Plant Gene 42 (2025) 100509

Contents lists available at ScienceDirect

Plant Gene

journal homepage: www.elsevier.com/locate/plantgene

Somatic drought stress memory affects leaf morpho-physiological traits of plants via epigenetic mechanisms and phytohormonal signalling☆

Franklin Alongi [a], Anja Petek-Petrik [b], Mohammad Mukarram [c], Hülya Torun [d], Bernhard Schuldt [b], Peter Petrík [b,*]

[a] *Karlsruhe Institute of Technology (KIT), Institute of Meteorology and Climate Research—Atmospheric Environmental Research (IMK-IFU), 82467 Garmisch-Partenkirchen, Germany*
[b] *Chair of Forest Botany, Institute of Forest Botany and Forest Zoology, Technical University of Dresden (TUD), Pienner Str. 7, 01737 Tharandt, Germany*
[c] *Department of Plant Biology, Universidad de la República, Av. Gral. Eugenio Garzón 780, Montevideo 12900, Uruguay*
[d] *Department of Biosystem Engineering, Faculty of Agriculture, Düzce University, Düzce, Türkiye*

ARTICLE INFO

Edited by A Rooney

Keywords:
Antioxidants
Cuticle
Stomata
Stress priming
Photosynthesis
Phytohormones
Water-use efficiency

ABSTRACT

Drought stress memory in plants is an adaptive mechanism that enhances resilience to future water stress through physiological and molecular modifications triggered by previous drought events. This review explores somatic drought stress memory within a plant's lifespan, with a specific focus on leaf and stomatal morphology, minimum leaf conductance, photosynthetic efficiency, water-use efficiency, antioxidant capacity, and leaf senescence. We examine how epigenetic mechanisms—such as DNA methylation, histone modifications, and non-coding RNAs—regulate gene expression in coordination with hormonal signalling pathways. Phytohormones, including abscisic acid, jasmonic acid, ethylene, salicylic acid, auxins and cytokinins, are central to these processes, influencing key morphological and physiological adaptations, such as stomatal regulation, cuticle thickness, water retention, and improved water-use efficiency. The review synthesizes current knowledge on the molecular and hormonal networks underlying these adaptations and their impact on leaf architecture and metabolism. Despite advancements, critical gaps remain in identifying the specific genes and pathways involved, understanding the longevity of epigenetic marks, and elucidating the intricate cross-talk between phytohormones during drought stress memory. This review emphasizes the need for integrated -omics approaches to map epigenetic modifications and uncover their roles in developing drought-resistant plants through targeted stress priming strategies.

1. Introduction

Drought stress is becoming a major driver of ecosystem disturbances worldwide (Allen et al., 2010; Seidl et al., 2017; Hammond et al., 2022). Moreover, drought stress is also threatening global food security due to negative effects on crops production (Cotrina Cabello et al., 2023; Wahab et al., 2023). The frequency and severity of the drought spells is expected to increase under current climate change scenarios (Vicente-Serrano et al., 2022). Drought stress memory in plants refers to the physiological and molecular changes that plants undergo after experiencing drought, which then influence their response to future drought events (Wojtyla et al., 2020; Jacques et al., 2021; Kambona et al., 2023). This "memory" or stress priming can lead to various adaptive changes in leaf morpho-physiological traits, enhancing the plant's ability to cope with subsequent water stress. We can distinguish between three main categories of stress memory which are somatic, inter-generational and transgenerational (Sharma et al., 2022; Lukić et al., 2023). This review focuses solely on somatic stress memory within the lifespan of the plant and is not exploring transfer of the stress priming response to subsequent generations. Drought exposure can also induce lasting negative impacts on leaf physiology, often referred to as drought legacy (Müller and Bahn, 2022), but here we focus mainly on evidence of positive adaptive acclimation.

Drought stress can lead to epigenetic changes, such as DNA methylation and histone modification, which alter gene expression in response to future droughts (Kinoshita and Seki, 2014; Zhang et al.,

---

☆ This article is part of a Special issue entitled: 'Multi-scale landscape' published in Plant Gene.

* Corresponding author.

E-mail address: peter.petrik@tu-dresden.de (P. Petrík).

https://doi.org/10.1016/j.plgene.2025.100509
Received 30 October 2024; Received in revised form 21 December 2024; Accepted 2 April 2025

2018). These modifications can make plants more resilient by enabling faster and more robust activation of stress-responsive genes during subsequent drought events. Moreover, histone modifications can enhance or decrease the expression of genes in phytohormonal signalling pathways, enabling plants to respond more robustly to perceived drought conditions (Chinnusamy and Zhu, 2009; Banerjee and Roychoudhury, 2017). Another drought memory mechanism, non-coding RNAs (ncRNAs), are largely involved in the post-transcriptional regulation of gene expression. ncRNAs can target mRNAs of phytohormone-related genes, modulating their stability and translation during and after drought stress (Contreras-Cubas et al., 2012; Gelaw and Sanan-Mishra, 2021). These epigenetic modifications are often reversible but can persist across cell divisions, allowing plants to 'remember' previous stress conditions and respond more effectively to recurrent droughts.

Drought memory epigenetic changes affect multiple phytohormones, among others abscisic acid (ABA), auxin, ethylene, jasmonic acid (JA), salicylic acid (SA) and cytokinin, that help improve and fine-tune future drought response by modifying leaf morphology and physiology (Fig. 1). Of these major phytohormones at play during progressive drought, ABA is the primary hormone involved in the regulation of drought responses (Sussmilch and McAdam, 2017; Sircaik et al., 2021; Húdoková et al., 2023). Plants with drought stress memory often exhibit increased sensitivity to ABA, which can further regulate epigenetic mechanisms of drought tolerance (Kaya et al., 2024). This means that during subsequent drought events, these plants more rapidly accumulate ABA, leading to faster stomatal closure and reduced water loss (Virlouvet et al., 2018; Forestan et al., 2020). ABA also influences cell division and expansion rate, with increased ABA leading to smaller and thicker leaves in plants with a history of drought stress (Sah et al., 2016; Ost et al., 2023). Similarly, drought-primed auxin signalling, largely through cross talk with ABA, can affect leaf size, stomatal patterning and cuticular structure, reducing water lost through transpiration during subsequent drought (Yuan et al., 2019; Jiang et al., 2022; Khoudi, 2023). Another phytohormone that can be positively affected by drought memory and improve future drought resistance is ethylene. Drought primed plants can show more efficient nutrient reabsorption from leaves before leaf senescence via altered ethylene signalling pathways (Peerzada and Iqbal, 2021). JA is also a key hormone involved in drought stress response. In plants diplaying drought stress memory, JA levels may increase to enhance stress tolerance by increasing antioxidant production (Ahmad et al., 2016; Liu et al., 2016). SA contributes to drought stress resistance via systemic acquired resistance and can modulate various physiological processes under stress conditions (Miura and Tada, 2014; Torun et al., 2024). Plants displaying drought stress memory may show altered SA signalling pathways, where SA help maintain higher chlorophyll and antioxidant levels during subsequent droughts, thereby improving stability of the photosynthetic apparatus (Brito et al., 2018; Kohli et al., 2022). These epigenetic and phytohormonal changes can influence leaf size, shape, cuticle formation, stomatal behaviour, phenology, photosynthesis, transpiration and water-use efficiency, which are vital for water retention and stress adaptation capability of a plant.

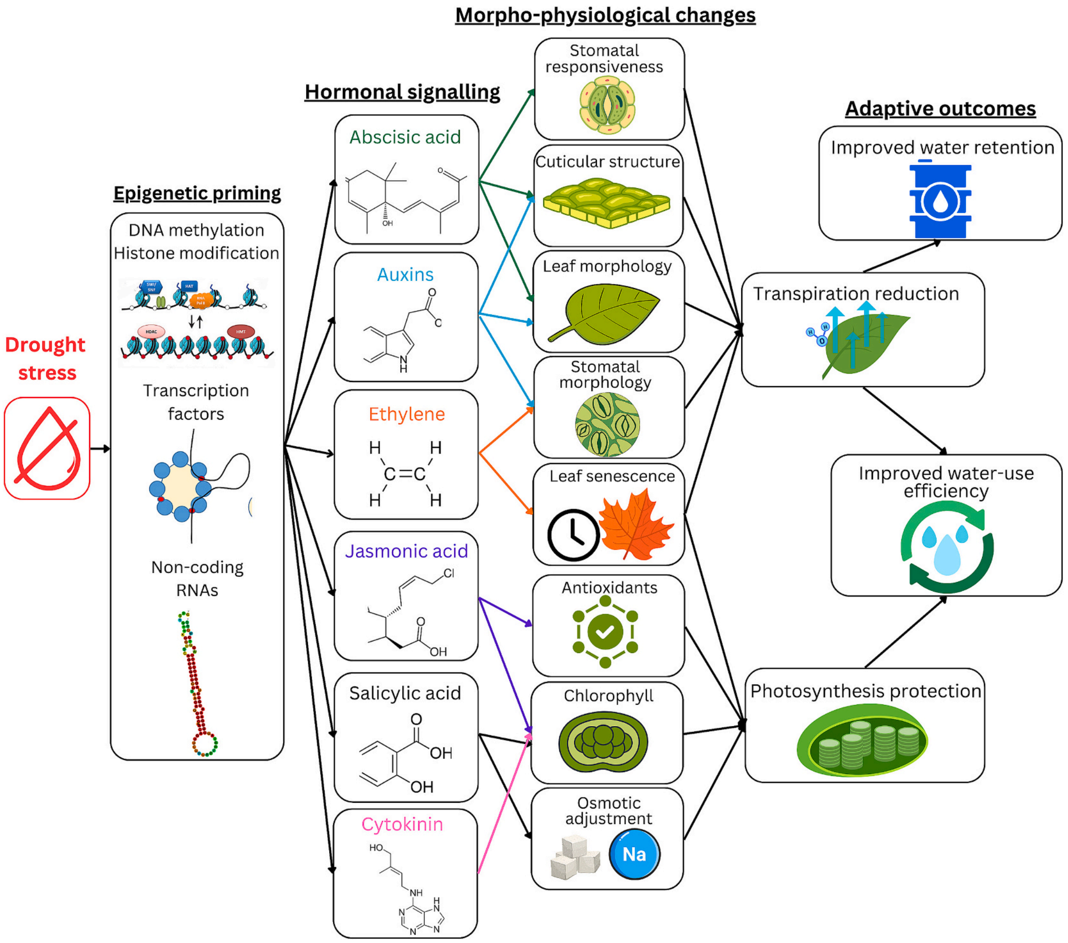

Fig. 1. Overview of drought memory pathways from epigenetic priming to adaptive outcomes at leaf level via hormonal signalling and leaf morpho-physiological changes. The "DNA methylation and histone modification" image is adapted from previously adapted figure by Luong, P. Basic Principles of Genetics, Connexions Web site (2009). The "transcription factors" image is adapted from a figure by Adrian Baily. The "non-coding RNAs" image is authored by Paul Gardner. All three images are shared under a Creative Commons Attribution License (CC-BY 3.0). The figure was created in Canva software.

