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Deciphering the Mechanisms Behind the Molecular Memory of Drought Stress in Plants

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Abstract

The initial drought, plants develop a memory that results in partial stomatal opening during the watered recovery interval, increased levels of osmoprotectants and abscisic acid (ABA), and a dampened photosynthesis response during the subsequent drought. This short-term memory is regulated by ABA and other phytohormones, with transcriptional memory observed in various genes through the deposition of methylated histones at drought-tolerance genes. RNA polymerase activity is stalled during the recovery interval, ready to be activated promptly in the subsequent drought by a pause-breaking factor. Drought stress also induces DNA demethylation near drought-response genes, indicating a genetic control of the process. Progenies of drought-exposed plants inherit specific methylation patterns, which enhances their adaptation to drought conditions. However, an extended watered recovery interval can lead to the loss of drought memory, facilitated by certain demethylases and chromatin accessibility factors. Small RNAs play a crucial role in regulating drought memory by modulating transcript levels of drought-responsive target genes. Future research is expected to delve further into the genetic regulation of drought memory and explore the interplay between genetic and epigenetic factors in its inheritance. Studying plants from extreme environments can provide valuable insights into robust memory responses at the ecosystem level.

Keywords: ABA, DNA methylation, Drought memory, Epigenetics, Histone modifcations.

Introduction:

By the year 2050, the world's population is expected to reach nearly 10 billion, posing a significant challenge to agricultural production in meeting the growing food demand. Global warming, increased frequencies of drought [1], and desertification further exacerbate the issue

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[2]. Drought stress adversely affects nutrient availability and makes plants more susceptible to pests and diseases. Countries like India and the USA already experience significant yield losses in agriculture due to drought, and these losses are projected to worsen in the future [3].

Plants have evolved various adaptive strategies to survive droughts, including drought avoidance, endurance, and tolerance mechanisms [4]. While severe drought can lead to plant damage and even death, short-term moderate droughts may allow for plant recovery upon stress withdrawal [5]. Plants possess the ability to "remember" past drought events, adjusting their physiology to respond more effectively to subsequent droughts [6]. This adaptive process, known as priming, memory, and acclimation, enables plants to enhance their resilience.

Figure 1 illustrates the different types of drought memory in plants. Plants can remember exposure to drought for several days to weeks through changes in their transcriptomic and metabolomic profiles [7]. This short-term memory results in the accumulation of specific signaling molecules, such as transcription factors, which are activated upon subsequent stress exposure [8]. These molecular changes lead to physiological responses like partial stomatal closure and reduced photosynthesis as preparatory measures for the next drought [9] .

Epigenetic regulation of chromatin plays a crucial role in both short-term and transgenerational drought memories[10]. It allows for the passage of memory to future generations through germ cells developing during drought exposure [11]. Understanding the molecular mechanisms of plant drought memory is essential for crop improvement and enhancing resilience to climate change [12].

While plants lack a centralized brain like higher animals, they possess the capacity for memorization, a fundamental aspect of adaptive evolution [13]. Ongoing research in this area will help fill gaps in our understanding of plant drought memory and pave the way for innovative applications in crop improvement [14].

Transcriptional memory of plants:

Transcriptional memory of drought in plants refers to their ability to retain a memory of past drought events at the transcriptional level [15]. After exposure to drought stress, plants undergo changes in gene expression that persist even after the stress is alleviated [16]. This memory allows plants to respond more effectively to subsequent drought exposures [17], with quicker and more robust defense mechanisms [18]. The memory is regulated by specific genes,

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transcription factors, and signaling pathways, and it can be passed on to future generations through epigenetic modifications [19]. Understanding this process has significant implications for crop improvement and breeding programs to develop more drought-tolerant varieties and ensure food security in the face of climate change [20].

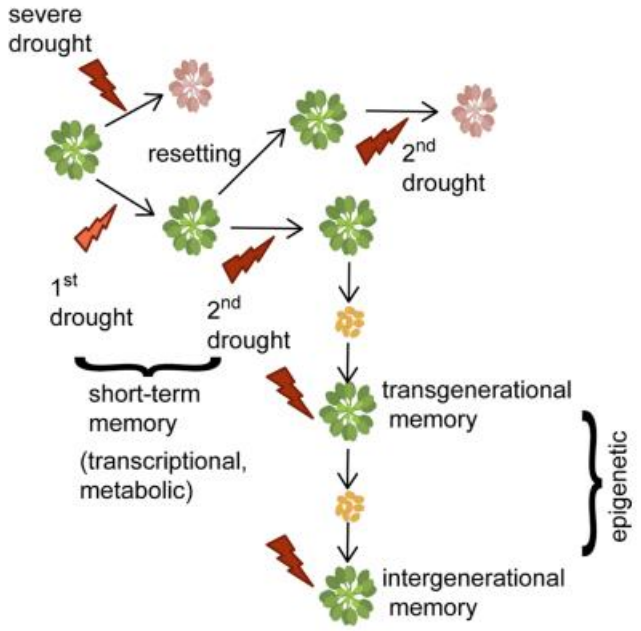

Fig. 1 Drought memory in plants. Severe drought may kill a plant, but a mild drought or a drought for a short duration can trigger short-term memory, usually established by transcriptional training or metabolic reprogramming, leading to survival under a subsequent drought. Sometimes, the memory may be 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

