



# How do plants remember drought?

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Received: 19 March 2022 / Accepted: 21 May 2022 / Published online: 10 June 2022  
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## Abstract

**Main conclusion** Plants develop both short-term and transgenerational memory of drought stress through epigenetic regulation of transcription for a better response to subsequent exposure.

**Abstract** Recurrent spells of droughts are more common than a single drought, with intermittent moist recovery intervals. While the detrimental effects of the first drought on plant structure and physiology are unavoidable, if survived, plants can memorize the first drought to present a more robust response to the following droughts. This includes a partial stomatal opening in the watered recovery interval, higher levels of osmoprotectants and ABA, and attenuation of photosynthesis in the subsequent exposure. Short-term drought memory is regulated by ABA and other phytohormone signaling with transcriptional memory behavior in various genes. High levels of methylated histones are deposited at the drought-tolerance genes. During the recovery interval, the RNA polymerase is stalled to be activated by a pause-breaking factor in the subsequent drought. Drought leads to DNA demethylation near drought-response genes, with genetic control of the process. Progenies of the drought-exposed plants can better adapt to drought owing to the inheritance of particular methylation patterns. However, a prolonged watered recovery interval leads to loss of drought memory, mediated by certain demethylases and chromatin accessibility factors. Small RNAs act as critical regulators of drought memory by altering transcript levels of drought-responsive target genes. Further studies in the future will throw more light on the genetic control of drought memory and the interplay of genetic and epigenetic factors in its inheritance. Plants from extreme environments can give queues to understanding robust memory responses at the ecosystem level.

**Keywords** ABA · DNA methylation · Drought memory · Epigenetics · Histone modifications

Communicated by Gerhard Leubner.

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## Introduction

By the year 2050, the world population will reach near 10 billion. On the other hand, agricultural production may not be sufficient to feed the growing billions due to global warming and increased frequencies of drought and desertification (Salinger 2005). Drought will complicate matters further by reducing the nutrient availability and altering the patterns of pest and disease infestations of plants. It is estimated that India and the USA currently experience a 15–20% yield loss in agriculture due to drought, projected to increase in the future (Leng and Hall 2019). Severe drought usually causes damage to a plant, preventing reproduction, causing senescence, and ultimately leading to death. However, a short-term moderate drought may permit plant recovery upon stress withdrawal. Sessile plants have evolved several adaptive strategies to survive droughts, viz., drought

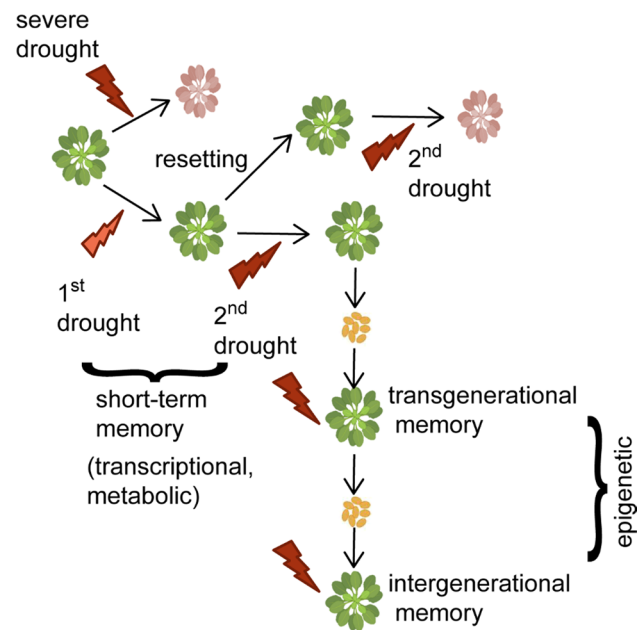
avoidance with deeper roots, succulent stems, stomatal closure at high water potentials, high tissue elasticity, and crassulacean acid metabolism (CAM) mode of photosynthesis, drought endurance by leaf shedding, and drought tolerance by stomatal closure at low water potentials, low hydraulic conductance of xylem, leaf size reduction and accumulation of osmoprotectants. In addition, some ephemerals like *Arabidopsis* bypass stress altogether by temporal control of their life cycles (Ward 2016).

But the catch is that single stress events are rare. Plants practically experience frequent spells of drought, often with intermittent recovery intervals. In such a fluctuating stress scenario, the survival of plants critically depends on the ability to “remember” or “learn” and “recall” the past events of drought, altering its physiology to present a more rapid and robust response to the subsequent drought. This adaptive process is designated by priming, memory, and acclimation. It is perplexing that plants have “memory,” usually considered a monopoly of higher animals having a centralized “brain” and complex neuronal networks. However, this assumption is entirely wrong, as all living beings, including plants, are equipped with memorization capacity, the basis of adaptive evolution (Galviz et al. 2020).

Figure 1 describes the various types of drought memory in plants. Plants remember exposure to drought for several days to weeks. This is due to transcriptomic and metabolic alterations within the somatic cells and is effective within the same generation. Accumulation of specific dormant signaling molecules like transcription factors (TFs) activated upon the subsequent stress exposure has been found for short-term memory of drought. These molecular events are reflected in physiological events like partial stomatal closure and slowing down photosynthesis as preparatory strategies for the next drought. However, the ultimate level of control of various genes for drought memory lies in the epigenetic regulation of the chromatin, which leads to both short-term memories and the passage of memory to future generations through germ cells developing during the drought exposure. In this review, we look into our current understanding of the molecular mechanisms of plant memory to drought—both in the short term and across generations. We explore gaps in our current knowledge of plant drought memory and promising areas of future explorations and applications for crop improvement.

