (Sanchez-Martin et al. 2015). These changes are likely to maintain plant water status, with any photo-inhibitory effect being counteracted by an efficient antioxidant capacity, thereby representing an integrated mechanism of drought tolerance in oats (Sanchez-Martin et al. 2015). It was also documented that *SIZ1*-mediated endogenous SA accumulation plays an important role in stomatal

closure and drought tolerance (Miura et al. 2013). In this study, the *siz1* mutation showed drought tolerance, while *nahG siz1* decreased the tolerance to drought stress. Drought stress also induced expression of SA-responsive genes, such as *PR1* and *PR2* (Miura et al. 2013). Furthermore, other SA-accumulating mutants, *cpr5* and *acd6*, exhibited stomatal closure and drought tolerance, and *nahG* suppressed the phenotypes *cpr5* and *acd6*, as did *siz1* and *nahG siz1* (Miura et al. 2013).

Treatment with 0.5 mM SA significantly alleviated growth inhibition induced by drought in wheat seedlings, manifested by less decreased plant biomass, root length, and less increased lipid peroxidation (Kang et al. 2013). In addition, SA significantly increased the content of ASA and GSH under drought stress. Analysis of protein expression patterns revealed that proteins associated with signal transduction, stress defense, photosynthesis, carbohydrate metabolism, protein metabolism, and energy production could be involved in SA-induced drought tolerance in wheat seedlings (Kang et al. 2012).

Melatonin

Melatonin (*N*-acetyl-5-methoxytryptamine) is a potent, naturally occurring antioxidant that effectively scavenges both ROS and reactive nitrogen species (RNS) in animals and plants (Zhang et al. 2015; Manchester et al. 2015; Arnao and Hernandez-Ruiz 2015). Melatonin pretreatment significantly increases the drought tolerance of both drought-tolerant *Malus prunifolia* and drought-sensitive *M. hupehensis* plants. Melatonin application results in better water conservation in leaves, less electrolyte leakage, steady chlorophyll contents, and greater photosynthetic performance under stress conditions (Li et al. 2015a). In addition, melatonin selectively downregulates *MdNCED3*, an ABA synthesis gene, and upregulates its catabolic genes, *MdCYP707A1* and *MdCYP707A2*, thereby reducing ABA contents in drought-stressed plants. Melatonin also directly scavenges H₂O₂ and enhances the activities of antioxidant enzymes to detoxify H₂O₂ indirectly (Li et al. 2015a).

N-acetylserotonin-*O*-methyltransferase (ASMT) is a specific enzyme required for melatonin synthesis (Lee et al. 2015). An ASMT gene was cloned from apple rootstock (*Malus zumi* Mats) and designated as *MzASMT1* (KJ123721). The *MzASMT1* expression in apple leaves can be induced by drought stress. Melatonin levels in *MzASMT1* transgenic *Arabidopsis* plants were 2–4 times higher than those in the wild type. The transgenic *Arabidopsis* plants had significantly lower intrinsic ROS than the wild type and therefore these plants exhibited greater tolerance to drought stress than that of wild type (Zuo et al. 2014). When melatonin was added to soils under drought conditions, the resultant oxidative stress was eased and leaf senescence was delayed (Wang et al. 2013b). Transgenic Micro-Tom tomato plants overexpressing the homologous ovine arylalkylamine *N*-acetyltransferase (AANAT) and hydroxyindole-*O*-methyltransferase (HIOMT) genes display loss of apical dominance and enhanced drought tolerance (Wang et al. 2014a). The melatonin application significantly reduces chlorophyll degradation and suppresses the upregulation of senescence-associated gene 12 (*SAG12*) and pheophorbide *a* oxygenase (*PAO*).

It also alleviates the inhibition of photosynthesis brought on by drought stress (Wang et al. 2013b). In order to better understand the roles of this molecule in induction of drought tolerance, further investigations are needed.

Nitric Oxide

Nitric oxide (NO), a key signaling molecule, is involved in mediation of drought stress-induced physiological responses in plants (Fig. 2.3). In marigold (*Tagetes erecta* L.), it was found that the promoting effect of NO on rooting under drought stress was dose-dependent. NO treatment attenuated the destruction of mesophyll cell ultrastructure by drought stress, and increased leaf chlorophyll content, maximal PSII efficiency and quantum efficiency of PSII electron transport, and hypocotyls soluble carbohydrate and protein content (Liao et al. 2012). It is suggested that the protection of mesophyll cell ultrastructure by NO under drought conditions improves the photosynthetic performance of leaves and alleviates the negative effects of drought. In rice, drought tolerance of plants was strongly related to the maintenance of tissue water potential and enhanced capacity of antioxidants, improved stability of cellular membranes and enhanced photosynthetic capacity, plausibly by signaling action of NO (Farooq et al. 2009a, b). In addition, the exogenous sodium nitroprusside (SNP, nitric oxide donor) treatment could significantly alleviate the stress injury and accelerate the progress of recovery (Wang et al. 2011). Using two NO donors, SNP and S-nitroso-N-acetylpenicillamine, it was documented that NO induces stomatal closure and

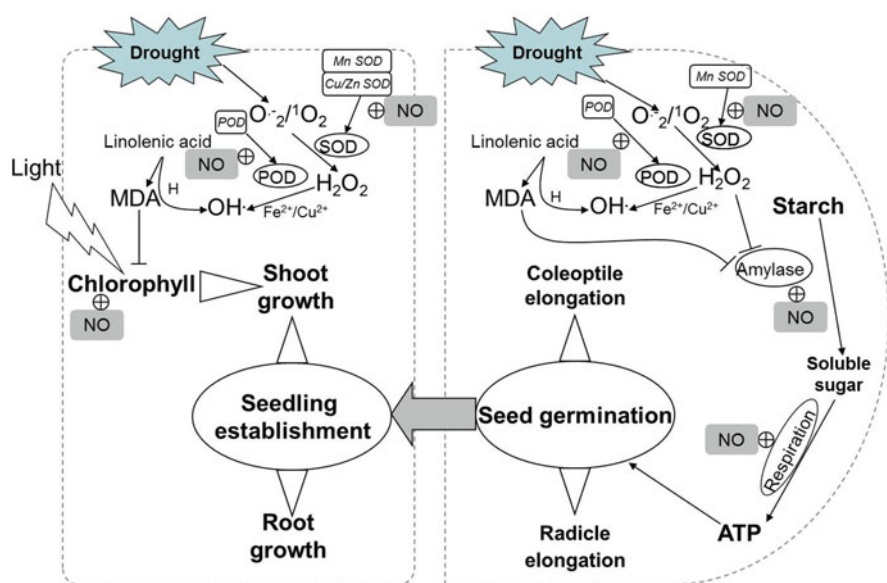


Fig. 2.3 Schematic representation of drought tolerance induced by nitric oxide during germination and the seedling growth stages in wheat

enhances the adaptive plant responses against drought stress (Mata and Lamattina 2001). In SNP-treated leaves of *Tradescantia sp.*, the stomatal closure was associated with a 10 % increase of RWC. Ion leakage, a cell injury index, was 25 % lower in SNP-treated wheat leaves compared with the controls after the recovery period (Mata and Lamattina 2001). A study on the interaction between polyamine (PA) and nitric oxide signaling in adaptive responses to drought in cucumber showed that seedlings pretreated with PAs and subjected to water deficit possessed early and transient NO production (Arasimowicz-Jelonek et al. 2009). However, NO donor administration preceding drought had no effect on endogenous PA levels but was positively correlated with an alleviation of water deficit-induced membrane permeability and lipid peroxidation (Arasimowicz-Jelonek et al. 2009).