Information regarding past drought stress can be imprinted in the new leaf buds, which therefore affects the morpho-physiological characteristics of leaves in the subsequent vegetation season (Sadhukhan et al., 2022). In the following growing season, plants that have previously experienced drought stress may develop smaller, thicker leaves with higher leaf-mass per area (LMA, kg m^{-2}), i.e. lower specific leaf area (SLA, cm^{-2} g^{-1}), in order to reduce total transpiration and improve their water-use efficiency (WUE) (Auler et al., 2021; Petrik et al., 2022). Drought stress memory can lead to long-term reductions in stomatal density (fewer stomata per unit area) or adjustments in stomatal aperture (opening size) (Mantoan et al., 2020). These changes help plants regulate gas exchange more efficiently under water-limited conditions, reducing water loss while maintaining some level of CO_2 uptake for photosynthesis. Reduction of stomatal density without an increase in stomatal size also lowers total maximal stomatal opening area and therefore limits potential transpiration (Rathnasamy et al., 2023). This may be additionally critical during severe drought stress, as a lower minimum stomatal conductance (g_{min}) can reduce passive water loss when stomata are completely closed. The reduction of stomatal size can have positive impact on stomatal responsiveness (Kardiman and Ræbild, 2018) and water-use efficiency (Petrík et al., 2024). The cuticle, a waxy layer on the leaf surface, often becomes thicker in plants with drought stress memory (Spieß et al., 2012; Sintaha et al., 2022). This adaptation might reduce water loss by enhancing the boundary layer barrier to evaporation (Hasanuzzaman et al., 2023). Reducing transpiration improves the water retention ability of plants, leading to higher resiliency to drought conditions (Petek-Petrik et al., 2023; Petek-Petrik et al., 2024).

While drought typically reduces photosynthesis due to stomatal closure, plants with drought stress memory may exhibit a more efficient photosynthetic response under mild stress (Gallé et al., 2007; Arend et al., 2016). This could be due to changes in the expression of genes involved in photosynthesis, allowing the plant to maintain productivity even under water-limited conditions. Drought stress memory often leads to an increase in WUE through tighter regulation of stomatal opening, allowing the plant to maximize carbon gain while minimizing water loss (Sintaha et al., 2022). Some plants may maintain higher Rubisco content in their leaves after a drought, which can help sustain photosynthetic activity during subsequent drought events (Lukić et al., 2020). Plants exhibiting drought stress memory may also accumulate higher levels of protective metabolites, sugars, and antioxidants, which help protect cellular integrity and maintain osmotic balance, reducing the damaging effects of drought on leaf tissues and decreasing hydraulic vulnerability (Wang et al., 2019; Liu et al., 2022; Vuković et al., 2022). Epigenetic modifications under water limitation can also increase proline synthesis, which assists in both stress response and recovery (Hayat et al., 2012). Recurrent drought stress can prime plants to enhance their antioxidant defences, which help mitigate oxidative radicals that can accumulate during drought (Lukić et al., 2020; Kashyap et al., 2024). This includes increased activity of enzymes like superoxide dismutase, catalase, and peroxidase in the leaves. In plants displaying drought memory, the epigenetic alterations can persist, leading to a long-term improvement in water retention, photosynthetic efficiency, and faster responses to phytohormonal signalling (Balao et al., 2018).

Taken together, drought stress memory equips plants with enhanced photosynthetic efficiency, improved water-use regulation, and bolstered protective mechanisms, allowing them to maintain productivity, limit water loss, and mitigate oxidative damage in the case of recurrent drought events. The objective of this review was to summarise the latest research and find gaps in knowledge regarding drought stress memory mechanisms at the leaf level of plants. Understanding these mechanisms is crucial for developing effective strategies to prime crops, tree seedlings, and other plants for enhanced drought tolerance in order to provide greater resilience and productivity in the face of increasing climate challenges (Seth et al., 2024).

2. Epigenetic mechanisms in drought stress memory

Epigenetic mechanisms, including DNA methylation, histone modifications, and non-coding RNAs (ncRNAs), play a pivotal role in establishing and maintaining drought stress memory in plants. These mechanisms enable plants to modulate gene expression in response to drought (Fig. 2), leading to both immediate and long-term adjustments (drought memory) in leaf morphology and physiology.

2.1. DNA methylation and histone modification

DNA methylation, typically occurring at cytosine residues, can lead to the repression of gene expression by altering chromatin structure or by directly inhibiting the binding of transcription factors (Keshet et al., 1986; Mattei et al., 2022). In the context of drought stress, methylation patterns can change dynamically, allowing for the upregulation or downregulation of specific genes involved in stress responses (Luo et al., 2018; Wang et al., 2016). DNA methylation often works in conjunction with other epigenetic mechanisms, such as histone modifications and small RNAs (e.g., siRNAs and miRNAs), to regulate gene expression and maintain genome stability (Wang et al., 2022a, 2022b). Major proportion (30 %) of drought-induced DNA methylation/demethylation sites (e.g. *DK151, IR64*) stay present even after drought release in rice (Wang et al., 2011). The differentially methylated DNA regions are one of the essential mechanisms of drought memory of plants (Kou et al., 2022b). Drought stress induced methylation reduces gene accessibility (e.g. *MYC2*) and persists after drought release, positively affects jasmonic acid biosynthesis and antioxidant capacity of Arabidopsis (Liu et al., 2016). The drought induced DNA methylation/demethylation is gene specific and contributes as building block of drought memory in plants (Sun et al., 2021; Zi et al., 2024; Sadhukhan et al., 2022). Histone

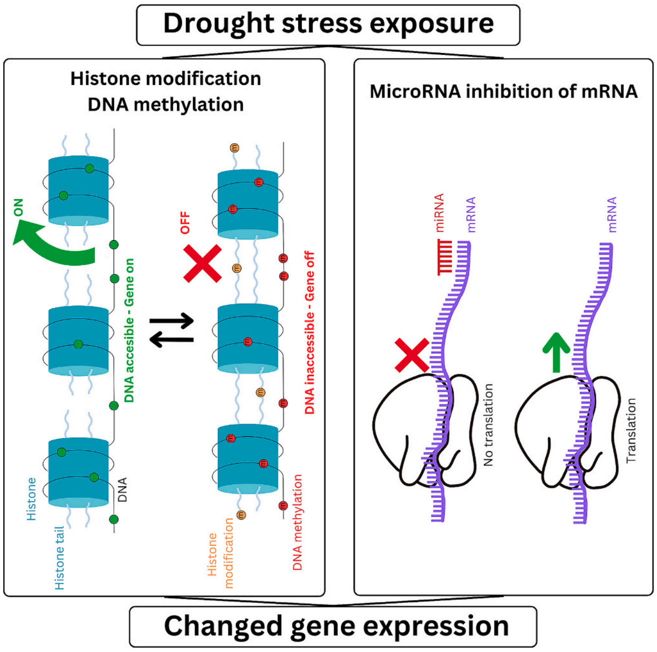

Fig. 2. Drought stress exposure and altered gene expression mechanisms in plants. Left Panel: Histone modifications and DNA methylation regulate gene accessibility. When histone modifications promote DNA accessibility (green circles), gene expression is turned “ON.” Conversely, DNA methylation and histone modifications (red marks) make DNA inaccessible, turning gene expression “OFF.” Right Panel: miRNA binds to target mRNA, preventing translation (red cross). In the absence of miRNA inhibition, mRNA is successfully translated into protein (green arrow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

modifications, such as acetylation, methylation, phosphorylation, and ubiquitination, further influence chromatin accessibility and gene expression. Acetylation of histones, for instance, generally correlates with transcriptional activation by loosening chromatin structure, making DNA more accessible for transcription (Wang et al., 2024a, 2024b). Conversely, histone methylation can either activate or repress transcription, depending on the specific residues modified. During drought stress, these epigenetic marks can be selectively added or removed to fine-tune the expression of genes involved in stress response, such as via improved water retention, stomatal regulation, and modified leaf architecture (Liu et al., 2010; Luo et al., 2012). If these epigenetic modifications persist beyond the initial stress period, they can contribute to the plant's ability to "remember" drought conditions and respond more effectively to subsequent stress. Histone modifications can provide a persistent epigenetic transmission mechanism associated with drought memory in plants (Luo et al., 2012; Avramova, 2015; Lämke and Bäurle, 2017). Histone modifications help plants "remember" drought by regulating stress-responsive genes, enabling quicker and more effective responses to future drought events (Wang et al., 2024a, 2024b).

2.2. *Role of non-coding RNAs*

Non-coding RNAs (ncRNAs) are regulatory molecules that do not encode proteins but play critical roles in gene expression regulation (Gelaw and Sanan-Mishra, 2021; Abdulraheem et al., 2024). Among these, micro RNAs (miRNAs) and small interfering RNAs (siRNAs) are RNA molecules most commonly involved in post-transcriptional gene silencing, and function by guiding the degradation or inhibition of specific mRNA targets (Carthew and Sontheimer, 2009). During drought, ncRNAs fine-tune gene expression, allowing plants to modulate their growth and stress response effectively. The involvement of ncRNAs in epigenetic regulation contributes to drought memory by establishing chromatin modifications, DNA methylation patterns, and histone acetylation changes that "store" stress information, enabling faster and more efficient responses to subsequent drought stress (Nguyen et al., 2022; Abdulraheem et al., 2024). Several miRNAs have been identified to play crucial roles in drought memory, impacting leaf development, morphology, and physiological processes. Specific miRNAs are upregulated or downregulated, influencing genes that affect stomatal density, leaf size, leaf xylem anatomy, cuticular structure, ABA signalling, ROS regulation and photosynthetic efficiency (Table 1). Apart from miRNAs, siRNAs also play a vital role in drought memory, particularly through their involvement in RNA-directed DNA methylation (RdDM) pathways (Rao et al., 2024). siRNAs can guide DNA methylation at specific genomic loci. siRNAs through modulating the activity of transposable elements (TEs) aid in the maintenance of genome stability during drought stress, protecting against deleterious effects caused by TE mobilization (Gelaw and Sanan-Mishra, 2021), leading to long-lasting transcriptional silencing of genes involved in stress responses (Castel and Martienssen, 2013).

3. Crosstalk between epigenetic mechanisms and phytohormones

Phytohormones, such as abscisic acid (ABA), jasmonic acid (JA), ethylene, and auxins, are integral to plant stress responses, including drought. The interaction between epigenetic modifications and phytohormone signalling pathways allows plants to coordinate complex responses that modulate leaf morphology and physiology (Lu et al., 2017; Jiang et al., 2023; Kapoor et al., 2023; Rudolf et al., 2024). The interplay of phytohormones during and after drought stress involves crosstalk at molecular, genetic, and physiological levels, modulated by epigenetic mechanisms (Shaffique et al., 2023; Kaya et al., 2024). The complex impact of DNA methylation/demethylation, histone acetylation/deacetylation and non-coding RNAs on the mentioned phytohormones is visualized in Fig. 3. A coordinated epigenetic and hormonal response is essential for establishing drought stress memory, enabling plants to adapt to recurring drought conditions by fine-tuning gene expression and physiological processes to optimize survival and resilience.