## Transcriptional memory of drought

To understand how plants remember drought in the short term within a single generation, most researchers followed a simple experimental setup, wherein watered plants (W) were given a first drought treatment (D1) followed by a watered recovery interval (R1). Subsequently, more droughts and



**Fig. 1** Drought memory in plants. Severe drought may kill a plant, but a mild drought or a drought for a short duration can trigger short-term memory, usually established by transcriptional training or metabolic reprogramming, leading to survival under a subsequent drought. Sometimes, the memory may be reset or erased upon a prolonged watered recovery interval, leading to drought sensitivity in the subsequent exposure. The memory of stressed plants is carried over to the next generation, termed transgenerational memory, which is usually attributed to epigenetic changes like DNA methylations. The persistence of memory in two or more generations is intergenerational memory

recovery intervals followed (i.e., D2, R2, D3, etc.). Under these conditions, researchers carried out transcriptome analyses to identify the expression patterns of different genes, revealing four distinct types of memory (Ding et al. 2013). Those genes that exhibited progressively higher expression levels under subsequent droughts were designated as [+ / +]. Genes belonging to abscisic acid (ABA)-dependent signaling, TFs, late embryogenesis abundant (LEA) genes, lipid transfer proteins, chaperones, ion transporters, and membrane protectants belonged to this category. A higher expression of these genes in D2 signifies their higher protective functions in the subsequent drought. Genes for ribosome assembly and protein synthesis, and the chlorophyll-binding light-harvesting protein complex of photosystem II (PSII), were progressively downregulated in a [− / −] fashion, signifying attenuation of chloroplast functions. The third class of memory genes included other chloroplast membrane proteins and those belonging to the electron transport chain, which, although downregulated in D1, had increased levels in D2, exhibiting a [− / +] pattern. This signifies the restoration of photosynthetic functions under subsequent drought. The fourth category of transcriptional memory behavior was

of the [+/-] type, including genes of phytohormone signaling, ion transporters, and aquaporins, whose expression gets induced in D1 but reduces in D2, possibly functioning to readjust ion homeostasis under re-iterated drought (Ding et al. 2013).

### Alteration of photosynthesis under recurrent droughts

The exposure of the plant to the first drought causes an increase in the drought stress hormone ABA leading to stomatal closure, reduced carbon dioxide intake, decreased photosynthesis capacity, and photoinhibition of PS. As a result, accumulating energy in the chloroplast leads to reactive oxygen species (ROS) production, causing cellular damage and further degradation of photosynthetic pigments. To counter this, plants exposed to drought reduce the light-harvesting complex of PSII to minimize the energy accumulation and resultant ROS in the chloroplast (Fleta-Soriano and Munné-Bosch 2016; Godwin and Farrona 2020). Also, as an immediate measure to reduce photosystem damage, a drop in photosynthesis is accompanied by increased heat dissipation and chlorophyll fluorescence. In sugar beet, photosynthesis was drastically reduced in all three cycles of recurrent drought, displaying unexpected increase in chlorophyll fluorescence (Leufen et al. 2016). In potato, the genes encoding chlorophyll a/b binding protein of PSII and proteins involved in chlorophyll biosynthesis had reduced expression in D1. However, the level of these PSII genes increased in D2 through a memory response in both potato and rice (Chen et al. 2020; Auler et al. 2021). In another study in rice, several pigment biosynthesis genes and those encoding photosystem I reaction center proteins were suppressed in D1 but maintained at constant levels in D2. In addition, genes of chloroplast retrograde signaling also displayed memory behavior, suggesting their possible role in drought acclimation (Li et al. 2019).

However, *Dipteryx alata*, endemic to the Brazilian savanna and adapted to a recurrent drought environment, memorized and acclimated to drought differently, without compromising photosynthesis. Plants exposed to three drought cycles (D3) maintained higher carbon fixation rates than only D1-exposed plants by keeping the stomata open and maintaining higher stomatal conductivity and leaf hydraulic conductance. However, chlorophyll did not degrade in any of the drought cycles. Maintained photosynthesis could fuel cellular defense and respiratory processes in D3 plants, comparable to control levels. In contrast, the D1 plants had higher visible ROS-induced damage due to the stomatal closure, impairment of photosynthesis, and higher respiration rates than control or D3 plants, shunning metabolites from other processes to the Krebs cycle (Alves

et al. 2020). Despite having a higher stomatal conductance leading to more water loss, D3 *D. alata* plants survived drought by increasing the accumulation of solutes for osmotic adjustment (Martorell et al. 2015).

### Role of osmolytes under recurrent droughts

Plants can survive droughts for a more extended period by synthesizing and accumulating osmolytes in the cell. These are small-sized, water-soluble neutral molecules, helpful in maintaining positive turgor pressure of the cell, stabilizing the proteins and membranes, and protecting the photosynthesis machinery from ROS (Yancey 2005; Szabados and Savaure 2010; Meena et al. 2019). These include small non-reducing sugars and other amine compounds (Lahuta et al. 2022). Soluble sugars increased along with recurrent drought stresses (Woodruff and Meinzer 2011; Sala et al. 2012; Li and Liu 2016). While a fivefold increase of proline was observed in the D1, it was 50-fold after D2 in pea plants (Lahuta et al. 2022). Expression of the proline biosynthesis gene *P5CS* was higher in subsequent droughts after acclimation in potato (Chen et al. 2020). Switchgrass exposed to multiple droughts upregulated the trehalose and proline biosynthesis genes. Trehalose plays a vital role in the osmotic adjustment of cells during secondary stress (Zhang et al. 2018a, b). Similarly, the levels of another osmolyte myoinositol increased with drought exposure but decreased after re-watering (Galiano et al. 2017). Plants produce glycine-rich hydrophilic LEA proteins that accumulate in the intracellular spaces to tolerate drought stress by stabilizing the cell membrane and protein structure (Magwanga et al. 2018), a common mechanism to handle dehydration in all life forms (Hundertmark and Hincha 2008). *LEA* genes were induced to higher levels under D2 in potato, indicating their roles in drought acclimation (Chen et al. 2020).