2.3 Drought Stress Memory

Drought and other abiotic stresses are recurring environmental stresses experienced by plants throughout their life (Avramova 2015). To survive the repeated stresses, plants can response to later stress events in a way that may be different from their response during the first encounter with the stress. A different response to a similar stress represents the concept of “stress memory” (Avramova 2015). During this process, a coordinated reaction at the organismal, cellular, and genome levels is considered contribute to the improved tolerance in plants. In order to test the long-term stress memory on tuber yield and drought tolerance related traits in potato under drought, seed tubers produced by plants grown under well-water (non-primed tubers) and drought (primed tubers) conditions were sown and exposed to similar watering treatments (Ramírez et al. 2015). Higher tuber yield was produced by primed plants under both nonrestricted and restricted water regimes. The decrease in tuber yield and tuber carbon isotope discrimination with water restriction was lower in primed plants. In addition, it was also found that long-term stress memory consequently appears to be highly genotype-dependent in potato (Ramírez et al. 2015). In grasses, the responses of *Arrhenatherum elatius* plants under a second, later drought (pre-exposed to an earlier drought), to plants exposed to a single (only later) drought were compared (Walter et al. 2011). The results showed that the percentage of living biomass after a late drought was higher for plants that were exposed to drought earlier in the growing season compared to single-stressed plants, even after harvest and resprouting after the first drought. Recently, the effects of drought priming were exemplified with sustaining ROS homeostasis, increasing photosynthetic rate, and higher grain yield when plants exposed to later abiotic stress, such as low temperature, drought, and heat (Li et al. 2015b; Wang et al. 2014c, 2015). Interestingly, *Arabidopsis* plants subjected to a daily dehydration cycle display physiological and transcriptional stress memory: previously stressed plants showed partially closed stomata during a watered recovery period, facilitating water conservation during a subsequent dehydration stress (Virlouvet and Fromm 2015).

Many experiments have proven that the short- and long-term drought stress memory exist in plants (Hu et al. 2015a, b; Berry and Dean 2015; Avramova 2015;

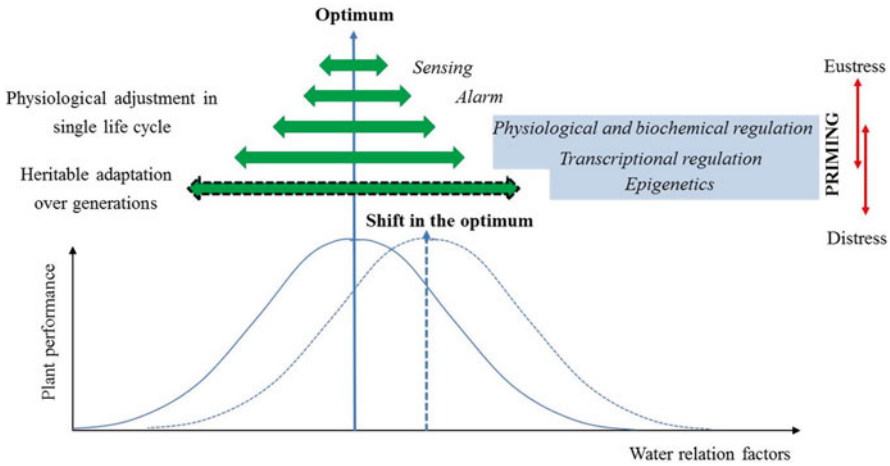


Fig. 2.4 Sensing and adjustment of plants to drought stress by regulations in physiological, transcriptional, and epigenetic levels

Thellier and Luttge 2012; Guan et al. 2012; Pecinka et al. 2009; Molinier et al. 2006). It should be noted that the mechanisms establishing short- or long-term acquisition of stress-induced states may be different (Fig. 2.4). For short-term drought memory, the mechanisms related to morphological adaptation, physiological and biochemical changes, and transcriptional modifications have been reviewed above. In order to understand the mechanism of long-term drought memory in *Arabidopsis*, chromatin marks, such as histone modifications, have been tested in primed and non-primed plants. Primed plants are identical to non-primed plants in growth and development, yet they display enhanced drought tolerance after a second stress exposure (Sani et al. 2013). ChIP-seq analysis of four histone modifications revealed that the priming treatment altered the epigenomic landscape; the changes were small but they were specific for the treated tissue, varied in number and direction depending on the modification, and preferentially targeted transcription factors (Sani et al. 2013). Although some of the mechanisms underlying stress memory in plants have been illustrated, such as morphological changes, the accumulation of specific transcription factors and protective metabolites, and epigenetic modifications, it is still important to understand cross-stress tolerance and stress memory from gene to ecosystem (Munné-Bosch and Alegre 2013).

2.4 Molecular Mechanisms of Drought Memory and Epigenetics

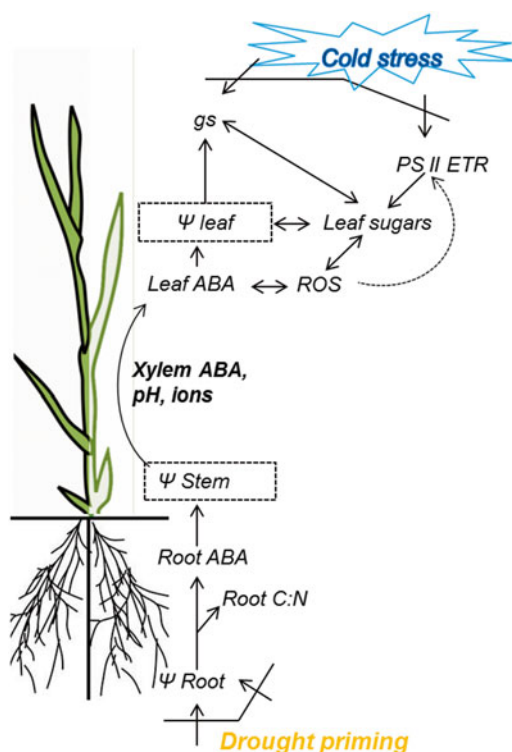
Transcriptional evidences for drought stress memory indicate that the molecular mechanisms regulating production of different transcript amounts in response to single stress stimulation and repeated stress stimulation are different (Avramova 2015;

Berry and Dean 2015). Epigenetic mechanisms are now known to play a critical role in regulating gene expression through small RNAs, histone modifications, and DNA methylation (Kinoshita and Seki 2014). These are inherited through mitotic cell divisions and probably can be transmitted to the next generation (Kinoshita and Seki 2014). In *Arabidopsis*, it was found that drought signals are transduced into effects on gene expression (Yamaguchi-Shinozaki and Shinozaki 2005). The study on changes of histone tails in response to dehydration showed that *RD29A*, *RD20*, and *AtGOLS2* transcripts accumulate under drought stress, while the amounts of these transcripts fall to the basal level when rehydration (Kim et al. 2008, 2012). In addition, alterations to trimethylated histone H3 lysine 4 (H3K4me3), which is correlated with active transcription, suggest that this chromatin mark may play a role in transcription memory for these genes since it is enriched by drought stress and maintained at same levels during the rehydration process (Kim et al. 2012). It was also reported that multiple exposures to drought stress enable plants to respond to a new stress by more rapid adaptive changes to gene expression patterns compared with plants not previously exposed to a drought stress (Ding et al. 2012, 2014; Liu et al. 2014; Alvarez-Venegas et al. 2014). Genome-wide DNA methylation profiles were investigated with regard to a possible role in memory of drought stress; however, no correlation has been identified between gene expression patterns and DNA methylation levels in *Arabidopsis* (Colaneri and Jones 2013).