Table 1
Overview of micro-RNAs and their regulation targets that affect leaf morpho-physiological traits in relations to drought memory in plants.

RNA code	Regulation target	Hormonal or morpho-physiological target	References
miR159	*MYB* transcription factors	ABA signalling, stomatal closure	Reyes and Chua, 2007; Millar et al., 2019
miR166	*HD-ZIP III* transcription factors	Leaf xylem anatomy, transpiration, WUE	Li et al., 2017; Yadav et al., 2024
miR168	*AGO1* from RNA-induced silencing complex	ABA signalling	Li et al., 2012; Singroha et al., 2021
miR171	*SCL6* transcription factors	Gibberellin, leaf morphology	Huang et al., 2017; Pei et al., 2023
miR319	*TCP* transcription factors	Leaf size and shape	Koyama et al., 2017; Lu et al., 2023
miR393	Auxin receptors of *TIR1*	Stomatal density, ABA signalling	Yuan et al., 2019; Jiang et al., 2022
miR396	*GRF*	Leaf size	Liu et al., 2009; Liebsch and Palatnik, 2020
miR398	*APX6, CSD*	Leaf senescence, ROS regulation	Chen et al., 2020a, 2020b; Li et al., 2022a, 2022b
miR399	Phosphate homeostasis	Stomatal responsiveness	Pant et al., 2008; Zhu et al., 2020
miR408	Plastocyanin	Photosynthetic efficiency, stomatal responsiveness	Zhang et al., 2017; Balyan et al., 2023; Yang et al., 2024
siRNAs	*CER3* silencing	Cuticular structure and biosynthesis	Lam et al., 2015; Sajeevan et al., 2017

3.1. *Abscisic acid*

Abscisic acid (ABA) is the central hormone regulating plant responses to drought stress. It is responsible for inducing stomatal closure, reducing water loss, cuticle biosynthesis and activating stress-responsive genes (Martin et al., 2017). The crosstalk between epigenetic modifications and ABA signalling pathways enhances the plant's ability to respond to drought stress, both immediately and during subsequent drought episodes. During drought stress, DNA demethylation of key genes involved in ABA biosynthesis, such as 9-*cis*-epoxycarotenoid dioxygenase 3 (*NCED3)* (Virlouvet and Fromm, 2015), Ras-associated binding 18 (*RAB18)* (Ding et al., 2014) or Zeaxanthin Epoxidase 1 (*ZEP1)* (Forestan et al., 2020), lead to an increase in ABA production. This rapid accumulation of ABA triggers the closure of stomata, minimizing water loss. After stress release, these demethylated regions can remain active, priming the plant for quicker ABA synthesis in future droughts (Godwin and Farrona, 2020), and therefore a more sensitive response of ABA-mediated drought tolerance. Additional histone acetylation at ABA-responsive genes, such as *ABF2* (ABA-responsive element-binding factor 2), enhances their expression, promoting faster and more robust drought responses (Alves de Freitas et al., 2019). The memory of drought is partially encoded in these epigenetic marks, allowing the plant to respond more rapidly to future stress by activating the ABA signalling cascade (Ma et al., 2019). Epigenetic regulation of ABA receptors, such as PYR/PYL proteins, ensures that the ABA signalling pathway remains primed, with faster ABA-mediated stomatal closure even under milder future drought conditions (Lim et al., 2013; Fidler et al., 2022; Jiang et al., 2024).

3.2. *Jasmonic acid*

Jasmonic acid (JA) is associated with responses to biotic stress but

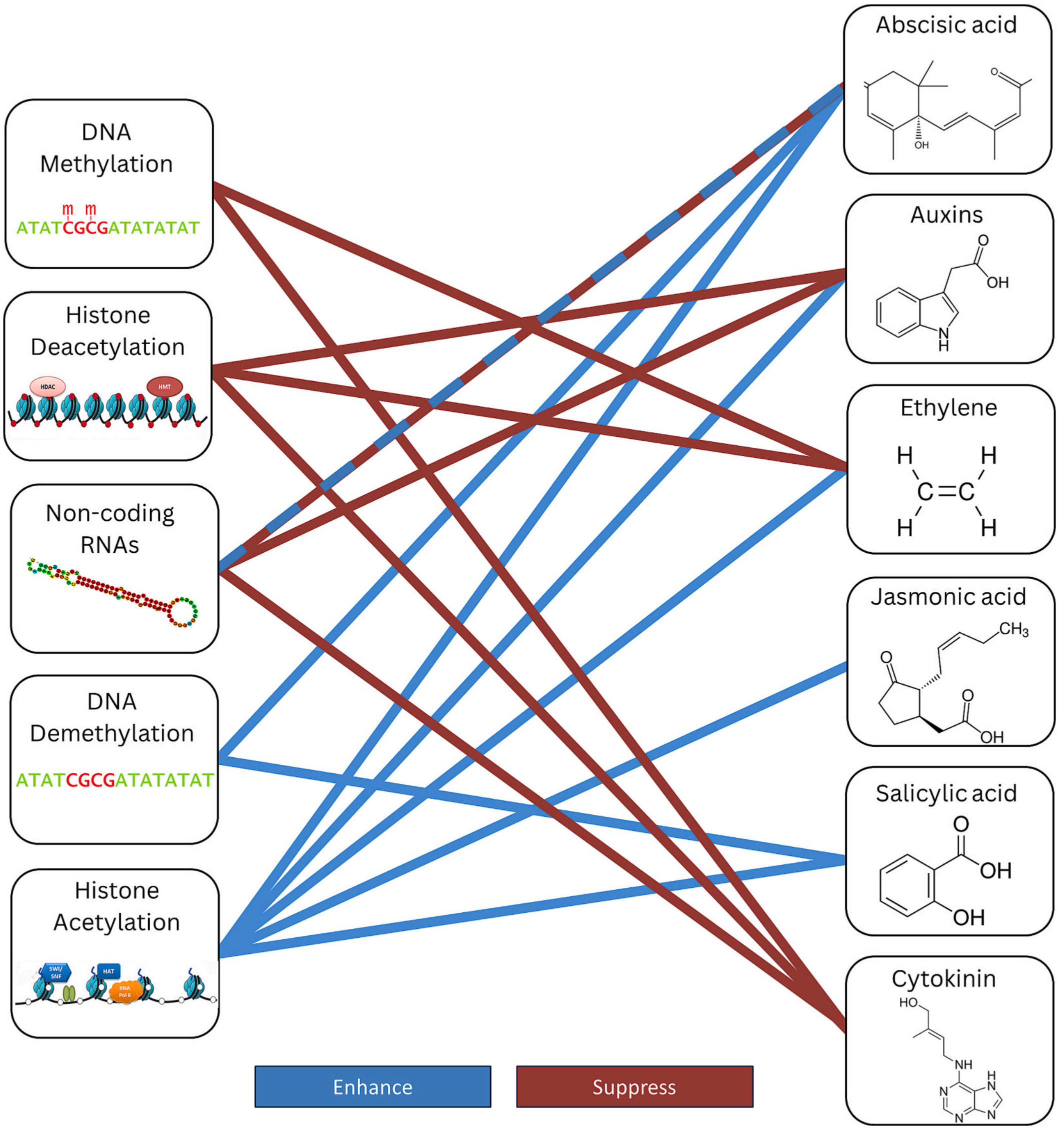

Fig. 3. Graphical overview of epigenetic pathways of phytohormone control as drought memory components after drought stress. Epigenetic modifications can result in enhanced (blue) or suppressed (red) phytohormone levels. Note: displayed relationships are restricted to specific mechanisms discussed in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

also play roles in drought tolerance. JA levels increase during drought, modulating antioxidant defences to help plants cope with higher oxidative stress (Alam et al., 2014; Mukarram et al., 2021; Kebert et al., 2023). The crosstalk between JA and epigenetic mechanisms helps fine-tune the plant's drought response. Histone acetylation at the promoters of JA biosynthesis genes, such as *LOX3* (lipoxygenase 3) and *AOS* (allene oxide synthase), can enhance JA production during and after drought (Avramova, 2017; Su et al., 2023). This leads to an increase in antioxidant enzyme activity and ROS scavenging, which protect the plant from oxidative damage. Epigenetic marks, such as histone methylation at specific loci in JA-responsive genes, regulate the plant's ability to modulate growth and defence mechanisms. After drought release, these marks can persist, ensuring that the plant maintains elevated antioxidant levels and is better prepared for future oxidative stress associated with drought (Ali and Baek, 2020; Wang et al., 2021; Kaya et al., 2024). Conversely, cross-talk between ABA and JA pathways can lead to the repression of genes related to biotic defence during subsequent drought periods (Avramova, 2019), allowing plants to prioritize their physiological and metabolic resources toward drought-specific responses, thereby enhancing water-use efficiency and stress resilience. These interactions can lead to changes in leaf morphology, such as reduced leaf size and altered leaf architecture, which help conserve water. While the longevity of these epigenetic modifications remains largely unclear, initial transcriptional changes to drought stress are known to persist throughout subsequent watering and dehydration cycles (Liu et al., 2016).

3.3. Ethylene

Ethylene interacts with epigenetic mechanisms to regulate leaf senescence under drought stress. The epigenetic repression or activation of ethylene-responsive genes can modulate this process, influencing leaf lifespan and function under drought conditions (Tan et al., 2023). Ethylene also modulates stomatal development by crosstalk with gibberellins, affecting stomatal size (Saibo et al., 2003). Epigenetic regulation of ethylene signalling pathways ensures that plants optimize resource use during and after drought (Nazir et al., 2024). DNA methylation of ethylene biosynthesis genes, such as *ACS* (ACC synthase), can lower ethylene production during drought. This regulation helps balance ethylene levels, preventing premature senescence and ensuring that the plant can retain functional leaves during stress (Khan et al., 2024). Histone modifications in ethylene signalling genes, such as *EIN3* (ethylene-insensitive 3), regulate the timing and extent of leaf senescence (Jan et al., 2019). This ensures that plants only shed leaves when necessary, allowing for optimal nutrient reallocation and prolonged leaf function after drought conditions (Drenovsky et al., 2019). During drought, ethylene levels increase to facilitate senescence and nutrient reallocation from older leaves to younger tissues (Munné-Bosch and Alegre, 2004). The explicit timing of leaf senescence during drought stress is critical to optimize both the continued photosynthetic function of leaves and to ensure the complete remobilization of nutrients upon leaf shedding (Tan et al., 2023). After drought release, plants with drought memory may exhibit delayed senescence, allowing them to maintain photosynthetically active leaves longer, particularly when the successful remobilization of nutrients from shed to persisting leaves occurs. Epigenetic regulation of ethylene pathways enables plants to fine-tune the timing of leaf senescence based on water availability and stress history (Li et al., 2014).