### Role of phytohormones in drought memory

ABA levels increase under drought, playing critical roles in tolerance response. These include regulation of stomatal closure to prevent water loss and triggering signal cascades that lead to the transcriptional activation of downstream genes via the ABA-responsive *cis*-element (ABRE) in their promoters (Osakabe et al. 2014). The genes downstream to ABA encode proteins that lead to membrane protection and detoxification of ROS and osmolytes, which synergistically protect the plant cell from damage (Todaka et al. 2019). Many ABA-responsive downstream genes, e.g., *RD29B*, encoding LEA-like proteins acting as warning signals (Msanne et al. 2011) and *RAB18*, encoding a cell-protective dehydrin (Hallouin et al. 2002) exhibited [+/+] memory that

persisted 5–7 days in *Arabidopsis* and maize (Ding et al. 2013, 2014). Several ABA-responsive *LEA*-like genes that code for hydrophilic proteins, protecting plants from desiccation tolerance (Hand et al. 2011), had increasing levels of transcripts and proteins in subsequent droughts and recovery intervals in the desiccation-tolerant plant *Craterostigma plantagineum* (Liu et al. 2019). Interestingly, in an invasive CAM xerophyte, *Aptenia cordifolia*, and the C4 switchgrass, even higher ABA levels were produced under D2 than in D1, suggesting significant roles of ABA in drought memory (Fleta-Soriano et al. 2015; Zhang et al. 2018a, b). Following ABA levels, the ABA biosynthesis *NCED* gene family transcripts in switchgrass displayed superinduced [+/+] behavior. In contrast, the ABA catabolism gene *CYP703A3* was downregulated in D1 and D2 (Zhang et al. 2018a, b). ABA is primarily synthesized in the roots, which sense drought in the soil and is transported through the xylem to the leaves to induce stomatal closure (Zhu 2002). This is why rootstock genotypes strongly influence re-iterated drought acclimation in grafted citrus plants due to the difference in their ABA synthesis capacities (Neves et al. 2017).

### ABA regulates drought memory of stomatal guard cells

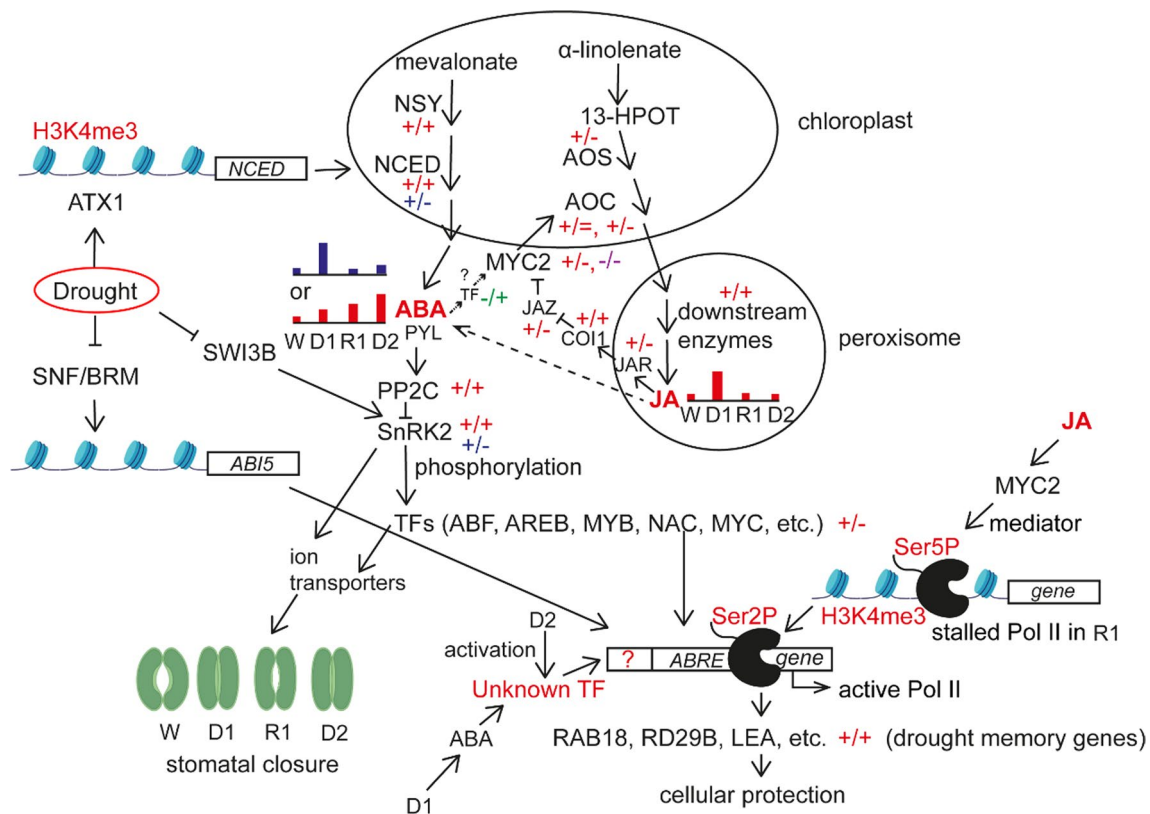
The guard cells surrounding the stomatal aperture play critical roles in stomatal closure and display different transcriptional memory than the surrounding mesophyll cells (Virilouvet and Fromm 2015). Stomata close on every drought exposure to minimize water loss, but interestingly, stomatal reopening is partial in R1, showing evidence of drought memory (Fig. 2). Under prolonged water availability, however, this memory is lost. Guard cell memory is dependent on ABA levels as the transpiration rates from stomata are the same in D1 and D2 in the ABA-deficient *aba2* mutant (Nambara et al. 1998). A higher expression of *NCED3* and *AAO3* and resultant higher ABA synthesis in guard cells leads to higher levels of ABA during R1 than the surrounding mesophyll cells. Even though mesophyll cell transcript levels of these genes return to W values during R1, the guard cell-specific transcript levels remain high, explaining partial stomatal closure in R1. On the other hand, higher transcript levels of ABA-dependent TFs regulating stomatal closure (Li et al. 2008) and lower transcript levels of TFs regulating stomatal opening (Oh et al. 2011; Rusconi et al. 2013) in guard cells during R1 bring about the partial stomatal closure. Finally, the downstream ion transporters for stomatal opening have lower transcript levels in D1 in guard cells, decreasing stomatal opening in D1. During R1, their transcript levels return to that in W. On the other hand, a subset of ion transporter genes for stomatal closure has higher R1-expression in guard cells, facilitating partial stomatal closure. Moreover, different

ABA-regulated drought-tolerance genes have higher transcript levels during D2 in guard cells. (Virilouvet and Fromm 2015).