2.5 Cross-Stress Memory

It is well known that temperate plants including wheat have the ability to obtain cold tolerance by cold acclimation (Theocharis et al. 2012). Cold acclimation in plant is a complex process involving many morphological, physiological, and biochemical changes (Theocharis et al. 2012), including a significant reduction in tissue hydration during cold hardening (Rajashekar and Panda 2014). Besides, evidence shows that drought stress alone, in the absence of low temperatures, can also induce cold tolerance in different plant species such as *Arabidopsis*, wheat, oats, rye, and strawberry (Rajashekar and Panda 2014). As similar effects and plant responses were noticed at cellular and transcriptional levels, the hardening and stress memory mechanisms may be connected (Mahajan and Tuteja 2005). Thus, hardening and acquisition of stress memory will also prevent attack of other stresses (Walter et al. 2013). Recent studies found that preceding exposure to a drought stress could enhance later frost tolerance in several plant species (Kreyling et al. 2012). For example, the freezing tolerance in Norway spruce (*Picea abies*) progenies was physiologically correlated with drought tolerance (Blödner et al. 2005). In our study, drought priming at vegetative stages alleviated photodamage due to drought and heat stresses during reproductive stage (Wang et al. 2015). Compared to the non-hardened plants, the hardened plant obtained higher grain yield, which was mainly attributed to a higher kernel number under drought stress and to a higher kernel weight under heat stress (Wang et al. 2014c). In addition, our recent study found that drought priming at

Fig. 2.5 Drought priming improves the cold tolerance by modification of antioxidant capacity and photosynthesis performance in wheat



vegetative stage improves the antioxidant capacity and photosynthesis performance of wheat exposed to a short-term low temperature stress at jointing stage (Fig. 2.5) (Li et al. 2015b). Another kind of cross-stress tolerance towards herbivore induced by drought was caused by modifications of secondary compounds (Herms and Mattson 1992). However, the mechanisms underlying the cross-stress memory remain largely unknown.

2.6 Transgenerational Stress Memory

Sufficient evidence indicates that the modifications induced by former stress events could stimulate a faster immune mechanism to improve stress tolerance in face of repeated events, while some modifications could be inherited to the next generation (Molinier et al. 2006). Transgenerational transmission of information about stress exposure is manifested as an increase in the somatic homologous recombination frequency in plants. Upregulated activity of antioxidative enzymes in maternal plants under drought was reported to be inherited to the next generation of *Arabidopsis thaliana* (Čuk et al. 2010). The activity of catalase was significantly decreased in the irradiated plants in comparison to the non-irradiated control plants,

while the activity of guaiacol peroxidase was increased. In irradiated plants, there was an induction of a new HSP70 protein isoform. In the non-irradiated progeny of irradiated plants, a significant decrease in catalase and ascorbate peroxidase activity was noticed in comparison to plants whose parents were not irradiated (Čuk et al. 2010). There was no significant change in guaiacol peroxidase activity or induction of HSP70 isoforms in the progeny. This indicates that results indicate that, besides the already known increase in frequency of somatic homologous recombination, transmission of information about stress exposure can also include changes in activities of antioxidative enzymes catalase and ascorbate peroxidase. The transgenerational stress memory was also found in mild heat stress, where F3 generation plant showed a heat-specific fitness enhancement after parental plant and F1 generation had been treated with mild heat (Whittle et al. 2009).

It has been suggested that the epigenetic mechanisms, such as histone modifications and DNA methylation and acetylation, can be inherited through mitotic or meiotic cell divisions (Chinnusamy and Zhu 2009), which support the transgenerational stress memory in cellular biochemistry. Recent evidence suggests that exposure of *Arabidopsis* plants to abiotic stresses, including salt, UV, flooding and extreme temperatures (heat and cold), led to an increased homologous recombination frequency (HRF) and global genome methylation, and showed higher tolerance to the abiotic stress in their untreated progeny (Boyko et al. 2010; Pecinka et al. 2009). It was also proved that the stress-induced transgenerational responses in *Arabidopsis* depend not only on altered DNA methylation but also on smRNA silencing pathways, revealed by using *dcl2* and *dcl3* deficiency mutants (Boyko et al. 2010; Pecinka et al. 2009). However, the heritability of epigenetic change induced by stress exposure was not confirmed in *Arabidopsis*, indicating strict requirement to specific conditions of transgenerational epigenetic memory (Pecinka et al. 2009).

2.7 An Integrated View and Future Prospects

As one of main focuses in plant-abiotic stress research, studies on plant drought priming and stress memory are still rare. To date, most of results on plant drought priming were obtained in controlled lab experiments, which might be different from the natural conditions. Thus, in future studies, a combination of experiments from controlled lab evaluations with observations and simulation under field conditions should be performed. In addition, certain environmental responses in many seed crops can persist in the next sexual generation. These transgenerational effects have potential significance in agronomy, thus it is essential to elucidate the mechanisms of transgenerational stress memory and to understand the possible regulation pathways. Collectively, to further understanding the processes and mechanisms of priming effects, ecophysiologists and molecular biologists should work together in order to reveal the complete regulation network at different levels and scales, such that management strategies could be developed to sustain crop productivity under future climate changes scenarios.