3.4. Salicylic acid

Salicylic acid (SA) is a key hormone in regulating systemic acquired resistance and defence responses, and plays a crucial role in mitigating the negative effects of stress, particularly in the context of drought (Zhang et al., 2010). SA is involved in photosynthetic stability, osmotic adjustment, and antioxidant defences, as well as helping plants maintaining chlorophyll levels and reducing oxidative damage (Khan et al., 2015; Gao et al., 2023; Torun et al., 2024). The crosstalk between SA and epigenetic mechanisms enables the integration of these defence responses, ensuring an efficient acclimation to drought stress and contributing to the plant's overall resilience during and after recovery. Histone acetylation at the promoters of SA biosynthesis genes, such as *ICS1* (isochorismate synthase 1), enhances SA production during and after drought stress (Kumazaki and Suzuki, 2019). This increased SA production helps plants maintain higher chlorophyll levels, reduce oxidative damage, and improve photosynthetic efficiency under stress conditions. After the release of drought stress, persistent epigenetic marks such as DNA methylation and histone modifications at SA-responsive genes allow plants to maintain elevated antioxidant levels (Ullah et al., 2024). These marks ensure that the photosynthetic apparatus remains protected, enabling plants to recover more efficiently and maintain defence readiness against future stress. SA-influenced epigenetic regulation of osmolyte-related genes enhances solute production and retention, allowing plants to adjust osmotically during and after drought (de Souza Neta et al., 2024). Epigenetic mechanisms regulate the expression of osmolyte-related genes such as *P5CS* (Safari et al., 2022), *RD29A* (Jia et al., 2012; Kinoshita and Seki, 2014) and *DREB* (Santos et al., 2011; Shriti et al., 2024). This adjustment is critical for stabilizing cell membranes and proteins, preventing damage from dehydration, and ensuring proper cellular function.

3.5. Auxins

Auxins are primarily involved in plant growth and development but also play important roles in modulating leaf expansion, stomatal patterning, and cuticular development under drought conditions (Teale et al., 2006; Higashide et al., 2014; Verma et al., 2022). Epigenetic regulation of auxin pathways allows plants to balance growth and stress responses effectively. miRNAs, such as miR393, target auxin receptors like *TIR1* (transport inhibitor response 1), modulating auxin signalling during and after drought (Jiang et al., 2022). The interaction between miRNAs and DNA methylation fine-tunes auxin responses, leading to altered leaf morphology and improved drought resilience. Histone modifications in auxin-responsive genes, such as *ARFs* (auxin response factors), ensure that the auxin signalling pathways remain active or suppressed as needed during stress and after stress release (Marzi et al., 2024). This epigenetic regulation affects leaf size, stomatal density, and cuticle formation (Guo et al., 2019; Yuan et al., 2019; Torii, 2021). Auxin epigenetic adjustment during drought stress can also affect mesophyll cell expansion after stress release and therefore increase photosynthetic capacity due to mesophyll conductance constraints (Batista-Silva et al., 2024). After drought release, epigenetic changes in auxin signalling allow plants to modulate leaf growth and stomatal patterning, ensuring that the plant maintains conservative water-use strategies while resuming growth (Wang et al., 2022a, 2022b).

3.6. Cytokinins

Cytokinins play a key role in maintaining chlorophyll content and antioxidant capacity under and after drought conditions (Gujjar et al., 2020; Mughal et al., 2024). In plants with drought memory, cytokinins help delay leaf senescence and prevent chlorophyll degradation, supporting sustained photosynthesis (Efroni et al., 2013; Vankova, 2014; Prasad, 2022). Drought-induced DNA methylation changes at *ARR* gene promoters can downregulate cytokinin responses during stress, reducing chlorophyll loss (Cortleven et al., 2016). Higher cytokinin levels during drought reduce chlorophyll loss, while cytokinin signalling recovery after stress promotes chlorophyll retention, enhancing the plant's ability to cope with future droughts (Prerostova et al., 2018). Cytokinins can also induce physiological changes at leaf level via nitric oxide (NO) signalling affecting photosynthetic performance, electron transport rate and stomatal regulation (Shao et al., 2010; Ahmad et al., 2024). Subsequent changes in NO can persist for days following stress release, allowing for the continued enhancement of drought tolerance (Fan and Liu, 2012). This dynamic regulation of cytokinin signalling, mediated by both hormonal adjustments and epigenetic modifications, helps to maintain photosynthetic efficiency and delay senescence during recurrent droughts, reinforcing the plant's ability to 'remember' previous stress events and mount a more effective response to future drought conditions.

4. Leaf morpho-physiological changes after drought stress release

After a period of drought stress, plants undergo significant morpho-physiological adjustments when water availability is restored. These changes are strongly influenced by the memory of previous drought episodes, which allows plants to adapt more effectively to subsequent stress events. Drought memory, established through mechanisms such as epigenetic modifications, transcriptional reprogramming, and hormonal adjustments, ensures that certain stress-responsive traits persist even after rehydration. For example, genes involved in stomatal regulation, cuticle composition, or antioxidant defence may remain primed for rapid activation during future droughts (Fig. 4). Additionally, morphological traits such as altered leaf thickness, stomatal density, and cuticular wax are often retained to some degree, improving water retention during subsequent drought events.

Understanding how drought memory shapes leaf morpho-physiological responses highlights the balance plants maintain between recovery and resilience. These memory-driven adaptations not only contribute to efficient stress recovery but also enhance long-term plant fitness, particularly in environments where drought stress is recurrent.

4.1. Leaf morphology: size and thickness

During drought stress, leaf growth is typically suppressed as plants focus on conserving water and prioritize resources toward water-acquisition in root tissues (Kou et al., 2022a). When stress is relieved, plants often resume leaf expansion, but the rate of recovery depends on the severity and duration of the prior stress (Xu et al., 2010). In plants exhibiting drought memory, this resumption may be delayed or occur at

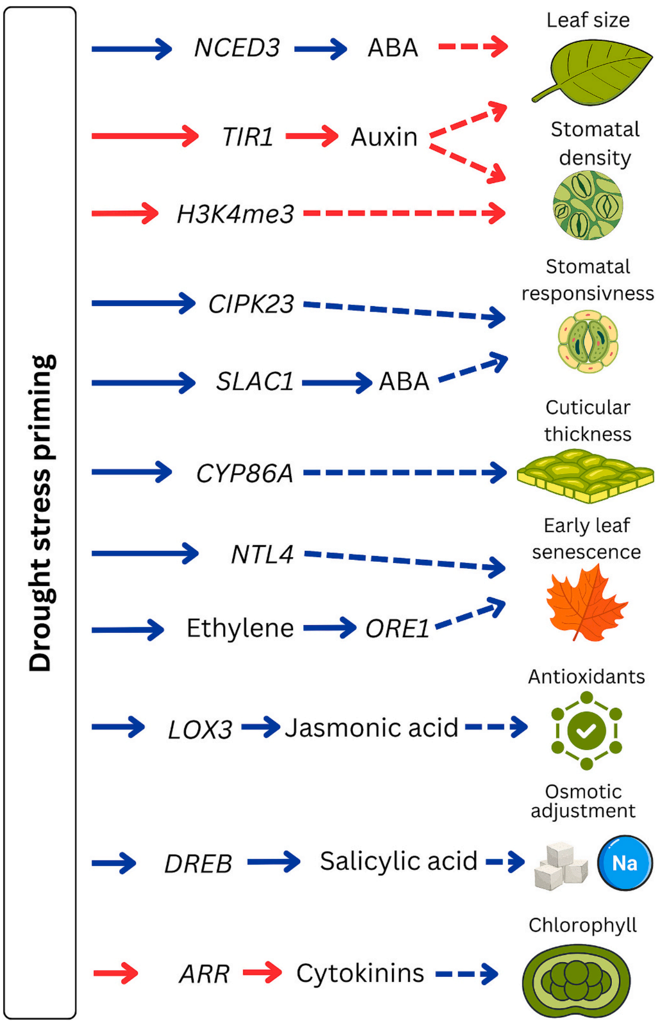

Fig. 4. Example for specific genes and phytohormonal signals regulating drought priming responses such as stomatal density, cuticular thickness, antioxidants, osmotic adjustment, chlorophyll maintenance, and leaf senescence to enhance drought tolerance in plants.

a reduced rate to prevent excessive water loss during any subsequent stress events. Persistent reductions in leaf size are commonly observed in plants following drought events (Fleta-Soriano and Munné-Bosch, 2016; Metz et al., 2020). Smaller leaves reduce transpiration and water loss, serving as a protective adaptation even after water becomes available again (Smith and Geller, 1980; Zhu et al., 2020). Moreover, smaller leaves are more efficient at cooling down under high temperatures, reducing unnecessary water loss (Konrad et al., 2021). SLA, which represents the leaf area relative to its dry mass, often remains lower (or higher leaf mass per area $LMA = SLA^{-1}$) in plants that have experienced drought (Fleta-Soriano and Munné-Bosch, 2016; Weithmann et al., 2022). This is indicative of thicker leaves with higher tissue density, which can aid in water retention and increase hydraulic safety margins. Reduction of leaf area post drought release, particularly when accompanied by an increased resource sink in roots, also often means increase in root:shoot ratio, which can positively affect drought resistance of plants (Fleta-Soriano and Munné-Bosch, 2016). The drought memory pathways leading to reduction of leaf size after drought release are usually mediated by epigenetic crosstalk with phytohormones like ABA and Auxins (discussed in sections 3.1 and 3.4). Especially epigenetic upregulation of *NCED3* leads to ABA biosynthesis and reduced leaf growth (Lee et al., 2021) Furthermore, upregulation of *DREB/CBF* suppresses leaf growth during and after drought (Morran et al., 2011). This intricate balance between growth suppression and adaptive resource allocation underscores the importance of understanding the molecular and physiological mechanisms behind drought memory.

4.2. *Stomatal morphology: size and density*

Stomatal morphology, including stomatal density and stomatal size, plays a critical role in regulating gas exchange and water loss (Hetherington and Woodward, 2003). Stomatal density shows higher phenotypic plasticity than stomatal size in response to precipitation conditions or drought stress (Stojnić et al., 2015; Petrík et al., 2020; Petek-Petrik et al., 2024). Therefore, any drought memory impact on stomatal morphology is often more visible in changes of stomatal density than size (Petrik et al., 2022). After drought stress release, stomatal characteristics may only partially revert to pre-stress conditions, as plants with drought memory retain modifications to minimize water loss. Drought memory induced long-term reduction of stomatal density in sorghum, which was connected with the methylated *H3K4me3* epigenetic memory marker (Mantoan et al., 2020). Moreover, methylation of *NCED3* (Virlouvet and Fromm, 2015), *RAB18* (Ding et al., 2014) or *ZEP1* (Forestan et al., 2020) increases ABA synthesis and subsequently reduces stomatal density. This reduction in stomatal density helps plants regulate water loss more effectively in anticipation of future drought episodes, reducing the effective surface area through which water can be lost via transpiration (Doheny-Adams et al., 2012). Drought memory can also lead to prolonged reduction of stomatal guard cell length, which can be also linked to increased water-use efficiency of plants (Herrera et al., 2024; Petrík et al., 2023; Petrík et al., 2024). This retention of drought-induced stomatal modifications highlights the role of epigenetic memory in optimizing water-use efficiency, allowing plants to better prepare for and withstand future water-limiting conditions.