### ABA regulates signaling and transcription for drought memory

ABA exerts its role in the memory patterns of drought-responsive genes, e.g., *RD29B*, through the ABRE (Uno et al. 2000). Deleting the ABREs from the promoter led to the abolition of transcriptional memory of *RD29B*. However, ABRE-flanking sequences have some role in the variation in memory behavior of two genes, both containing ABRE in their promoters (Virilouvet et al. 2014). Analysis of memory patterns in *Arabidopsis* ABA-signaling mutants suggests that ABA controls drought memory through the SnRK2/ABF/ABRE signaling pathway (Fujii et al. 2009; Ding et al. 2013; Fujita et al. 2013; Karle et al. 2020). Corroborating these results, several *SNRK2* orthologs displayed memory behavior in rice and switchgrass, increasing transcripts in D2 and decreasing in R1 (Zhang et al. 2018a, b; Li et al. 2019). On the other hand, the ABA-independent SnRK2s exert opposite repressive roles to transcriptional memory (Fujii et al. 2011; Virilouvet et al. 2014). Protein levels of TFs, ABF3, and ABF4 slightly increased in D2, and after posttranslational modifications, they regulate memory of *RD29B*. In switchgrass, ABF genes behaved as non-memory gene, i.e., maintained at constant levels after their induction during D1 [+/=] (Zhang et al. 2018a, b). ABA, once bound to its co-receptors *PYL* and *PP2C*, prevents the inhibitory action of *PP2Cs*, leading to the activation of SnRKs (Umezawa et al. 2009; Karle et al. 2020). Three *PP2C* orthologs behaved as a superinduced memory gene, i.e., with progressively higher expression in D1 and D2 [+/+] in maize, switchgrass, and soybean, while some other orthologs showed induction in D1, but suppression in D2 [+/-] or transcript levels maintained equally in D2 after their induction in D1 [+/=] (Ding et al. 2014; Zhang et al. 2018a, b; Kim et al. 2020). LRR-like kinases of ABA signaling showed [+/-] memory in coffee (Guedes et al. 2018). LRR-proteins interact with heat shock proteins (Lopes-Caitar et al. 2016), which although suppressed in D1, was induced during D2 [-/+ ] in coffee, indicating their function in the proper folding of proteins during drought acclimation (Guedes et al. 2018). Different ABA-responsive MYB TFs displayed memory under re-iterated drought. In *Arabidopsis*, MYBs showed [+/+] memory (Ding et al. 2013). In coffee, drought and ABA-suppressed transcriptional activator MYBs displayed [-/+ ] behavior, while repressor MYBs, showed a [+/-] pattern, being suppressed in D2 (Guedes et al. 2018).





**Fig. 2** Role of abscisic acid and jasmonate in transcriptional drought memory. The early steps of abscisic acid (ABA) and jasmonate (JA) synthesis occur in the chloroplast from the mevalonate and  $\alpha$ -linolenate pathways. The first drought exposure (D1) leads to induction in ABA biosynthesis genes *NSY* and *NCED* with respect to the watered control condition (W). After a water recovery interval (R1), a second drought (D2) leads to even higher transcript levels in these genes. This is indicative of a superinduced [+/+] memory behavior. Similar memory behavior is observed in the downstream genes of ABA signaling, viz. *PP2C* and *SnRK2*. In the absence of ABA, *PP2C* negatively regulates the signaling Kinase *SnRK2*. ABA binds to its receptor *PYL* and the co-receptor *PP2C* and this removes the negative regulation of *PP2C* on *SnRK2* kinases. Once *SnRK2* is activated by phosphorylation, it can activate downstream target proteins. The dynamics of *SnRK2*-activated ion transporters in the guard cells lead to stomatal closure in D1 and D2, but only partial closure in R1 (see main text). The transcript levels of the transcription factors (TFs) regulated by ABA via *SnRK2* are reduced in D2 than in D1 [+/-]. These TFs binds to the ABA-responsive element (ABRE) in the promoter of +/+ downstream drought-response genes, e.g., *RAB18*, *RD29B*, *LEA*, etc. whose gene products lead to protection of the cell under drought. In some plant species, ABA levels are reduced in D2, concomitant with the [+/-] memory behavior of *NCED* and *SnRK2* (shown in blue). In addition, drought-induced changes in the chromatin remodellers *ATX1*, *SNF/BRM* and *SWI3B* lead to their activation or abolition of inhibitory activity, causing activation of the transcription of *NCED*, *ABI5* *SnRK2* genes, respec-

tively. The upstream JA biosynthesis genes follow [+/-] behavior, but the downstream genes, whose products are localized in the peroxisome, observe [+/+] patterns. The net effect is the increased levels of JA in D1 but the reduction in D2. The TF *MYC2* is positioned at the crossroads of both ABA and JA-mediated signaling. *MYC2* follows a [+/-] memory pattern or progressive downregulation in both D1 and D2 [-/-] (shown in purple) and is regulated by JA through the *JAR*, *COI-1* and *JAZ*-mediated pathway. ABA also regulates *MYC2* via *PYL6* and by another unknown transcription factor which is suppressed in D1 but induced in D2 [-/+]. ABA triggers JA biosynthesis via *MYC2*, regulating the upstream biosynthesis genes of JA, *AOC* and *AOS*. The expression of JA biosynthesis genes of the  $\alpha$ -linolenate pathway in the chloroplast are induced in D1 but suppressed in D2 [+/-], while downstream JA biosynthesis genes in the peroxisome follow [+/+] patterns, with a net effect of increased JA levels in D1 followed by a decrease in D2. Again, JA is also found to trigger ABA biosynthesis. JA also causes recruitment of the transcriptional machinery to the promoters of ABA-responsive genes via *MYC2* and mediator protein complexes. But the RNA polymerase II is stalled in R1, marked by Serine 5 phosphorylation of the C-terminal tail of Pol II (Ser5P), and an unknown additional factor produced during D1 but activated only in D2 through an ABA-independent pathway triggers activation of the Pol II in forwarding motion, marked by serine 2 phosphorylation of Pol II C-terminal tail (Ser2P). Direct regulations are shown by bold lines and indirect regulations by dashed lines

**ABA alone is not sufficient for drought memory**

Surprisingly, the *aba2* mutant retains drought memory, although it fails to produce ABA (Virouvet et al. 2014).