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References

- Ahmad I, Basra SMA, Hussain S, Hussain SA, Rehman HU, Rehman A, Ali A. Priming with ascorbic acid, salicylic acid and hydrogen peroxide improves seedling growth of spring maize at suboptimal temperature. *J Environ Agr Sci*. 2015;3:14–22.
- Ali M, Jensen CR, Mogensen VO. Early signals in field grown wheat in response to shallow soil drying. *Funct Plant Biol*. 1998;25:871–82.
- Alvarez-Venegas R, Abdallat AA, Guo M, Alfano JR, Avramova Z. Epigenetic control of a transcription factor at the cross section of two antagonistic pathways. *Epigenetics*. 2014;2:106–13.
- Arasimowicz-Jelonek M, Floryszak-Wieczorek J, Kubiś J. Interaction between polyamine and nitric oxide signaling in adaptive responses to drought in cucumber. *J Plant Growth Regul*. 2009;28:177–86.
- Arnao MB, Hernandez-Ruiz J. Functions of melatonin in plants: a review. *J Pineal Res*. 2015;59:133–50.
- Ashoub A, Beckhaus T, Berberich T, Karas M, Brüggemann W. Comparative analysis of barley leaf proteome as affected by drought stress. *Planta*. 2013;237:771–81.
- Atkin OK, Macherel D. The crucial role of plant mitochondria in orchestrating drought tolerance. *Ann Bot*. 2009;103:581–97.
- Atkin O, Scheurwater I, Pons T. High thermal acclimation potential of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an alpine congeneric. *Glob Chang Biol*. 2006;12:500–15.
- Atkin O, Scheurwater I, Pons T. Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures. *New Phytol*. 2007;174:367–80.
- Avramova Z. Transcriptional ‘memory’ of a stress; transient chromatin and memory (epigenetic) marks at stress response genes. *Plant J*. 2015;83:149–59.
- Baerenfaller K, Massonnet C, Walsh S, Baginsky S, Bühlmann P, Hennig L, Hirsch-Hoffmann M, Howell KA, Kahlau S, Radziejowski A. Systems-based analysis of *Arabidopsis* leaf growth reveals adaptation to water deficit. *Mol Syst Biol*. 2012;8:606.
- Basra S, Farooq M, Tabassam R, Ahmad N. Physiological and biochemical aspects of pre-sowing seed treatments in fine rice (*Oryza sativa* L.). *Seed Sci Technol*. 2005;33:623–8.
- Berry S, Dean C. Environmental perception and epigenetic memory: mechanistic insight through FLC. *Plant J*. 2015;83:133–48.
- Blödner C, Skroppa T, Johnsen Ø, Polle A. Freezing tolerance in two Norway spruce (*Picea abies* L. Karst.) progenies is physiologically correlated with drought tolerance. *J Plant Physiol*. 2005;162:549–58.
- Boyko A, Blevins T, Yao Y, Golubov A, Bilichak A, Illynskyy Y, Hollander J, Frederick Meins J, Kovalchuk I. Transgenerational adaptation of *Arabidopsis* to stress requires DNA methylation and the function of Dicer-Like proteins. *PLoS One*. 2010;5, e9514.
- Bruce TJA, Matthes MC, Napier JA, Pickett JA. Stressful “memories” of plants: evidence and possible mechanisms. *Plant Sci*. 2007;173:603–8.
- Chen K, Arora R. Dynamics of the antioxidant system during seed osmopriming, post-priming germination, and seedling establishment in Spinach (*Spinacia oleracea*). *Plant Sci*. 2011;180:212–20.
- Chen K, Arora R. Priming memory invokes seed stress-tolerance. *Environ Exp Bot*. 2012;94:33–45.
- Chen K, Fessehaie A, Arora R. Selection of reference genes for normalizing gene expression during seed priming and germination using qPCR in *Zea mays* and *Spinacia oleracea*. *Plant Mol Biol Rep*. 2012;30:478–87.

- Chen K, Fessehaie A, Arora R. Aquaporin expression during seed osmopriming and post-priming germination in spinach. *Biol Plantarum*. 2013;57:193–8.
- Chinnusamy V, Zhu J-K. Epigenetic regulation of stress responses in plants. *Curr Opin Plant Biol*. 2009;12:133–9.
- Colaneri AC, Jones AM. Genome-wide quantitative identification of DNA differentially methylated sites in *Arabidopsis* seedlings growing at different water potential. *PLoS One*. 2013;8, e59878.
- Conrath U. Molecular aspects of defence priming. *Trends Plant Sci*. 2011;16:524–31.
- Čuk K, Gogalo M, Tkalec M, Vidaković-Cifrek Ž. Transgenerational stress memory in *Arabidopsis thaliana* (L.) Heynh.: antioxidative enzymes and HSP70. *Acta Bot Croat*. 2010;69:183–97.
- Ding Y, Fromm M, Avramova Z. Multiple exposures to drought ‘train’ transcriptional responses in *Arabidopsis*. *Nat Commun*. 2012;3:740.
- Ding Y, Virlouvet L, Liu N, Riethoven JJ, Fromm M, Avramova Z. Dehydration stress memory genes of *Zea mays*; comparison with *Arabidopsis thaliana*. *BMC Plant Biol*. 2014;14:141.
- Doheny-Adams T, Hunt L, Franks PJ, Beerling DJ, Gray JE. Genetic manipulation of stomatal density influences stomatal size, plant growth and tolerance to restricted water supply across a growth carbon dioxide gradient. *Philos Trans R Soc Lond B Biol Sci*. 2012;367:547–55.
- Eisvand H, Tavakkol-Afshari R, Sharifzadeh F, Maddah Arefi H, Hesamzadeh Hejazi S. Effects of hormonal priming and drought stress on activity and isozyme profiles of antioxidant enzymes in deteriorated seed of tall wheatgrass (*Agropyron elongatum* Host). *Seed Sci Technol*. 2010;38:280–97.
- Eldem V, Akcay UC, Ozhuner E, Bakır Y, Uranbey S, Unver T. Genome-wide identification of miRNAs responsive to drought in peach (*Prunus persica*) by high-throughput deep sequencing. *PLoS One*. 2012;7(12):502–98.
- Elkoca E, Haliloglu K, Esitken A, Ercisli S. Hydro- and osmopriming improve chickpea germination. *Acta Agric Scand Sect B Soil Plant Sci*. 2007;57:193–200.
- Faghani E, Gharechahi J, Komatsu S, Mirzaei M, Khavarinejad RA, Najafi F, Farsad LK, Salekdeh GH. Comparative physiology and proteomic analysis of two wheat genotypes contrasting in drought tolerance. *J Proteomics*. 2014;114:1–15.
- Farooq M, Basra SMA, Wahid A, Rehman H. Exogenously applied nitric oxide enhances the drought tolerance in fine grain aromatic rice (*Oryza sativa* L.). *J Agron Crop Sci*. 2009a;195:254–61.
- Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA. Plant drought stress: effects, mechanisms and management. *Agron Sustain Dev*. 2009b;29:185–212.
- Farooq M, Basra SM, Wahid A, Ahmad N. Changes in nutrient-homeostasis and reserves metabolism during rice seed priming: consequences for seedling emergence and growth. *Agr Sci China*. 2010;9:191–8.
- Franks PJ, Doheny-Adams WT, Britton-Harper ZJ, Gray JE. Increasing water-use efficiency directly through genetic manipulation of stomatal density. *New Phytol*. 2015;207:188–95.
- Frazier TP, Sun G, Burklew CE, Zhang B. Salt and drought stresses induce the aberrant expression of microRNA genes in tobacco. *Mol Biotechnol*. 2011;49:159–65.
- Gao P, Bai X, Yang L, Lv D, Li Y, Cai H, Ji W, Guo D, Zhu Y. Over-expression of *osa-MIR396c* decreases salt and alkali stress tolerance. *Planta*. 2010;231:991–1001.
- Giri GS, Schillinger WF. Seed priming winter wheat for germination, emergence, and yield. *Crop Sci*. 2003;43:2135–41.
- Guan Q, Haroon S, Bravo DG, Will JL, Gasch AP. Cellular memory of acquired stress resistance in *Saccharomyces cerevisiae*. *Genetics*. 2012;192:495–505.
- Guan XK, Song L, Wang TC, Turner NC, Li FM. Effect of drought on the gas exchange, chlorophyll fluorescence and yield of six different-era spring wheat cultivars. *J Agron Crop Sci*. 2015;201:253–66.
- Hackenberg M, Gustafson P, Langridge P, Shi BJ. Differential expression of microRNAs and other small RNAs in barley between water and drought conditions. *Plant Biotechnol J*. 2015;13:2–13.
- Hajheidari M, Eivazi A, Buchanan BB, Wong JH, Majidi I, Salekdeh GH. Proteomics uncovers a role for redox in drought tolerance in wheat. *J Proteome Res*. 2007;6:1451–60.