4.3. *Stomatal responsiveness and transpiration*

Stomatal closure is a key response to drought that limits water loss but also restricts carbon dioxide uptake and photosynthesis. Drought stressed plants often reduce their stomatal conductance and transpiration in order to prevent excessive water loss (Střelcová et al., 2013; Rui et al., 2024). Upon drought stress release, stomata typically reopen, restoring gas exchange. However, in plants exhibiting drought memory, stomatal behaviour often remains altered, with stomata showing a more conservative response to water availability (Virlouvet and Fromm, 2015). Stomatal reopening is often more gradual in plants recovering from drought stress, allowing them to maintain a balance between gas exchange and water conservation (Rui et al., 2024). The delayed stomatal opening can be partially attributed to changes in the trafficking protein SYP121, which regulates ion channel activity in stomatal guard cells (Eisenach et al., 2012). This behaviour may lead to increased intrinsic water-use efficiency (iWUE) which can persist long-term, as iWUE is largely linked to the plant's methylation status (Zhong et al., 2021). Drought stress primed plants close their stomata faster under subsequent drought stress exposure due to higher accumulation of ABA and increased Ca^{2+} influx rate, which was connected to higher expression of *CIPK23* and higher expression of the *SLAC1* gene (Yang et al., 2023). Plants with drought memory are better capable of fine-tuning their stomatal control with ABA and therefore exhibit enhanced iWUE with sustained biomass or yield gains (Yao et al., 2021). Long-term exposure to water-deficit reduces the transpiration sensitivity to soil water content and VPD, resulting in plants maintaining low transpiration even under well-watered conditions (Grossiord et al., 2018; Zavadilová et al., 2023). This sustained reduction in transpiration enhances future drought tolerance by enabling a conservative approach to survive subsequent drought episodes and maintain physiological function.

4.4. Cuticular structure and residual water losses

The cuticle is a waxy layer preventing excessive water loss. The water loss after stomatal closure under drought conditions is dominated by cuticular pathway and through leaky stomata, which together comprise minimum leaf conductance (g_{min}). Minimum leaf conductance has been characterised as one of the most critical traits affecting drought survival time of plants and biomass accumulation capacity under drought (Petek-Petrik et al., 2023; Petek-Petrik et al., 2024; Ziegler et al., 2024). Drought memory can have significant impacts on cuticular wax composition via the aliphatic wax biosynthetic pathway, including *CER1, CER2, CER3, CER4, CER10* and *WSD1* (Dimopoulos et al., 2020). Nevertheless, changes of cuticular waxes are not necessarily translated into changes in minimum leaf conductance. There are few studies suggest that g_{min} may be plastic, with plants potentially acclimating to drought stress by reducing g_{min} (Le Provost et al., 2013; Chen et al., 2020a, 2020b) or that changes in cuticular waxes are related more to temperature stability of the cuticular layer (VanderWeide et al., 2022). On the other hand, several studies have found very limited phenotypic plasticity of g_{min} and no response pattern to drought stress (Schuster et al., 2017; Slot et al., 2021; Petek-Petrik et al., 2024; Wang et al., 2024a, 2024b). Therefore, the acclimation potential of g_{min} reduction as part of drought memory mechanisms is still unknown. *CYP86A* family genes, which are essential for cutin and wax biosynthesis, are regulated by auxin and are important for cuticle formation (Kong et al., 2020). The *CYP86A* genes can be epigenetically altered following drought stress, but the precise hormonal signalling pathway is still not known (Duan and Schuler, 2005). There is lack of studies directly linking drought priming or drought memory to changes in cuticular structure and residual water losses or minimum leaf conductance. As g_{min} is a critical component of drought tolerance, it is essential that future research focuses on how drought memory influences potential g_{min} acclimation, identifying epigenetic and physiological pathways that regulate long-term reductions in minimal stomatal conductance under recurrent drought conditions.

4.5. Photosynthetic recovery and chlorophyll retention

Drought stress can impair photosynthesis due to reduced stomatal conductance and by damaging the photosynthetic apparatus. Upon stress release, photosynthesis usually resumes, but the recovery process is modulated by drought memory. Plants with drought memory often exhibit enhanced photosynthetic efficiency during subsequent drought compared to non-primed plants (Fig. 5), allowing them to maintain productivity with limited water loss (Zhou et al., 2016). Specifically, plants may exhibit higher Rubisco activity and antioxidant capacity which supports photosynthetic rates (Menezes-Silva et al., 2017). Leaf level photosynthesis, electron transport rate and photosystem II performance index can be also significantly higher after drought release compared to the pre-stress state (Arend et al., 2016; Kannenberg et al., 2019; Antunović Dunić et al., 2023). Plants with drought memory have often reduced stomatal conductance, but if able to maintain their photosynthetic capacity may achieve higher water-use efficiency post drought release (Herrera et al., 2024). The faster recovery of photosynthetic rates after drought may result from altered gene expression related to photosynthetic machinery (*PSBS*, *LHCB*, *PGR5*), especially efficiency of photosystem II (Li et al., 2000; Damkjær et al., 2009; Arend et al., 2016; Yamamoto and Shikanai, 2019). Drought stress primed plants also show increased chlorophyll and carotenoid contents under subsequent drought stress compared to non-primed plants (Ben Abdallah et al., 2017), which is intricately linked to the epigenetic silencing of genes involved in pigment decomposition and upregulation of pigment synthases (Zhang et al., 2015; Anwar et al., 2021). Drought stress priming can also lead to increase of Rubisco content, which helps maintain photosynthetic rate under subsequent drought stress (Abid et al., 2016). Drought memory can be also associated with accumulation of the D_1 protein which improves the photoprotection under subsequent drought stress (Gadzinowska et al., 2021). As such, persistent epigenetic control enables plants to maintain photosynthetic function through the maintenance of pigment and Rubisco activity, allowing for a more resilient photosynthetic apparatus during subsequent stress event.

4.6. Antioxidant defences and osmolyte accumulation

Plants exposed to drought stress typically increase the production of antioxidants and osmoprotectants (e.g., proline, soluble sugars) to mitigate oxidative damage and maintain osmotic balance (Ditmarova et al., 2010; Vuksanović et al., 2023). Higher antioxidant capacity under drought helps plants to protect photosynthetic apparatus (Hasanagić et al., 2020; Alongi et al., 2024). In plants with drought memory, antioxidant enzyme classes such as superoxide dismutase, peroxidase, glutathione reductase and catalase continue to function at higher levels, helping the plant recover from stress and defend against future oxidative damage (Alves et al., 2020; Lukić et al., 2020; Carvalho et al., 2024). Drought priming can increase antioxidant capacity and is also linked to higher $d^{13}C$, reflecting higher water-use efficiency of plants (Ramírez et al., 2015). Higher leaf antioxidant content after drought priming can also enable plants to accumulate more biomass in subsequent drought stress exposure by reducing ROS agents, which would otherwise weaken cellular membrane integrity (Amini et al., 2023). Increased antioxidant capacity in cotton was linked to *H3K4me3* methylation (Tian et al., 2024). Drought stress memory positively affects leaf soluble sugars and proline content, therefore improving osmotic balance of drought stress primed plants under subsequent drought (Ben Abdallah et al., 2017). The study also found a positive impact of drought memory on antioxidant capacity in subsequent drought. The drought memory osmotic adjustment in wheat was associated with demethylation of *TaP5CS* and *TaBADH* (Li et al., 2023). Therefore, sustained epigenetic control from drought priming can lead to both antioxidant and osmotic adjustment to improve future drought tolerance.

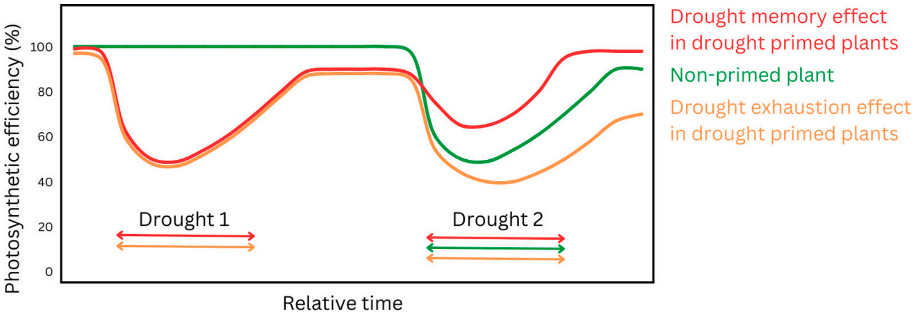

Fig. 5. Conceptual figure showing potential pathways of photosynthetic efficiency for drought primed plants that exhibit drought memory or drought exhaustion effects, compared with non-primed plant.

4.7. Leaf senescence: water loss avoidance, nutrient reallocation or assimilation recovery

Drought can both accelerate to prevent water losses and delay leaf senescence to conserve resources. The premature defoliation under extreme drought events is often attributed to tissue dehydration damage, rather than controlled process (Arend et al., 2022). Nevertheless, leaf senescence is largely regulated by epigenetic mechanisms, such as through the increased methylation of senescence-specific histones (Rudy et al., 2024). Overexpression of *NTL4* during and after drought stress response accelerates leaf senescence (Tan et al., 2023). Moreover, upregulation of ORE1 during drought stress can lead to faster leaf senescence (Yu et al., 2021). Nevertheless, the longevity of the epigenetic changes after stress release is still unknown. On the other hand, in plants exhibiting drought memory, leaf senescence may be delayed, allowing leaves to remain photosynthetically active for longer, which aids in the recovery of growth and productivity after stress (Arend et al., 2016). Selective leaf senescence, when plants reallocate nutrients such as nitrogen (N) from older to younger leaves, may further optimize resource allocation for new growth when conditions improve (Touche et al., 2024). Epigenetic modifications such as DNA methylation and siRNA are known to help regulate N responses, particularly under nutrient deficient conditions (Zhang et al., 2023). This is especially critical for ecosystems that experience repeated drought stress periods which can negatively affect access of plants to soil nutrients (Gessler et al., 2017; Joseph et al., 2021; Touche et al., 2022). However, impaired or incomplete nutrient reallocation during leaf senescence may occur, particularly during severe drought stress when leaf senescence is expedited due to rapidly sustained hydraulic damage (Estiarte and Peñuelas, 2015). Effective epigenetic regulation of leaf senescence processes may therefore be critical to optimize the trade-off between efficient nutrient scavenging and the timely senescence of damaged or older tissues.