Also, D1 plants cannot trigger memory if treated only with ABA but not D2. These observations, coupled with no observed specific *cis*-element for transcriptional memory, suggest that although necessary, ABA is insufficient for

triggering memory by itself. In *Arabidopsis*, rice, maize, and soybean, ABA levels increased during D1, D2, D3, etc. but returned to W levels in the water recovery intervals. In these cases, ABA levels in D2 and D3 were not higher than D1 (Ding et al. 2014; Virilouvet et al. 2018; Li et al. 2019; Thuy Quynh Nguyen et al. 2020). This is due to a [+/>+] behavior of the ABA catabolism genes *CYP707A3* and *CYP76C2* in these species (Ding et al. 2014). There was a sharp spike in ABA levels in D1, but ABA levels reduced in the subsequent droughts in rice. Similarly, all ABA-signaling genes, including *NCED3* and the rice orthologs of *SNRK2s*, *SAPKs*, followed [+/>-] behavior, indicating a species-specific alteration in drought memory behavior (Li et al. 2019).

The memory of superinduced genes was lost if the recovery intervals lasted more than seven days, even though ABA levels were retained (Ding et al. 2012). ABA levels were slightly higher than W, but insufficient to maintain the memory in R1, R2, and R3. In this case, neither ABA nor the ABA-dependent TFs (Yoshida et al. 2010) can explain the memory behavior, although essential for the superinduction of memory genes. It is speculated that ABA generated from D1 triggers an unknown factor activated by ABA-independent signaling, which leads to the superinduction of memory genes in D2 (Virilouvet et al. 2014). Even though transcription of the memory genes goes down in R1, R2, and R3 back to W levels, certain epigenetic marks are still maintained, and the RNA polymerase is stalled, only to be re-activated into transcription by some unknown ‘pause-breaking’ factor in D2 (Fig. 2) (Ding et al. 2012).

### Jasmonic acid and other phytohormones regulate drought memory

Jasmonic acid (JA) is another phytohormone rapidly produced during drought protecting plants from oxidative damage (Sasaki-Sekimoto et al. 2005; Ding et al. 2013; Wang et al. 2021). JA signals the TF MYC2 through the COI-1-JAR1-JAZ pathway to activate the [+/>-] JA-related drought memory genes (Fig. 2) (Ding et al. 2014; Liu et al. 2016). JA accumulates during D1 in most plants but is formed in low levels in R1 and D2, equivalent to W. JA is produced from  $\alpha$ -linolenate in chloroplasts, catalyzed by enzymes allene oxide cyclase (AOC) and allene oxide synthase (AOS), which followed [+/>-] memory patterns in switchgrass (Zhang et al. 2018a, b), and [+/>=] non-memory behavior in maize (Ding et al. 2014). But the peroxisome-localized downstream enzymes of JA biosynthesis were encoded by [+/>+] superinduced genes. Although there is a discrepancy between the transcript levels of the downstream biosynthesis genes and the JA levels in D2, unidirectional [+/>+], [-/>-], and [+/>-] memory response of many JA-responsive genes indicates that JA has a vital role in drought memory (Ding et al. 2013). On the other hand, the chloroplast-localized

upstream JA biosynthesis genes, *AOC* and *AOS*, are regulated by the bHLH TF MYC2 in S1, but not in S2, because MYC2 orthologs follow [+/>-] and [-/>-] memory patterns. This can partially explain why JA levels reduce in D2 despite the [+/>+] behavior of the downstream genes of JA biosynthesis in the peroxisome. Most JA signaling genes, including an AP2/ERF family TF, showed conserved [+/>-] memory behavior in most plants (Ding et al. 2014). It is speculated that an unknown ABA-responsive TF activated by drought, possibly having an opposite [-/>+] memory, induces MYC2 in D1 but suppresses it in D2, leading to [+/>-] memory behavior of most of the JA-related genes (Liu et al. 2016; Avramova 2018). The cross-talk of ABA and JA in drought memory is explained graphically in Fig. 2.

MYC2 is a focal point of the cross-talk between various phytohormone signaling, ABA, JA, salicylate (SA), gibberellic acid (GA), and auxin (Kazan and Manners 2013). ABA triggers the JA biosynthesis genes through MYC2, which physically binds the ABA receptor PYL6 (Adie et al. 2007; Aleman et al. 2016; Avramova 2018). Among other phytohormones, the biosynthesis genes of GA, auxin, ethylene, and zeatin (cytokinin) of potato, switchgrass, and the resurrection plant *Boea hygrometrica* display superinduced memory behavior (Zhang et al. 2018a, b; Chen et al. 2020; Sun et al. 2021). This coupled with the observed increase of auxin levels (Neves et al. 2017) and reduction in salicylic acid in roots under re-iterated drought (Miura et al. 2013), indicates the roles of a myriad of phytohormones in drought memory. In *B. hygrometrica*, along with *CTK* genes encoding cytokinin biosynthesis enzymes, high-affinity nitrate transporters were superinduced in D2 (Sun et al. 2021). Nitrate signals upregulate cytokinin biosynthesis affecting plant development under stress (Sakakibara et al. 2006; Wang et al. 2016). In *A. cordifolia*, GA levels reduced progressively in D1 and D2, which synergistically with the steady increase in ABA levels in D1 and D2, increase production of ROS for stress signaling without causing photo-oxidative damage (Fleta-Soriano et al. 2015).

### Epigenetic regulation of drought memory

Epigenetic modifications include heritable changes in gene expression via chromatin modifications through DNA methylation and histone modifications, e.g., methylation and phosphorylation, and post-transcriptional regulation of RNAs via RNA interference (Hirayama and Shinozaki 2010; Santos et al. 2011). DNA methylation, chromatin modifications, and small interfering RNAs (siRNAs) play vital roles in the epigenetic regulation of genes involved in stress memory. Memory can be inherited to the offspring through mitotic cell divisions, as plants develop germ cells late in their life cycle (Kinoshita and Seki 2014). So, any

epigenetic modifications occurring in the juvenile phase can be transferred to the next generations. But maladaptive epigenetic marks at one part of the plant are prevented from getting inherited by future generations if the plant produces seeds many times in its life cycle. Also, seeds arising from different meristems add to the variability of the epialleles (Galviz et al. 2020).