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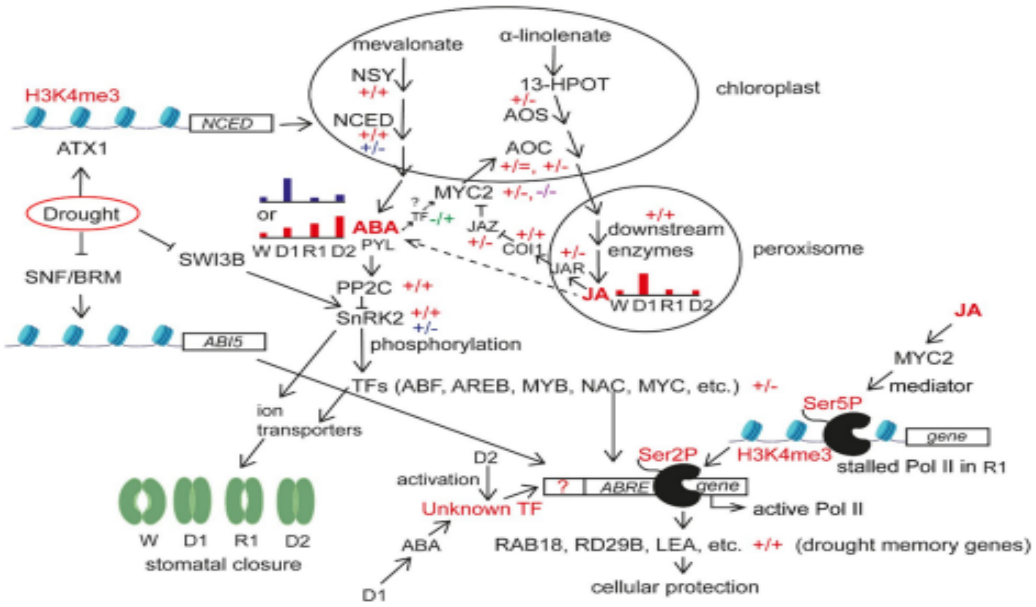

Fig. 2 Role of abscisic acid and jasmonate in transcriptional drought memory. The early steps of abscisic acid (ABA) and jasmonate (JA) synthesis occur in the chloroplast from the mevalonate and α-linolenate pathways. The first drought exposure (D1) leads to induction in ABA biosynthesis genes *NSY* 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, respectively. 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 supressed in D1 but induced in D2 [−/+] (shown in green). ABA triggers JA biosynthesis via MYC2, regulating the upstream biosynthesis genes of JA, *AOC* and *AOS*. The expression of JA biosynthesis genes of the α-linolenate pathway in the chloroplast are induced in D1 but supressed in D2 [+/−], or remain at constant levels in D2 after their initial induction in D1 [+/=], 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

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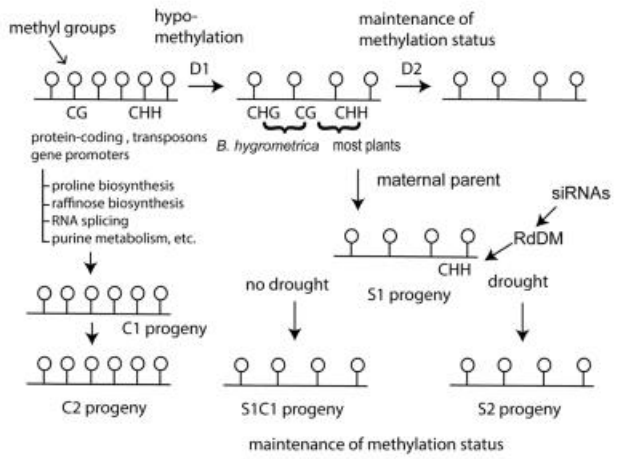

Fig. 3 Maintenance of DNA methylation for drought memory. Drought (D1) causes demethylation in most plants' CG and CHH sequence contexts, but in the CG and CHG sequences in *Boea hygrometrica*. The change in methylation status in the promoter of protein-coding genes leads to their activation causing 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 inherited 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

Conclusion:

Transcriptional memory of drought in plants refers to their ability to retain a memory of past drought events at the transcriptional level. After exposure to drought stress, plants undergo changes in gene expression that persist even after the stress is alleviated. This memory allows plants to respond more effectively to subsequent drought exposures, with quicker and more robust defense mechanisms.

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