- Hamanishi ET, Thomas BR, Campbell MM. Drought induces alterations in the stomatal development program in *Populus*. *J Exp Bot*. 2012;63:4969–71.
- Hao P, Zhu J, Gu A, Lv D, Ge P, Chen G, Li X, Yan Y. An integrative proteome analysis of different seedling organs in tolerant and sensitive wheat cultivars under drought stress and recovery. *Proteomics*. 2015;15:1544–63.
- Hepworth C, Doheny-Adams T, Hunt L, Cameron DD, Gray JE. Manipulating stomatal density enhances drought tolerance without deleterious effect on nutrient uptake. *New Phytol*. 2015. doi:10.1111/nph.13598.
- Hermes DA, Mattson WJ. The dilemma of plants: to grow or defend. *Q Rev Biol*. 1992;67:283–335.
- Hu T, Jin Y, Li H, Amombo E, Fu J. Stress memory induced transcriptional and metabolic changes of perennial ryegrass (*Lolium perenne*) in response to salt stress. *Physiol Plant*. 2015a. doi:10.1111/ppl.12342.
- Hu T, Liu SQ, Amombo E, Fu JM. Stress memory induced rearrangements of HSP transcription, photosystem II photochemistry and metabolism of tall fescue (*Festuca arundinacea* Schreb.) in response to high-temperature stress. *Front Plant Sci*. 2015b;6:403–25.
- Ibáñez H, Ballester A, Muñoz R, José Quiles M. Chlororespiration and tolerance to drought, heat and high illumination. *J Plant Physiol*. 2010;167:732–8.
- Jacobsen S-E, Liu F, Jensen CR. Does root-sourced ABA play a role for regulation of stomata under drought in quinoa (*Chenopodium quinoa* Willd.). *Sci Hortic*. 2009;122:281–7.
- Janmohammadi M, Dezfali PM, Sharifzadeh F. Seed invigoration techniques to improve germination and early growth of inbred line of maize under salinity and drought stress. *Genet Appl Plant Physiol*. 2008;34:215–26.
- Jiang M, Zhang J. Effect of abscisic acid on active oxygen species, antioxidative defence system and oxidative damage in leaves of maize seedlings. *Plant Cell Physiol*. 2001;42:1265–73.
- Jisha KC, Vijayakumari K, Puthur JT. Seed priming for abiotic stress tolerance: an overview. *Acta Physiol Plant*. 2012;35:1381–96.
- Kaminski KP, Kørup K, Kristensen K, Nielsen KL, Liu F, Tophjerg HB, Kirk HG, Andersen MN. Contrasting water-use efficiency (WUE) responses of a potato mapping population and capability of modified ball-berry model to predict stomatal conductance and WUE measured at different environmental conditions. *J Agron Crop Sci*. 2015;201:81–94.
- Kang H-G, Kim J, Kim B, Jeong H, Choi SH, Kim EK, Lee H-Y, Lim PO. Overexpression of FTL1/DDF1, an AP2 transcription factor, enhances tolerance to cold, drought, and heat stresses in *Arabidopsis thaliana*. *Plant Sci*. 2011;180(4):634–41.
- Kang G, Li G, Xu W, Peng X, Han Q, Zhu Y, Guo T. Proteomics reveals the effects of salicylic acid on growth and tolerance to subsequent drought stress in wheat. *J Proteome Res*. 2012;11:6066–79.
- Kang G, Li G, Liu G, Xu W, Peng X, Wang C, Zhu Y, Guo T. Exogenous salicylic acid enhances wheat drought tolerance by influence on the expression of genes related to ascorbate-glutathione cycle. *Biol Plantarum*. 2013;57:718–24.
- Kaur S, Gupta A, Kaur N. Effect of osmo- and hydropriming of chickpea seeds on seedling growth and carbohydrate metabolism under water deficit stress. *Plant Growth Regul*. 2002;37:17–22.
- Kidokoro S, Watanabe K, Ohori T, Moriwaki T, Maruyama K, Mizoi J, Myint Phyu Sin Htwe N, Fujita Y, Sekita S, Shinozaki K, Yamaguchi-Shinozaki K. Soybean DREB1/CBF-type transcription factors function in heat and drought as well as cold stress-responsive gene expression. *Plant J*. 2015;81:505–18.
- Kim J-M, To TK, Ishida J, Morosawa T, Kawashima M, Matsui A, Toyoda T, Kimura H, Shinozaki K, Seki M. Alterations of lysine modifications on the histone H3 N-tail under drought stress conditions in *Arabidopsis thaliana*. *Plant Cell Physiol*. 2008;49:1580–8.
- Kim JY, Kwak KJ, Jung HJ, Lee HJ, Kang H. MicroRNA402 affects seed germination of *Arabidopsis thaliana* under stress conditions via targeting DEMETER-LIKE Protein3 mRNA. *Plant Cell Physiol*. 2010a;51:1079–83.
- Kim JY, Lee HJ, Jung HJ, Maruyama K, Suzuki N, Kang H. Overexpression of microRNA395c or 395e affects differently the seed germination of *Arabidopsis thaliana* under stress conditions. *Planta*. 2010b;232:1447–54.