### Histone modifications

Histones are essential components of the chromatin structure. Histone variations and posttranslational modifications play crucial roles in chromatin structure and accessibility of the RNA polymerase, regulating the transcriptional status of genes. The linker histone H1 variations play a significant role in chromatin remodeling. The variant H1.3 increases under stress, essential for normal stomatal function and adaptive developmental responses to light and water stress. ABA-mediated drought signaling causes H1.3 to be expressed in stomatal guard cells (Rutowicz et al. 2015).

Plants remember drought by modifying histones associated with numerous drought-induced genes. Enhanced H3K4 methylation marks the recently activated drought and ABA-response genes for enhanced reactivation in response to recurrent droughts (Kim et al. 2008; Zhang et al. 2009; Van et al. 2010; Levine 2011). Under drought stress, H3K4me3 modification redundantly by the methylase ATX1 triggers *NCED3* expression for ABA production (Ding et al. 2011). As these epigenetic marks are enriched during D1 and sustained throughout R1, they play a role in transcriptional memory (He and Li 2018).

Interestingly out of the [+/-] Arabidopsis superinduced genes, transcript levels of a subset remained high at R1. But, transcripts of the other subgroup decreased in R1. This is due to subset-specific histone modification by CLF, a subunit of polycomb-group proteins. Although the histone modifications H3K27me3 and H3K4me3 antagonize each other in developmental genes, these modifications were not antagonistic in the drought memory genes. H3K27me3 could not prevent transcription, possibly due to the effects of other activating TFs produced under drought, but limit the full expression potential of memory genes. This suggests that histone modifications have completely different regulatory dynamics between developmental versus memory genes (Liu et al. 2014).

In addition, a linker histone variant H1-S was upregulated by drought through ABA signaling in tomato (Scippa et al. 2004; Chinnusamy and Zhu 2009). The SWI/SNF nucleosome remodeling protein alters gene expression of ABA-signaling genes. In the absence of stress, SWI3B interacts with HABI1, a PP2C inhibiting ABA signaling. The SNF/Brahma chromatin remodeling complexes negatively regulate drought tolerance by repression of ABI5 (Han et al.

2012). Drought stress inhibits SWI/SNF complexes leading to the activation of ABA-regulated stress response genes. Thus, ABA is intricately linked with histone modifications for drought memory (Mehrotra et al. 2014). This relationship of ABA with histone modifications is graphically explained in Fig. 2.

### DNA methylation changes for short-term drought memory

DNA methylation at the cytosine residues is an epigenetic mark that regulates gene expression and is one of the means for drought memory to be transmitted to the next (intergenerational memory) or more subsequent generations (transgenerational memory). DNA methylation in plants occurs by various methyltransferases, at CG sequences (gene body methylation), at CHG (H = A, C or T), and methylation de novo at asymmetrical CHH sequences triggered by the RNA-directed DNA methylation (RdDM) pathway. Methylation at the regulatory regions of a gene shuts off gene expression, while demethylation by demethylases turns it on (Zhang et al. 2018a). Drought induces a change in methylation patterns of the genomic DNA in various plant species (Wojtyla et al. 2020). Consistent with DNA hypermethylation under drought (Labra et al. 2002), in drought-tolerant clones of coffee, a methyltransferase showed [-/+ ] transcriptional memory (Guedes et al. 2018).

By contrast, the promoters of proline biosynthesis genes are demethylated, activating transcription, leading to higher proline contents for enhanced protection under D2 (Zhang et al. 2013). Drought-tolerant rice genotypes were associated with cytosine demethylation, whereas the sensitive genotypes showed hypermethylation (Gayacharan 2013; Kou et al. 2021). DNA methylation in Arabidopsis and rice was found to have a wide variation with the genotype, and the sequence variations within specific methylases and argonautes, regulating this trait, were identified by a genome-wide association study (GWAS) (Kawakatsu et al. 2016; Rajkumar et al. 2020; Zhang et al. 2020). The sensitive genotypes of rice had more differentially methylated regions (DMRs), indicating the role of methylation in the short-term drought memory of rice. Interestingly most of these DMRs were within the CHH sequences and in transposons, showing the most significant role of the RdDM pathway, which affects CHH methylation. However, repeated drought stress led to the stable maintenance of methylation patterns sculpted by the first drought exposure. Besides transposons, memory DMRs were also associated with osmolyte biosynthesis and JA signaling (Li et al. 2019). Cytosine methylation in *B. hygrometrica* is more robustly maintained than Arabidopsis and other crops. DNA demethylation was found in drought-acclimated plants at all symmetrical sites, viz. CG and CHG, but the asymmetrical CHH sequences remained

hypermethylated. DNA demethylation was observed in the promoters of memory genes, guiding alternative splicing under stress, producing raffinose, and maintaining homeostasis of amino acids between the vacuole and cytoplasm, leading to the upregulation of these genes in D2 (Fig. 3) (Sun et al. 2021).