5. Conclusion and future prospects

While DNA methylation, histone modifications, and non-coding RNAs have been linked to drought stress memory, the specific genes and pathways regulated by these epigenetic marks at the leaf level are not fully mapped. Additionally, current studies have largely focused on a handful of model or crop species such as *Arabidopsis* or *Populus*, which benefit from the existence of complete and relatively simple genome maps (Ding et al., 2013; Georgii et al., 2019). Hence, species of which genomes are not completely available, particularly in perennial plants with relatively large and highly repeated genomes, remain understudied. While many epigentic mechanisms are conserved across species, an increased focus of future research on these understudied species will likely identify orthologous genes, which enable epigenetic control. Such studies will help to elucidate the longevity of such modifications and overall duration of stress-memory. There is also a need for comprehensive profiling of both epigenetic and metabolomic processes to understand how stress memory translates to physiological responses in leaves. The interplay between different phytohormones (e.g., ABA, auxins, cytokinins) in the context of drought memory at the leaf level is complex and not fully understood. It is unclear how epigenetic modifications influence the dynamic balance of these hormones during repeated drought events and how these interactions are integrated to produce a coordinated response toward drought memory. Although some ncRNAs are known to be involved in drought responses, their specific roles in establishing and maintaining drought stress memory at the leaf level are not well defined. Identifying key ncRNAs within drought memory acquisition and understanding their targets and regulatory networks in leaf tissues is an ongoing challenge. The specific changes in leaf anatomy (e.g., cuticle thickness, vascular structure), ion homeostasis (Pesacreta et al., 2021; Acharya and Pesacreta, 2022) that contribute to drought stress memory are not fully understood. More research is needed to link anatomical changes with physiological and molecular responses exhibited via drought memory, and to identify how long such modifications persist and therefore lead to increased stress tolerance during subsequent droughts. Integrating metabolomic and transcriptomic studies is essential for identifying how epigenetic changes translate into stress-related metabolites and gene expression patterns that sustain stress responses and result in drought memory. These -omics approaches will help clarify the connections between epigenetic modifications, metabolic pathways, and long-term stress tolerance in plants.

Understanding drought memory in plants has become increasingly critical due to the escalating impacts of climate change. With global warming driving more frequent and severe drought events, the ability of plants to “remember” previous stress episodes and adapt accordingly is vital for ensuring their survival and productivity. In agriculture, identifying and breeding crops with enhanced drought memory traits could improve food security by enabling stable yields under water-limiting conditions. Similarly, for forest ecosystems, understanding how long-lived trees retain drought memory could inform reforestation efforts and the selection of resilient species for afforestation projects in drought-prone regions.

Declaration of generative AI in scientific writing

During the preparation of this work Peter Petrík used ChatGPT-4o for grammatical and stylistic correction of the text. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

CRediT authorship contribution statement

Franklin Alongi: Writing – original draft. **Anja Petek-Petrik:** Writing – review & editing. **Mohammad Mukarram:** Writing – review & editing. **Hülya Torun:** Writing – review & editing. **Bernhard Schuldt:** Writing – original draft. **Peter Petrík:** Writing – original draft, Supervision, Conceptualization.

Funding

FA acknowledges funding by the Helmholtz Initiative and Networking fund (W2/W3–156).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

References

Abdulraheem, M.I., Xiong, Y., Moshood, A.Y., Cadenas-Pliego, G., Zhang, H., Hu, J., 2024. Mechanisms of plant epigenetic regulation in response to plant stress: recent discoveries and implications. Plants 13, 163. https://doi.org/10.3390/plants13020163.

Abid, M., Tian, Z., Ata-Ul-Karim, S.T., Liu, Y., Cui, Y., Zahoor, R., Jiang, D., Dai, T., 2016. Improved tolerance to post-anthesis drought stress by pre-drought priming at vegetative stages in drought-tolerant and -sensitive wheat cultivars. Plant Physiol. Biochem. 106, 218–227. https://doi.org/10.1016/j.plaphy.2016.05.003.

Acharya, A., Pesacreta, T.C., 2022. Localization of seed-derived and externally supplied nutrients in peanut seedling root. Theor. Exp. Plant Physiol. 34, 37–51. https://doi.org/10.1007/s40626-021-00227-9.

Ahmad, P., Rasool, S., Gul, A., Sheikh, S.A., Akram, N.A., Ashraf, M., Kazi, A.M., Gucel, S., 2016. Jasmonates: multifunctional roles in stress tolerance. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00813.

Ahmad, B., Mukarram, M., Choudhary, S., Petrík, P., Dar, T.A., Khan, M.M.A., 2024. Adaptive responses of nitric oxide (NO) and its intricate dialogue with phytohormones during salinity stress. Plant Physiol. Biochem. 208, 108504. https://doi.org/10.1016/j.plaphy.2024.108504.

Alam, Md.M., Nahar, K., Hasanuzzaman, M., Fujita, M., 2014. Exogenous jasmonic acid modulates the physiology, antioxidant defense and glyoxalase systems in imparting drought stress tolerance in different Brassica species. Plant Biotechnol. Rep. 8, 279–293. https://doi.org/10.1007/s11816-014-0321-8.

Ali, Md.S., Baek, K.-H., 2020. Jasmonic acid signaling pathway in response to abiotic stresses in plants. IJMS 21, 621. https://doi.org/10.3390/ijms21020621.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Alongi, F., Petrík, P., Ruehr, N.K., 2024. Drought and heat stress interactions modify photorespiration and hydrogen peroxide content in Silver fir. Tree Physiol. https://doi.org/10.1093/treephys/tpae126 tpae126.

Alves, R.D.F.B., Menezes-Silva, P.E., Sousa, L.F., Loram-Lourenço, L., Silva, M.L.F., Almeida, S.E.S., Silva, F.G., Perez de Souza, L., Fernie, A.R., Farnese, F.S., 2020. Evidence of drought memory in Dipteryx alata indicates differential acclimation of plants to savanna conditions. Sci. Rep. 10, 16455. https://doi.org/10.1038/s41598-020-73423-3.

Amini, A., Majidi, M.M., Mokhtari, N., Ghanavati, M., 2023. Drought stress memory in a germplasm of synthetic and common wheat: antioxidant system, physiological and morphological consequences. Sci. Rep. 13, 8569. https://doi.org/10.1038/s41598-023-35642-2.

Antunović Dunić, J., Mlinarić, S., Pavlović, I., Lepeduš, H., Salopek-Sondi, B., 2023. Comparative analysis of primary photosynthetic reactions assessed by OJIP kinetics in three Brassica crops after drought and recovery. Appl. Sci. 13, 3078. https://doi.org/10.3390/app13053078.

Anwar, S., Brenya, E., Alagoz, Y., Cazzonelli, C.I., 2021. Epigenetic control of carotenogenesis during plant development. Crit. Rev. Plant Sci. 40, 23–48. https://doi.org/10.1080/07352689.2020.1866829.

Arend, M., Sever, K., Pflug, E., Gessler, A., Schaub, M., 2016. Seasonal photosynthetic response of European beech to severe summer drought: limitation, recovery and post-drought stimulation. Agric. For. Meteorol. 220, 83–89. https://doi.org/10.1016/j.agrformet.2016.01.011.

Arend, M., Link, R.M., Zahnd, C., Hoch, G., Schuldt, B., Kahmen, A., 2022. Lack of hydraulic recovery as a cause of post-drought foliage reduction and canopy decline in European beech. New Phytol. 234, 1195–1205. https://doi.org/10.1111/nph.18065.

Auler, P.A., Souza, G.M., da Silva Engela, M.R.G., do Amaral, M.N., Rossatto, T., Ziglio da Silva, M.G., Furlan, C.M., Maserti, B., Braga, E.J.B., 2021. Stress memory of physiological, biochemical and metabolomic responses in two different rice genotypes under drought stress: The scale matters. Plant Science 311, 110994. https://doi.org/10.1016/j.plantsci.2021.110994.

Avramova, Z., 2015. Transcriptional ‘memory’ of a stress: transient chromatin and memory (epigenetic) marks at stress-response genes. Plant J. 83, 149–159. https://doi.org/10.1111/tpj.12832.

Avramova, Z., 2017. The jasmonic acid-signalling and abscisic acid-signalling pathways cross talk during one, but not repeated, dehydration stress: a non-specific ‘panicky’ or a meaningful response? Plant Cell Environ. 40, 1704–1710. https://doi.org/10.1111/pce.12967.

Avramova, Z., 2019. Defence-related priming and responses to recurring drought: two manifestations of plant transcriptional memory mediated by the ABA and JA signalling pathways. Plant Cell Environ. 42, 983–997. https://doi.org/10.1111/pce.13458.

Balao, F., Paun, O., Alonso, C., 2018. Uncovering the contribution of epigenetics to plant phenotypic variation in Mediterranean ecosystems. Plant Biol. J. 20, 38–49. https://doi.org/10.1111/plb.12594.

Balyan, S., Kansal, S., Jajo, R., Behere, P.R., Chatterjee, R., Raghuvanshi, S., 2023. Delineating the tissue-mediated drought stress governed tuning of conserved miR408 and its targets in rice. Funct. Integr. Genomics 23, 187. https://doi.org/10.1007/s10142-023-01111-2.

Banerjee, A., Roychoudhury, A., 2017. Epigenetic regulation during salinity and drought stress in plants: histone modifications and DNA methylation. Plant Gene 11, 199–204. https://doi.org/10.1016/j.plgene.2017.05.011.

Batista-Silva, W., de Paiva Gonçalves, J., Siqueira, J.A., Martins, A.O., Ribeiro, D.M., Nunes-Nesi, A., Zsögön, A., Araújo, W.L., 2024. Auxin metabolism and the modulation of plant growth. Environ. Exp. Bot. 226, 105917. https://doi.org/10.1016/j.envexpbot.2024.105917.

Ben Abdallah, M., Methenni, K., Nouairi, I., Zarrouk, M., Youssef, N.B., 2017. Drought priming improves subsequent more severe drought in a drought-sensitive cultivar of olive cv. Chétoui. Sci. Hortic. 221, 43–52. https://doi.org/10.1016/j.scienta.2017.04.021.

Brito, C., Dinis, L.-T., Meijón, M., Ferreira, H., Pinto, G., Moutinho-Pereira, J., Correia, C., 2018. Salicylic acid modulates olive tree physiological and growth responses to drought and rewatering events in a dose dependent manner. J. Plant Physiol. 230, 21–32. https://doi.org/10.1016/j.jplph.2018.08.004.

Carthew, R.W., Sontheimer, E.J., 2009. Origins and mechanisms of miRNAs and siRNAs. Cell 136, 642–655. https://doi.org/10.1016/j.cell.2009.01.035.