- Kim J-M, To TK, Ishida J, Matsui A, Kimura H, Seki M. Transition of chromatin status during the process of recovery from drought stress in *Arabidopsis thaliana*. *Plant Cell Physiol.* 2012;53:847–56.
- Kinoshita T, Seki M. Epigenetic memory for stress response and adaptation in plants. *Plant Cell Physiol.* 2014;55:1859–63.
- Kreyling J, Wiesenberger GLB, Thiel D, Wohlfart C, Huber G, Walter J, Jentsch A, Konnerth M, Beierkuhnlein C. Cold hardiness of *Pinus nigra* Arnold as influenced by geographic origin, warming, and extreme summer drought. *Environ Exp Bot.* 2012;78:99–108.
- Lalk I, Dörfling K. Hardening, abscisic acid, praline and freezing resistance in two winter wheat varieties. *Physiol Plant.* 1985;63:287–92.
- Lee HY, Byeon Y, Tan D-X, Reiter RJ, Back K. Arabidopsis serotonin N-acetyltransferase knockout mutant plants exhibit decreased melatonin and salicylic acid levels resulting in susceptibility to an avirulent pathogen. *J Pineal Res.* 2015;58:291–9.
- Li W-X, Oono Y, Zhu J, He X-J, Wu J-M, Iida K, Lu X-Y, Cui X, Jin H, Zhu J-K. The *Arabidopsis NFYA5* transcription factor is regulated transcriptionally and posttranscriptionally to promote drought resistance. *Plant Cell.* 2008;20:2238–51.
- Li Y, Ren B, Yang X, Xu G, Shen Q, Guo S. Chloroplast downsizing under nitrate nutrition restrained mesophyll conductance and photosynthesis in rice (*Oryza sativa* L.) under drought conditions. *Plant Cell Physiol.* 2012;53:892–900.
- Li X, Jiang H, Liu F, Cai J, Dai T, Cao W, Jiang D. Induction of chilling tolerance in wheat during germination by pre-soaking seed with nitric oxide and gibberellin. *Plant Growth Regul.* 2013;71:31–40.
- Li X, Cai J, Liu F, Dai T, Cao W, Jiang D. Cold priming drives the sub-cellular antioxidant systems to protect photosynthetic electron transport against subsequent low temperature stress in winter wheat. *Plant Physiol Biochem.* 2014a;82:34–43.
- Li X, Cai J, Liu F, Dai T, Cao W, Jiang D. Exogenous abscisic acid application during grain filling in winter wheat improves cold tolerance of offspring's seedlings. *J Agron Crop Sci.* 2014b;200:467–78.
- Li X, Cai J, Liu F, Dai T, Cao W, Jiang D. Physiological, proteomic and transcriptional responses of wheat to combination of drought or waterlogging with late spring low temperature. *Funct Plant Biol.* 2014c;41:690–703.
- Li C, Tan DX, Liang D, Chang C, Jia D, Ma F. Melatonin mediates the regulation of ABA metabolism, free-radical scavenging, and stomatal behaviour in two *Malus* species under drought stress. *J Exp Bot.* 2015a;66:669–80.
- Li X, Topbjerg HB, Jiang D, Liu F. Drought priming at vegetative stage improves the antioxidant capacity and photosynthesis performance of wheat exposed to a short-term low temperature stress at jointing stage. *Plant and Soil.* 2015b;393:307–18.
- Liao WB, Huang GB, Yu JH, Zhang ML. Nitric oxide and hydrogen peroxide alleviate drought stress in marigold explants and promote its adventitious root development. *Plant Physiol.* 2012;58:6–15.
- Liu F, Andersen MN, Jensen CR. Root signal controls pod growth in drought-stressed soybean during the critical, abortion-sensitive phase of pod development. *Field Crops Res.* 2004;85:159–66.
- Liu F, Jensen CR, Andersen MN. A review of drought adaptation in crop plants: changes in vegetative and reproductive physiology induced by ABA-based chemical signals. *Aust J Agric Res.* 2005a;56:1245–52.
- Liu F, Jensen CR, Shahanzari A, Andersen MN, Jacobsen S-E. ABA regulated stomatal control and photosynthetic water use efficiency of potato (*Solanum tuberosum* L.) during progressive soil drying. *Plant Sci.* 2005b;168:831–6.
- Liu F, Shahnazari A, Andersen MN, Jacobsen SE, Jensen CR. Physiological responses of potato (*Solanum tuberosum* L.) to partial root-zone drying: ABA signalling, leaf gas exchange, and water use efficiency. *J Exp Bot.* 2006;57(14):3727–35.
- Liu H-H, Tian X, Li Y-J, Wu C-A, Zheng C-C. Microarray-based analysis of stress-regulated microRNAs in *Arabidopsis thaliana*. *RNA.* 2008;14(5):836–43.

- Liu L, Cang J, Wang X, Huang R, Wang J, Yu J, Lu B. Effects of exogenous abscisic acid on carbohydrate metabolism and the expression levels of correlative key enzymes in winter wheat under low temperature. *Biosci Biotech Biochem*. 2013;77:516–25.
- Liu N, Ding Y, Fromm M, Avramova Z. Different gene-specific mechanisms determine the ‘revised-response’ memory transcription patterns of a subset of *A. thaliana* dehydration stress responding genes. *Nucleic Acids Res*. 2014;42:5556–66.
- Liu C, Rubæk GH, Liu F, Andersen MN. Effect of partial root zone drying and deficit irrigation on nitrogen and phosphorus uptake in potato. *Agric Water Manage*. 2015;159:66–76.
- Loveys B, Scheurwater I, Pons T, Fitter A, Atkin O. Growth temperature influences the underlying components of relative growth rate: an investigation using inherently fast-and slow-growing plant species. *Plant Cell Environ*. 2002;25:975–88.
- Mahajan S, Tuteja N. Cold, salinity and drought stresses: an overview. *Arch Biochem Biophys*. 2005;444:139–58.
- Manchester LC, Coto-Montes A, Boga JA, Andersen LP, Zhou Z, Galano A, Vriend J, Tan DX, Reiter RJ. Melatonin: an ancient molecule that makes oxygen metabolically tolerable. *J Pineal Res*. 2015. doi:10.1111/jpi.12267.
- Massacci A, Nabiev SM, Pietrosanti L, Nematov SK, Chernikova TN, Thor K, Leipner J. Response of the photosynthetic apparatus of cotton (*Gossypium hirsutum*) to the onset of drought stress under field conditions studied by gas-exchange analysis and chlorophyll fluorescence imaging. *Plant Physiol Biochem*. 2008;46:189–95.
- Mata CG, Lamattina L. Nitric oxide induces stomatal closure and enhances the adaptive plant responses against drought stress. *Plant Physiol*. 2001;126:1196–204.
- Meena RP, Sendhil R, Tripathi S, Chander S, Chhokar R, Sharma R. Hydro-priming of seed improves the water use efficiency, grain yield and Net economic return of wheat under different moisture regimes. *SAARC J Agr*. 2014;11:149–59.
- Mishra KB, Iannacone R, Petrozza A, Mishra A, Armentano N, La Vecchia G, Trtílek M, Cellini F, Nedbal L. Engineered drought tolerance in tomato plants is reflected in chlorophyll fluorescence emission. *Plant Sci*. 2012;182:79–86.
- Miura K, Okamoto H, Okuma E, Shiba H, Kamada H, Hasegawa PM, Murata Y. *SIZ1* deficiency causes reduced stomatal aperture and enhanced drought tolerance via controlling salicylic acid-induced accumulation of reactive oxygen species in *Arabidopsis*. *Plant J*. 2013;73:91–104.
- Molinier J, Ries G, Zipfel C, Hohn B. Transgeneration memory of stress in plants. *Nature*. 2006;442.
- Munné-Bosch S, Alegre L. Cross-stress tolerance and stress “memory” in plants: an integrated view. *Environ Exp Bot*. 2013;94:1–2.
- Muscolo A, Junker A, Klukas C, Weigelt-Fischer K, Riewe D, Altmann T. Phenotypic and metabolic responses to drought and salinity of four contrasting lentil accessions. *J Exp Bot*. 2015;66:5467–80.
- Ni Z, Hu Z, Jiang Q, Zhang H. Overexpression of *gma-MIR394a* confers tolerance to drought in transgenic *Arabidopsis thaliana*. *Biochem Biophys Res Commun*. 2012;427:330–5.
- Pandita V, Anand A, Nagarajan S, Seth R, Sinha S. Solid matrix priming improves seed emergence and crop performance in okra. *Seed Sci Technol*. 2010;38:665–74.
- Pecinka A, Rosa M, Schikora A, Berlinger M, Hirt H, Luschig C, Scheid OM. Transgenerational stress memory is not a general response in *Arabidopsis*. *PLoS One*. 2009;4, e5202.
- Peuke A, Gessler A, Rennenberg H. The effect of drought on C and N stable isotopes in different fractions of leaves, stems and roots of sensitive and tolerant beech ecotypes. *Plant Cell Environ*. 2006;29:823–35.
- Plauborg F, Abrahamsen P, Gjettermann B, Møllerup M, Iversen BV, Liu F, Andersen MN, Hansen S. Modelling of root ABA synthesis, stomatal conductance, transpiration and potato production under water saving irrigation regimes. *Agr Water Manage*. 2010;98:425–39.
- Quarrie S, Jones H. Effects of abscisic acid and water stress on development and morphology of wheat. *J Exp Bot*. 1977;28:192–203.
- Rajashekar CB, Panda M. Water stress is a component of cold acclimation process essential for inducing full freezing tolerance in strawberry. *Sci Hortic*. 2014;174:54–9.