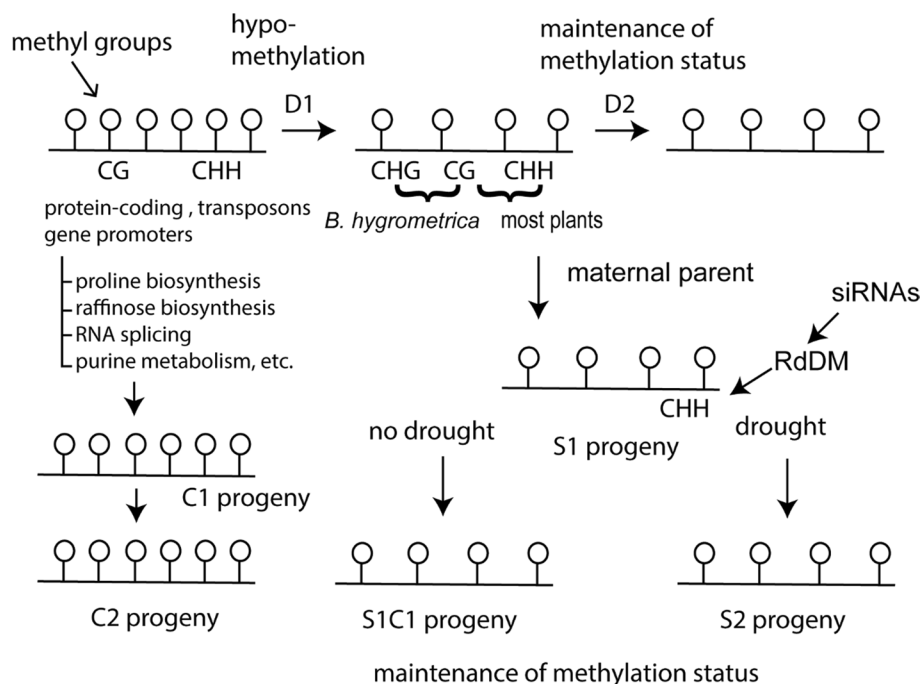
Apart from the influence of the genotype, drought alone can shape epigenomic diversity. In genetically identical poplar clones grown in varied geographic conditions, variation in DNA methylation due to prior drought exposures was observed. This variation guided differential transcriptomic changes determining the drought adaptability of the poplar clones (Raj et al. 2011). Environmentally-associated differences in methylation (epialleles) have also been identified in *Arabidopsis* (He et al. 2018).

### Role of DNA methylation in transgenerational drought memory

Ganguly et al. (2017) found transgenerational changes in DNA methylation are not correlated with drought memory in *Arabidopsis*. Sometimes, memory development requires

drought exposure for a minimum of two generations (Kron et al. 2008; Pecinka et al. 2012). But, in *Polygonum persicaria*, the inherited methylation patterns in the progeny of drought-exposed parents determined transgenerational drought memory. In this plant, the progenies of the drought-exposed parents were better equipped to counter drought, possessing longer roots than the progeny of the non-stressed parents, a phenotype abolished by methylation inhibitors. Different genotypes resulted in methylation and memory variations in the progeny, indicating genetic control of the process (Herman and Sultan 2016).

In *Arabidopsis*, homologous recombination frequency (HRF) and DNA methylation decreased by drought in the progeny of stressed plants (S1) relative to the progeny of the unstressed plants (C1). These changes in HRF were preserved in the next generation of stressed S1 plants (S2) but not in the second-generation progeny of the unstressed S1 plants (S1C1). However, the changes in DNA methylation due to drought stress exposure in the starting generation were maintained equally in all subsequent generations, S1, S2, and S1C1 regulated by RdDM-triggered CHH methylation (explained graphically in Fig. 3) (Boyko et al. 2010;



**Fig. 3** Maintenance of DNA methylation for drought memory. Drought (D1) causes demethylation in most plants' CG and CHH sequence contexts, but in the CG and CHG sequences in *Boea hygrometrica*. The change in methylation status in the promoter of protein-coding genes leads to their activation causing drought tolerance. A second drought (D2) does not change the methylation status further, which is maintained. The methylation patterns of stressed plants are inherited to the next generation (S1) through the maternal parent. No further change in methylation is observed, and this status is inher-

ited by the second generation of stressed (S2) or non-stressed plants (S1C1). On the other hand, the hypermethylated status of control non-stressed plants of the starting generation is transmitted to subsequent generations C1 and C2. Methylation levels of S1, S2 and S1C1 plants are lower than the control C1 and C2 plants. The role of siRNA-mediated methylation in the CHH context through the RNA-directed DNA methylation pathway is important for the transgenerational drought memory



Walter et al. 2011; Luna et al. 2012). Transgenerational memory is passed on to the offspring only from the maternal parent because a DNA glycosylase produced from the pollen vegetative cell and a central cell in the female gametophyte inhibits paternal inheritance (Choi et al. 2002; Park et al. 2020) through demethylation of transposons leading to the production of siRNAs which starts deactivating neighboring paternal genes through RNA-induced transcriptional silencing (Calarco et al. 2012; Zhang et al. 2018a, b; Park et al. 2020).

### Non-coding RNAs regulate drought memory

Small non-coding RNAs are also the vehicles that transmit the drought memory to the next generation (Brosnan and Voinnet 2011). Systemic movement of drought-triggered small RNAs via the symplast and vascular tissues to the meristem results in DNA methylation by the RdDM pathway (Melnik et al. 2011).

#### Long non-coding RNA

Long non-coding RNAs (lncRNAs) operate as precursors of microRNAs (miRNAs) and other siRNAs or as miRNA target mimics, regulating many biological processes (Kim and Sung 2012). Also, they influence chromatin dynamics and alternative splicing of pre-mRNA (Liu et al. 2015). Antisense lncRNAs were enriched in regions differentially methylated recurrent osmotic stress, suggesting the combined role of DNA methylation and lncRNA-mediated gene regulation for memory (Mozgova et al. 2019). In rice, 6% of lncRNAs show transcriptional drought memory. Among them, TCONS\_00028567 and its product miRNA showed strong induction at D2 but reduced levels after R3 and following droughts including ABA and ethylene signaling via *SAPK10* (Li et al. 2019). In switchgrass, levels of ABA and trehalose and that of the lncRNAs targeting their biosynthesis increased progressively in D1 and D2. However, ethylene signaling and its regulator lncRNAs were suppressed in D2, promoting plant development and preventing leaf senescence (Zhang et al. 2018a, b). Differentially expressed lncRNAs have also been identified under drought in other species (Urquiaga et al. 2021), wherein they post-transcriptionally regulate several drought-responsive TFs (Suksamran et al. 2020) or behave as target mimics of miRNAs (Shuai et al. 2014). In particular, the identified roles of lncRNAs in the regulation of DNA methylation via the RdDM pathway (Heo and Sung 2011; Yong-Villalobos et al. 2015; Ariel et al. 2020) place them as potent regulators of drought memory (Urquiaga et al. 2021).

### Micro RNA

MiRNAs regulate cellular processes of drought adaptation like development, phytohormone signaling, antioxidant defense, osmoprotection, photosynthesis, etc., through the upregulation and downregulation of positive and negative regulatory molecules. MiRNAs participate in stress memory through directed DNA methylation and various histone modifications (Sunkar and Zhu 2004; Sun et al. 2021). MiRNAs associate with Argonaute proteins to target complementary mRNA cleavage or translational inhibition (Gelaw and Sanan-Mishra 2021). MiRNAs amplify the silencing signal by generating siRNAs via RNA-dependent RNA polymerases (Creasey et al. 2014). Several miRNAs are upregulated under drought, targeting drought-responsive TFs (Liu et al. 2008; Jacques et al. 2021). In a unique example, grafting rapeseed scions into a more -tolerant turnip improved its drought memory, possibly due to the movement of miRNAs between the rootstock and scion (Pagliarani et al. 2017; Luo et al. 2020). Several miRNAs revealed distinct patterns of transcriptional memory behavior under repeated drought cycles in coffee and exerted complex regulation with their targets, the memory MYBs (Guedes et al. 2018).

### Resetting drought memory

Short-term drought memory is usually reset after a prolonged watered recovery. Like heat stress, autophagy genes may have critical roles in resetting short-term drought memory, possibly by clearing protective gene products like heat shock proteins (Sedaghatmehr et al. 2019). Moreover, since each generation of plants faces stress conditions different from the previous generation, the inherited memory is erased in the new generation in the early stages of development to ensure normal growth of the plant. Although the mechanism of erasing trans-generational drought memory is unknown, a screening of Arabidopsis mutants impaired in resetting stress memory indicated the involvement of chromatin accessibility factors and siRNA-mediated silencing (Yokthongwatana et al. 2010; Zhou et al. 2010; Iwasaki and Paszkowski 2014) in preventing transgenerational memory. However, how these proteins erase the epigenetic marks are not well understood. Histone demethylases may also play some role in resetting drought memory, as an ortholog of this enzyme in barley was induced under drought (Papaefthimiou and Tsaftaris 2012). In the sperm cells, histone methylases are silenced, demethylases are induced, and methylation-resistant histone variants are recruited to the chromatin to re-configure the paternal epigenome (Borg et al. 2020).

## Ecosystem-level drought memory

An intriguing question is whether plants remember a drought as an individual or a community. Recent studies hint towards the existence of ecological memory for drought. Entire juniper forests growing for centuries at drier sites of the Tibetan plateau are more susceptible to drought-induced damages than forests growing in wetter regions without prior history of droughts (Fang et al. 2021). This may be because detrimental effects of ecological drought memory last several decades after exposure, as observed in Mediterranean holm oaks (Lopez et al. 2009). Again, positive adaptations of an individual to drought can quickly be passed on to the community through seed dispersal leading to community adaptation to recurrent droughts. In the ecosystem, some plants growing at the edge of the forest or crop field serve as ‘sentinels,’ sending warning signals to their neighbors about the upcoming water deficit scenario (Ribeiro and Torres 2018). The detailed mechanisms of this type of community signaling remain largely unknown. Canarini et al. (2021) found recurrent drought-induced and ecosystem-level memory altering the soil microbiome. While drought can change plant exudates, affecting microbial stress response and survival, on the other hand, rainfall-regulated CO<sub>2</sub> emissions from the soil microbes can affect the photosynthesis efficiency of the plant community. Moreover, the epigenetic changes due to drought could be spread in whole plant communities in the ecosystem through seed dispersal from the maternal parent (Walter et al. 2013). Further research is needed in natural ecosystems to understand community drought memory in plants.

## The gap in our knowledge and where we are headed

We are just beginning the scientific understanding and appreciation of memory in plants, despite the perplexing absence of a nervous system in plants. The memory of drought and other stresses is of utmost importance for plant survival in the face of erratic precipitation caused due to global climate change. Several mechanisms have been identified that partly explain both short- and long-term drought memory of plants. Some are at the crossroads of other stresses, heat, pathogen attack, and herbivory (Liu et al. 2016).

GWAS is a robust forward genetic tool to identify novel genomic loci regulating complex stress phenotypes, including gene expression-level variation in plants (Kobayashi et al. 2016; Sadhukhan et al. 2017, 2021; Zhu

et al. 2022). GWAS on the methylome variation in many *Arabidopsis* natural accessions under control conditions revealed a strong association of the nucleotide sequence variation within several epigenetic modifiers (Kawakatsu et al. 2016). GWAS on the short-term and transgenerational drought phenotypes, including memory gene expression-level polymorphisms, will be powerful ways to identify new loci regulating drought stress memory.

Plants are more prone to inheriting environment-triggered epimutations due to the late development of germ cells by dedifferentiation of somatic cells under stress (He et al. 2018; Zhang et al. 2020). Moreover, the epigenetic states are not entirely erased from the germline (Minow and Colasanti 2020). But some questions remain. How do epimutations evolve under drought? Are inherited epigenetic marks and DNA polymorphisms associated, and do they co-segregate? Epigenome-wide association studies (EWAS) have recently been reported in plants to identify the epigenetic basis of complex phenotypes (Denkena et al. 2021). EWAS under drought conditions will throw more light on the epigenome evolution for a clear understanding of drought stress memory. On the other hand, the specific mechanisms of epigenetic drift and resetting drought memory in the next generation are unknown, needing future research.

We need to understand plant epigenome evolution influenced by drought to manipulate it to develop drought-resilient crops to meet future demand. Recent breeding programs have partly succeeded in selecting epigenetic states (Raju et al. 2018). Advancement of genome editing, including fusion of an epigenetic modifier with modified CRISPR-associated nuclease (dCas9), can guide favorable chromatin modifications in a gene-specific manner. Recent application of this technology has led to the development of drought-resistant plants without any changes in the nucleotide sequence (Paixão et al. 2019). Thus, epigenome engineering holds immense promise to develop plants with more robust memory responses. Research on plants naturally adapted to extreme environments such as deserts will further unravel novel molecular mechanisms regulating drought memory.

**Author contribution statement** AS and SSP wrote the article with inputs from the rest of the authors. AS prepared the figures. All authors read and approved the manuscript.

**Acknowledgements** The authors are grateful to their respective institutions for providing infrastructure support.

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