- Ramírez DA, Rolando JL, Yactayo W, Monneveux P, Mares V, Quiroz R. Improving potato drought tolerance through the induction of long-term water stress memory. *Plant Sci.* 2015;238:26–32.
- Rivas-Ubach A, Sardans J, Perez-Trujillo M, Estiarte M, Penuelas J. Strong relationship between elemental stoichiometry and metabolome in plants. *Proc Natl Acad Sci U S A.* 2012;109:4181–6.
- Sakurai N, Akiyama M, Kuraishi S. Irreversible effects of water stress on growth and stomatal development in cotyledons of etiolated squash seedlings. *Plant Cell Physiol.* 1986;27:1177–85.
- Sanchez-Martin J, Heald J, Kingston-Smith A, Winters A, Rubiales D, Sanz M, Mur LA, Prats E. A metabolomic study in oats (*Avena sativa*) highlights a drought tolerance mechanism based upon salicylate signalling pathways and the modulation of carbon, antioxidant and photo-oxidative metabolism. *Plant Cell Environ.* 2015;38:1434–52.
- Sani E, Herzyk P, Perrella G, Colot V, Amtmann A. Hyperosmotic priming of Arabidopsis seedlings establishes a long-term somatic memory accompanied by specific changes of the epigenome. *Genome Biol.* 2013;14:R59.
- Shahrokhi M, Tehranifar A, Hadizadeh H, Selahvarzi Y. Effect of drought stress and paclobutrazol-treated seeds on physiological response of *Festuca arundinacea* L. master and *Lolium perenne* L. barrage. *J Biol Environ Sci.* 2011;5:77–85.
- Shukla N, Awasthi RP, Rawat L, Kumar J. Seed biopriming with drought tolerant isolates of *Trichoderma harzianum* promote growth and drought tolerance in *Triticum aestivum*. *Ann Appl Biol.* 2015;166:171–82.
- Silva EC, Nogueira RJ, Vale FH, Araújo FP, Pimenta MA. Stomatal changes induced by intermittent drought in four umbu tree genotypes. *Brazil J Plant Physiol.* 2009;21:33–42.
- Silvente S, Sobolev AP, Lara M. Metabolite adjustments in drought tolerant and sensitive soybean genotypes in response to water stress. *PLoS One.* 2012;7(6), e38554.
- Su L, Dai Z, Li S, Xin H. A novel system for evaluating drought-cold tolerance of grapevines using chlorophyll fluorescence. *BMC Plant Biol.* 2015;15(1):82.
- Sun Y, Yan F, Cui X, Liu F. Plasticity in stomatal size and density of potato leaves under different irrigation and phosphorus regimes. *J Plant Physiol.* 2014;171:1248–55.
- Sun Y, Cui X, Liu F. Effect of irrigation regimes and phosphorus rates on water and phosphorus use efficiencies in potato. *Sci Hort.* 2015;190:64–9.
- Suseela V, Tharayil N, Xing B, Dukes JS. Warming and drought differentially influence the production and resorption of elemental and metabolic nitrogen pools in *Quercus rubra*. *Glob Chang Biol.* 2015. doi:10.1111/gcb.13033.
- Tavili A, Zare S, Moosavi SA, Enayati A. Effects of seed priming on germination characteristics of *Bromus* species under salt and drought conditions. *Amer-Eurasian J Agric Environ Sci.* 2011;10:163–8.
- Thellier M, Luttge U. Plant memory: a tentative model. *Plant Biol.* 2012;15:1–12.
- Theocharis A, Clement C, Barka EA. Physiological and molecular changes in plants grown at low temperatures. *Planta.* 2012;235:1091–105.
- Tombesi S, Nardini A, Frioni T, Soccolini M, Zadra C, Farinelli D, Poni S, Palliotti A. Stomatal closure is induced by hydraulic signals and maintained by ABA in drought-stressed grapevine. *Sci Rep.* 2015;5:12449.
- Tophjerg HB, Kaminski KP, Kørup K, Nielsen KL, Kirk HG, Andersen MN, Liu F. Screening for intrinsic water use efficiency in a potato dihaploid mapping population under progressive drought conditions. *Acta Agric Scand B Plant Sci.* 2015. doi:10.1080/09064710.2015.1015439.
- Udvardi MK, Kakar K, Wandrey M, Montanari O, Murray J, Andrianakaja A, Zhang J-Y, Benedito V, Hofer JM, Chueng F. Legume transcription factors: global regulators of plant development and response to the environment. *Plant Physiol.* 2007;144:538–49.
- Urano K, Kurihara Y, Seki M, Shinozaki K. 'Omics' analyses of regulatory networks in plant abiotic stress responses. *Curr Opin Plant Biol.* 2010;13:132–8.
- Valdes AE, Irar S, Majada JP, Rodríguez A, Fernandez B, Pages M. Drought tolerance acquisition in *Eucalyptus globulus* (Labill.): a research on plant morphology, physiology and proteomics. *J Proteomics.* 2013;79:263–76.

- Varga B, Varga-László E, Bencze S, Balla K, Veisz O. Water use of winter cereals under well-watered and drought-stressed conditions. *Plant Soil Environ.* 2013;59:150–5.
- Varga B, Vida G, Varga-László E, Bencze S, Veisz O. Effect of simulating drought in various phenophases on the water use efficiency of winter wheat. *J Agron Crop Sci.* 2015;201:1–9.
- Virlouvet L, Fromm M. Physiological and transcriptional memory in guard cells during repetitive dehydration stress. *New Phytol.* 2015;205:596–607.
- Walter J, Nagy L, Hein R, Rascher U, Beierkuhnlein C, Willner E, Jentsch A. Do plants remember drought? Hints towards a drought-memory in grasses. *Environ Exp Bot.* 2011;71:34–40.
- Walter J, Jentsch A, Beierkuhnlein C, Kreyling J. Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. *Environ Exp Bot.* 2013;94:3–8.
- Wang J, Vanlerberghe GC. A lack of mitochondrial alternative oxidase compromises capacity to recover from severe drought stress. *Physiol Plant.* 2013;149:461–73.
- Wang Y, Suo B, Zhao T, Qu X, Yuan L, Zhao X, Zhao H. Effect of nitric oxide treatment on antioxidant responses and psbA gene expression in two wheat cultivars during grain filling stage under drought stress and rewetting. *Acta Physiol Plant.* 2011;33:1923–32.
- Wang X, Liu Y, Jia Y, Gu H, Ma H, Yu T, Zhang H, Chen Q, Ma L, Gu A, Zhang J, Shi S. Transcriptional responses to drought stress in root and leaf of chickpea seedling. *Mol Biol Rep.* 2012a;39:8147–58.
- Wang Y, Liu F, Jensen CR. Comparative effects of deficit irrigation and alternate partial root-zone irrigation on xylem pH, ABA and ionic concentrations in tomatoes. *J Exp Bot.* 2012b;63:1907–17.
- Wang Z, Kang S, Jensen CR, Liu F. Alternate partial root-zone irrigation reduces bundle-sheath cell leakage to CO₂ and enhances photosynthetic capacity in maize leaves. *J Exp Bot.* 2012c;63:1145–53.
- Wang Z, Liu F, Kang S, Jensen CR. Alternate partial root-zone drying irrigation improves nitrogen nutrition in maize (*Zea mays* L.) leaves. *Environ Exp Bot.* 2012d;75:36–40.
- Wang M, Wang Q, Zhang B. Response of miRNAs and their targets to salt and drought stresses in cotton (*Gossypium hirsutum* L.). *Gene.* 2013a;530:26–32.
- Wang P, Sun X, Li C, Wei Z, Liang D, Ma F. Long-term exogenous application of melatonin delays drought-induced leaf senescence in apple. *J Pineal Res.* 2013b;54:292–302.
- Wang L, Zhao Y, Reiter RJ, He CJ, Liu GS, Lei Q, Zuo BX, Zheng XD, Li QT, Kong J. Changes in melatonin levels in transgenic 'Micro-Tom' tomato overexpressing ovine AANAT and ovine HIOMT genes. *J Pineal Res.* 2014a;56:134–42.
- Wang X, Cai J, Liu F, Dai T, Cao W, Wollenweber B, Jiang D. Multiple heat priming enhances thermo-tolerance to a later high temperature stress via improving subcellular antioxidant activities in wheat seedlings. *Plant Physiol Biochem.* 2014b;74:185–92.
- Wang X, Vignjevic M, Jiang D, Jacobsen S, Wollenweber B. Improved tolerance to drought stress after anthesis due to priming before anthesis in wheat (*Triticum aestivum* L.) var. Vinjett. *J Exp Bot.* 2014c;65:6441–56.
- Wang X, Vignjevic M, Liu F, Jacobsen S, Jiang D, Wollenweber B. Drought priming at vegetative growth stages improves tolerance to drought and heat stresses during grain filling in spring wheat (*Triticum aestivum* L. cv. Vinjett). *Plant Growth Regul.* 2015;75:677–87.
- Wei L, Zhang D, Xiang F, Zhang Z. Differentially expressed miRNAs potentially involved in the regulation of defense mechanism to drought stress in maize seedlings. *Int J Plant Sci.* 2009;170:979–89.
- Wei L, Wang L, Yang Y, Wang P, Guo T, Kang G. Absciscic acid enhances tolerance of wheat seedlings to drought and regulates transcript levels of genes encoding ascorbate-glutathione biosynthesis. *Front Plant Sci.* 2015;6:458.
- Whittle C, Otto S, Johnston M, Krochko J. Adaptive epigenetic memory of ancestral temperature regime in *Arabidopsis thaliana*. *Botany.* 2009;87(6):650–7.
- Windauer L, Altuna A, Benecch-Arnold R. Hydrotic analysis of *Lesquerella fendleri* seed germination responses to priming treatments. *Ind Crops Products.* 2007;25:70–4.
- Xiang Y, Tang N, Du H, Ye H, Xiong L. Characterization of *OsbZIP23* as a key player of the basic leucine zipper transcription factor family for conferring abscisic acid sensitivity and salinity and drought tolerance in rice. *Plant Physiol.* 2008;148:1938–52.

- Xie F, Stewart CN, Taki FA, He Q, Liu H, Zhang B. High-throughput deep sequencing shows that microRNAs play important roles in switchgrass responses to drought and salinity stress. *Plant Biotechnol J*. 2014;12:354–66.
- Xu Z, Zhou G. Responses of leaf stomatal density to water status and its relationship with photosynthesis in a grass. *J Exp Bot*. 2008;59:3317–25.
- Yamaguchi-Shinozaki K, Shinozaki K. Organization of cis-acting regulatory elements in osmotic- and cold-stress-responsive promoters. *Trends Plant Sci*. 2005;10:88–94.
- Yuan-Yuan S, Yong-Jian S, Ming-Tian W, Xu-Yi L, Xiang G, Rong H, Jun M. Effects of seed priming on germination and seedling growth under water stress in rice. *Acta Agron Sin*. 2010;36:1931–40.
- Zadraznik T, Hollung K, Egge-Jacobsen W, Meglic V, Sustar-Vozlic J. Differential proteomic analysis of drought stress response in leaves of common bean (*Phaseolus vulgaris* L.). *J Proteomics*. 2013;78:254–72.
- Zhang B. MicroRNA: a new target for improving plant tolerance to abiotic stress. *J Exp Bot*. 2015;66:1749–61.
- Zhang J, Davies W. Changes in the concentration of ABA in xylem sap as a function of changing soil water status can account for changes in leaf conductance and growth. *Plant Cell Environ*. 1990;13:277–85.
- Zhang X, Zou Z, Gong P, Zhang J, Ziaf K, Li H, Xiao F, Ye Z. Over-expression of microRNA169 confers enhanced drought tolerance to tomato. *Biotechnol Lett*. 2011;33:403–9.
- Zhang Z, Liu X, Wang X, Zhou M, Zhou X, Ye X, Wei X. An R2R3 MYB transcription factor in wheat, *TaPIMP1*, mediates host resistance to *Bipolaris sorokiniana* and drought stresses through regulation of defense- and stress-related genes. *New Phytol*. 2012;196:1155–70.
- Zhang JY, Cruz DECMH, Torres-Jerez I, Kang Y, Allen SN, Huhman DV, Tang Y, Murray J, Sumner LW, Udvardi MK. Global reprogramming of transcription and metabolism in *Medicago truncatula* during progressive drought and after rewatering. *Plant Cell Environ*. 2014;37:2553–76.
- Zhang N, Sun Q, Zhang H, Cao Y, Weeda S, Ren S, Guo YD. Roles of melatonin in abiotic stress resistance in plants. *J Exp Bot*. 2015;66:647–56.
- Zhou X, Wang G, Zhang W. UV-B responsive microRNA genes in *Arabidopsis thaliana*. *Mol Syst Biol*. 2007;3:103.
- Zhou L, Liu Y, Liu Z, Kong D, Duan M, Luo L. Genome-wide identification and analysis of drought-responsive microRNAs in *Oryza sativa*. *J Exp Bot*. 2010;61:4157–68.
- Zhou M, Li D, Li Z, Hu Q, Yang C, Zhu L, Luo H. Constitutive expression of a miR319 gene alters plant development and enhances salt and drought tolerance in transgenic creeping bentgrass. *Plant Physiol*. 2013;161:1375–91.
- Zhou S, Li M, Guan Q, Liu F, Zhang S, Chen W, Yin L, Qin Y, Ma F. Physiological and proteome analysis suggest critical roles for the photosynthetic system for high water-use efficiency under drought stress in *Malus*. *Plant Sci*. 2015;236:44–60.
- Zuo B, Zheng X, He P, Wang L, Lei Q, Feng C, Zhou J, Li Q, Han Z, Kong J. Overexpression of *MzASMT* improves melatonin production and enhances drought tolerance in transgenic *Arabidopsis thaliana* plants. *J Pineal Res*. 2014;57:408–17.

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