Carvalho, V., Gaspar, M., Nievola, C.C., 2024. Drought memory in Acanthostachys strobilacea, a CAM epiphytic bromeliad. Plant Biol. J. 26, 188–196. https://doi.org/10.1111/plb.13605.

Castel, S.E., Martienssen, R.A., 2013. RNA interference in the nucleus: roles for small RNAs in transcription, epigenetics and beyond. Nat. Rev. Genet. 14, 100–112. https://doi.org/10.1038/nrg3355.

Chen, C., Galon, Y., Rahmati Ishka, M., Malihi, S., Shimanovsky, V., Twito, S., Rath, A., Vatamaniuk, O.K., Miller, G., 2020a. ASCORBATE PEROXIDASE6 delays the onset of age-dependent leaf senescence. Plant Physiol., kiaa031 https://doi.org/10.1093/plphys/kiaa031.

Chen, M., Zhu, X., Zhang, Y., Du, Z., Chen, X., Kong, X., Sun, W., Chen, C., 2020b. Drought stress modify cuticle of tender tea leaf and mature leaf for transpiration barrier enhancement through common and distinct modes. Sci. Rep. 10, 6696. https://doi.org/10.1038/s41598-020-63683-4.

Chinnusamy, V., Zhu, J.-K., 2009. Epigenetic regulation of stress responses in plants. Curr. Opin. Plant Biol. 12, 133–139. https://doi.org/10.1016/j.pbi.2008.12.006.

Contreras-Cubas, C., Palomar, M., Arteaga-Vázquez, M., Reyes, J.L., Covarrubias, A.A., 2012. Non-coding RNAs in the plant response to abiotic stress. Planta 236, 943–958.

Cortleven, A., Marg, I., Yamburenko, M.V., Schlicke, H., Hill, K., Grimm, B., Schaller, G. E., Schmülling, T., 2016. Cytokinin regulates the etioplast-chloroplast transition through the two-component signaling system and activation of chloroplast-related genes. Plant Physiol. 172, 464–478. https://doi.org/10.1104/pp.16.00640.

Cotrina Cabello, G.G., Ruiz Rodriguez, A., Husnain Gondal, A., Areche, F.O., Flores, D.D. C., Astete, J.A.Q., Camayo-Lapa, B.F., Yapias, R.J.M., Jabbar, A., Yovera Saldarriaga, J., Salas-Contreras, W.H., Cruz Nieto, D.D., 2023. Plant adaptability to climate change and drought stress for crop growth and production. CABI Rev. https://doi.org/10.1079/cabireviews.2023.0004 cabireviews.2023.0004.

Damkjær, J.T., Kereïche, S., Johnson, M.P., Kovacs, L., Kiss, A.Z., Boekema, E.J., Ruban, A.V., Horton, P., Jansson, S., 2009. The photosystem II light-harvesting protein Lhcb3 affects the macrostructure of photosystem II and the rate of state transitions in Arabidopsis. Plant Cell 21, 3245–3256. https://doi.org/10.1105/tpc.108.064006.

de Freitas, Alves, Guedes, F., Menezes-Silva, P.E., DaMatta, F.M., Alves-Ferreira, M., 2019. Using transcriptomics to assess plant stress memory. Theor. Exp. Plant Physiol. 31, 47–58. https://doi.org/10.1007/s40626-018-0135-0.

de Souza Neta, M.L., Torres, S.B., de Paiva, E.P., Carvalho, S.M.C., de Sousa Leite, M., Guirra, B.S., de Morais, M.B., de Albuquerque, C.C., Pereira, K.T.O., Peixoto, T.D.C., da Silva Sá, F.V., 2024. Osmotic adjustment and antioxidant activity of cucumber seeds pre-treated with stress attenuators and subjected to drought stress during germination. J. Plant Growth Regul. 43, 1919–1933. https://doi.org/10.1007/s00344-023-11231-5.

Dimopoulos, N., Tindjau, R., Wong, D.C.J., Matzat, T., Haslam, T., Song, C., Gambetta, G. A., Kunst, L., Castellarin, S.D., 2020. Drought stress modulates cuticular wax composition of the grape berry. J. Exp. Bot. 71, 3126–3141. https://doi.org/10.1093/jxb/eraa046.

Ding, Y., Liu, N., Virlouvet, L., Riethoven, J.-J., Fromm, M., Avramova, Z., 2013. Four distinct types of dehydration stress memory genes in Arabidopsis thaliana. BMC Plant Biol. 13, 229. https://doi.org/10.1186/1471-2229-13-229.

Ding, Y., Virlouvet, L., Liu, N., Riethoven, J.-J., Fromm, M., Avramova, Z., 2014. Dehydration stress memory genes of Zea mays; comparison with Arabidopsis thaliana. BMC Plant Biol. 14, 141. https://doi.org/10.1186/1471-2229-14-141.

Ditmarova, L., Kurjak, D., Palmroth, S., Kmet, J., Strelcova, K., 2010. Physiological responses of Norway spruce (Picea abies) seedlings to drought stress. Tree Physiol. 30, 205–213. https://doi.org/10.1093/treephys/tpp116.

Doheny-Adams, T., Hunt, L., Franks, P.J., Beerling, D.J., Gray, J.E., 2012. 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. B 367, 547–555. https://doi.org/10.1098/rstb.2011.0272.

Drenovsky, R.E., Pietrasiak, N., Short, T.H., 2019. Global temporal patterns in plant nutrient resorption plasticity. Glob. Ecol. Biogeogr. 28, 728–743. https://doi.org/10.1111/geb.12885.

Duan, H., Schuler, M.A., 2005. Differential expression and evolution of the Arabidopsis CYP86A subfamily. Plant Physiol. 137, 1067–1081. https://doi.org/10.1104/pp.104.055715.

Efroni, I., Han, S.-K., Kim, H.J., Wu, M.-F., Steiner, E., Birnbaum, K.D., Hong, J.C., Eshed, Y., Wagner, D., 2013. Regulation of leaf maturation by chromatin-mediated modulation of cytokinin responses. Dev. Cell 24, 438–445. https://doi.org/10.1016/j.devcel.2013.01.019.

Eisenach, C., Chen, Z., Grefen, C., Blatt, M.R., 2012. The trafficking protein SYP121 of Arabidopsis connects programmed stomatal closure and K + channel activity with vegetative growth. Plant J. 69, 241–251. https://doi.org/10.1111/j.1365-313X.2011.04786.x.

Estiarte, M., Peñuelas, J., 2015. Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. Glob. Chang. Biol. 21, 1005–1017. https://doi.org/10.1111/gcb.12804.

Fan, Q.-J., Liu, J.-H., 2012. Nitric oxide is involved in dehydration/drought tolerance in Poncirus trifoliata seedlings through regulation of antioxidant systems and stomatal response. Plant Cell Rep. 31, 145–154. https://doi.org/10.1007/s00299-011-1148-1.

Fidler, J., Graska, J., Gietler, M., Nykiel, M., Prabucka, B., Rybarczyk-Płońska, A., Muszyńska, E., Morkunas, I., Labudda, M., 2022. PYR/PYL/RCAR receptors play a vital role in the abscisic-acid-dependent responses of plants to external or internal stimuli. Cells 11, 1352. https://doi.org/10.3390/cells11081352.

Fleta-Soriano, E., Munné-Bosch, S., 2016. Stress memory and the inevitable effects of drought: a physiological perspective. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00143.

Forestan, C., Farinati, S., Zambelli, F., Pavesi, G., Rossi, V., Varotto, S., 2020. Epigenetic signatures of stress adaptation and flowering regulation in response to extended drought and recovery in Zea mays. Plant Cell Environ. 43, 55–75. https://doi.org/10.1111/pce.13660.

Gadzinowska, J., Hura, K., Ostrowska, A., Hura, T., 2021. Activity of the photosynthetic apparatus in dehydrated leaves of a perennial shrub Rosa rubiginosa L. with different levels of drought memory. Environ. Exp. Bot. 187, 104493. https://doi.org/10.1016/j.envexpbot.2021.104493.

Gallé, A., Haldimann, P., Feller, U., 2007. Photosynthetic performance and water relations in young pubescent oak (Quercus pubescens) trees during drought stress and recovery. New Phytol. 174, 799–810. https://doi.org/10.1111/j.1469-8137.2007.02047.x.

Gao, Q., Liu, Yamin, Liu, Yumin, Dai, C., Zhang, Y., Zhou, F., Zhu, Y., 2023. Salicylic acid modulates the osmotic system and photosynthesis rate to enhance the drought tolerance of Toona ciliata. Plants 12, 4187. https://doi.org/10.3390/plants12244187.

Gelaw, T.A., Sanan-Mishra, N., 2021. Non-coding RNAs in response to drought stress. IJMS 22, 12519. https://doi.org/10.3390/ijms222212519.

Georgii, E., Kugler, K., Pfeifer, M., Vanzo, E., Block, K., Domagalska, M.A., Jud, W., AbdElgawad, H., Asard, H., Reinhardt, R., Hansel, A., Spannagl, M., Schäffner, A.R., Palme, K., Mayer, K.F.X., Schnitzler, J.-P., 2019. The systems architecture of molecular memory in poplar after abiotic stress. Plant Cell 31, 346–367. https://doi.org/10.1105/tpc.18.00431.

Gessler, A., Schaub, M., McDowell, N.G., 2017. The role of nutrients in drought-induced tree mortality and recovery. New Phytol. 214, 513–520. https://doi.org/10.1111/nph.14340.

Godwin, J., Farrona, S., 2020. Plant epigenetic stress memory induced by drought: A physiological and molecular perspective. In: Spillane, C., McKeown, P. (Eds.), Plant Epigenetics and Epigenomics, Methods in Molecular Biology. Springer, US, New York, NY, pp. 243–259. https://doi.org/10.1007/978-1-0716-0179-2_17.

Grossiord, C., Sevanto, S., Limousin, J.-M., Meir, P., Mencuccini, M., Pangle, R.E., Pockman, W.T., Salmon, Y., Zweifel, R., McDowell, N.G., 2018. Manipulative experiments demonstrate how long-term soil moisture changes alter controls of plant water use. Environ. Exp. Bot. 152, 19–27. https://doi.org/10.1016/j.envexpbot.2017.12.010.

Gujjar, R.S., Banyen, P., Chuekong, W., Worakan, P., Roytrakul, S., Supaibulwatana, K., 2020. A synthetic Cytokinin improves photosynthesis in rice under drought stress by modulating the abundance of proteins related to stomatal conductance, chlorophyll contents, and rubisco activity. Plants 9, 1106. https://doi.org/10.3390/plants9091106.

Guo, T., Wang, D., Fang, J., Zhao, J., Yuan, S., Xiao, L., Li, X., 2019. Mutations in the rice OsCHR4 gene, encoding a CHD3 family chromatin remodeler, induce narrow and rolled leaves with increased cuticular wax. IJMS 20, 2567. https://doi.org/10.3390/ijms20102567.

Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D.D., Allen, C.D., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. Nat. Commun. 13, 1761. https://doi.org/10.1038/s41467-022-29289-2.

Hasanagić, D., Koleška, I., Kojić, D., Vlaisavljević, S., Janjić, N., Kukavica, B., 2020. Long term drought effects on tomato leaves: anatomical, gas exchange and antioxidant modifications. Acta Physiol. Plant. 42, 121. https://doi.org/10.1007/s11738-020-03114-z.

Hasanuzzaman, Md., Zhou, M., Shabala, S., 2023. How does stomatal density and residual transpiration contribute to osmotic stress tolerance? Plants 12, 494. https://doi.org/10.3390/plants12030494.

Hayat, S., Hayat, Q., Alyemeni, M.N., Wani, A.S., Pichtel, J., Ahmad, A., 2012. Role of proline under changing environments: a review. Plant Signal. Behav. 7, 1456–1466. https://doi.org/10.4161/psb.21949.

Herrera, J.C., Savoi, S., Dostal, J., Elezovic, K., Chatzisavva, M., Forneck, A., Savi, T., 2024. The legacy of past droughts induces water-sparingly behaviour in Grüner Veltliner grapevines. Plant Biol. J. https://doi.org/10.1111/plb.13620 plb.13620.

Hetherington, A.M., Woodward, F.I., 2003. The role of stomata in sensing and driving environmental change. Nature 424, 901–908. https://doi.org/10.1038/nature01843.

Higashide, T., Narukawa, M., Shimada, Y., Soeno, K., 2014. Suppression of elongation and growth of tomato seedlings by auxin biosynthesis inhibitors and modeling of the growth and environmental response. Sci. Rep. 4, 4556. https://doi.org/10.1038/srep04556.

Huang, W., Peng, S., Xian, Z., Lin, D., Hu, G., Yang, L., Ren, M., Li, Z., 2017. Overexpression of a tomato miR171 target gene Sl GRAS 24 impacts multiple agronomical traits via regulating gibberellin and auxin homeostasis. Plant Biotechnol. J. 15, 472–488. https://doi.org/10.1111/pbi.12646.

Húdoková, H., Fleischer Jr., P., Ježík, M., Marešová, J., Pšidová, E., Mukarram, M., Ditmarová, Ľ., Sliacka-Konôpková, A., Jamnická, G., 2023. Can seedlings of Norway spruce (Picea abies L. H. Karst.) populations withstand changed climate conditions? Photosynt 61, 328–341. https://doi.org/10.32615/ps.2023.026.

Jacques, C., Salon, C., Barnard, R.L., Vernoud, V., Prudent, M., 2021. Drought stress memory at the plant cycle level: a review. Plants 10, 1873. https://doi.org/10.3390/plants10091873.

Jan, S., Abbas, N., Ashraf, M., Ahmad, P., 2019. Roles of potential plant hormones and transcription factors in controlling leaf senescence and drought tolerance. Protoplasma 256, 313–329. https://doi.org/10.1007/s00709-018-1310-5.

Jia, H., Zhang, S., Ruan, M., Wang, Y., Wang, C., 2012. Analysis and application of RD29 genes in abiotic stress response. Acta Physiol. Plant. 34, 1239–1250. https://doi.org/10.1007/s11738-012-0969-z.

Jiang, J., Zhu, H., Li, N., Batley, J., Wang, Y., 2022. The miR393-target module regulates plant development and responses to biotic and abiotic stresses. IJMS 23, 9477. https://doi.org/10.3390/ijms23169477.

Jiang, K., Guo, H., Zhai, J., 2023. Interplay of phytohormones and epigenetic regulation: a recipe for plant development and plasticity. JIPB 65, 381–398. https://doi.org/10.1111/jipb.13384.

Jiang, Y., Yue, Y., Wang, Zhaoxu, Lu, C., Wang, Zhizheng, Yin, Z., Li, Y., Hao, G.-F., Ding, X., 2024. A novel ABA structural analogues enhanced plant resistance by inducing the plant immunity and inactivating ABA signaling pathway. Adv. Agrochem. 3, 64–73. https://doi.org/10.1016/j.aac.2023.08.006.

Joseph, J., Luster, J., Bottero, A., Buser, N., Baechli, L., Sever, K., Gessler, A., 2021. Effects of drought on nitrogen uptake and carbon dynamics in trees. Tree Physiol. 41, 927–943. https://doi.org/10.1093/treephys/tpaa146.

Kambona, C.M., Koua, P.A., Léon, J., Ballvora, A., 2023. Stress memory and its regulation in plants experiencing recurrent drought conditions. Theor. Appl. Genet. 136, 26. https://doi.org/10.1007/s00122-023-04313-1.

Kannenberg, S.A., Novick, K.A., Alexander, M.R., Maxwell, J.T., Moore, D.J.P., Phillips, R.P., Anderegg, W.R.L., 2019. Linking drought legacy effects across scales: from leaves to tree rings to ecosystems. Glob. Chang. Biol. 25, 2978–2992. https://doi.org/10.1111/gcb.14710.

Kapoor, B., Kumar, P., Sharma, R., Irfan, M., 2023. Drought-induced plant miRNAome and phytohormone signaling cross-talk. In: Plant Hormones in Crop Improvement. Elsevier, pp. 235–247. https://doi.org/10.1016/B978-0-323-91886-2.00006-9.

Kardiman, R., Ræbild, A., 2018. Relationship between stomatal density, size and speed of opening in Sumatran rainforest species. Tree Physiol. 38, 696–705. https://doi.org/10.1093/treephys/tpx149.

Kashyap, S., Agarwala, N., Sunkar, R., 2024. Understanding plant stress memory traits can provide a way for sustainable agriculture. Plant Sci. 340, 111954. https://doi.org/10.1016/j.plantsci.2023.111954.

Kaya, C., Uğurlar, F., Adamakis, I.-D.S., 2024. Epigenetic modifications of hormonal signaling pathways in plant drought response and tolerance for sustainable food security. IJMS 25, 8229. https://doi.org/10.3390/ijms25158229.

Kebert, M., Kostić, S., Stojnić, S., Čapelja, E., Markić, A.G., Zorić, M., Kesić, L., Flors, V., 2023. A Fine-Tuning of the Plant Hormones, Polyamines and Osmolytes by Ectomycorrhizal Fungi Enhances Drought Tolerance in Pedunculate OakInt. J. Mol. Sci. 24 (8), 7510. https://doi.org/10.3390/ijms24087510.

Keshet, I., Lieman-Hurwitz, J., Cedar, H., 1986. DNA methylation affects the formation of active chromatin. Cell 44, 535–543. https://doi.org/10.1016/0092-8674(86)90263-1.

Khan, M.I.R., Fatma, M., Per, T.S., Anjum, N.A., Khan, N.A., 2015. Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. Front. Plant Sci. 6. https://doi.org/10.3389/fpls.2015.00462.

Khan, S., Alvi, A.F., Saify, S., Iqbal, N., Khan, N.A., 2024. The ethylene biosynthetic enzymes, 1-aminocyclopropane-1-carboxylate (ACC) synthase (ACS) and ACC oxidase (ACO): the less explored players in abiotic stress tolerance. Biomolecules 14, 90. https://doi.org/10.3390/biom14010090.

Khoudi, H., 2023. SHINE clade of ERF transcription factors: a significant player in abiotic and biotic stress tolerance in plants. Plant Physiol. Biochem. 195, 77–88. https://doi.org/10.1016/j.plaphy.2022.12.030.

Kinoshita, T., Seki, M., 2014. Epigenetic memory for stress response and adaptation in plants. Plant Cell Physiol. 55, 1859–1863. https://doi.org/10.1093/pcp/pcu125.

Kohli, S.K., Khanna, K., Bhardwaj, R., Corpas, F.J., Ahmad, P., 2022. Nitric oxide, salicylic acid and oxidative stress: is it a perfect equilateral triangle? Plant Physiol. Biochem. 184, 56–64. https://doi.org/10.1016/j.plaphy.2022.05.017.

Kong, L., Liu, Y., Zhi, P., Wang, X., Xu, B., Gong, Z., Chang, C., 2020. Origins and evolution of cuticle biosynthetic machinery in land plants. Plant Physiol. 184, 1998–2010. https://doi.org/10.1104/pp.20.00913.

Konrad, W., Katul, G., Roth-Nebelsick, A., 2021. Leaf temperature and its dependence on atmospheric CO 2 and leaf size. Geol. J. 56, 866–885. https://doi.org/10.1002/gj.3757.

Kou, X., Han, W., Kang, J., 2022a. Responses of root system architecture to water stress at multiple levels: a meta-analysis of trials under controlled conditions. Front. Plant Sci. 13, 1085409. https://doi.org/10.3389/fpls.2022.1085409.

Kou, S., Gu, Q., Duan, L., Liu, G., Yuan, P., Li, H., Wu, Z., Liu, W., Huang, P., Liu, L., 2022b. Genome-wide bisulphite sequencing uncovered the contribution of DNA methylation to rice short-term drought memory formation. J. Plant Growth Regul. 41, 2903–2917. https://doi.org/10.1007/s00344-021-10483-3.

Koyama, T., Sato, F., Ohme-Takagi, M., 2017. Roles of miR319 and TCP transcription factors in leaf development. Plant Physiol. 175, 874–885. https://doi.org/10.1104/pp.17.00732.

Kumazaki, A., Suzuki, N., 2019. Enhanced tolerance to a combination of heat stress and drought in Arabidopsis plants deficient in ICS1 is associated with modulation of photosynthetic reaction center proteins. Physiol. Plant. 165, 232–246. https://doi.org/10.1111/ppl.12809.

Lam, P., Zhao, L., Eveleigh, N., Yu, Y., Chen, X., Kunst, L., 2015. The exosome and trans-acting small interfering RNAs regulate cuticular wax biosynthesis during Arabidopsis inflorescence stem development. Plant Physiol. 167, 323–336. https://doi.org/10.1104/pp.114.252825.

Lämke, J., Bäurle, I., 2017. Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. Genome Biol. 18, 124. https://doi.org/10.1186/s13059-017-1263-6.

Le Provost, G., Domergue, F., Lalanne, C., Ramos Campos, P., Grosbois, A., Bert, D., Meredieu, C., Danjon, F., Plomion, C., Gion, J.-M., 2013. Soil water stress affects both cuticular wax content and cuticle-related gene expression in young saplings of maritime pine (Pinus pinaster Ait). BMC Plant Biol. 13, 95. https://doi.org/10.1186/1471-2229-13-95.

Lee, S.-U., Mun, B.-G., Bae, E.-K., Kim, J.-Y., Kim, H.-H., Shahid, M., Choi, Y.-I., Hussain, A., Yun, B.-W., 2021. Drought stress-mediated transcriptome profile reveals

NCED as a key player modulating drought tolerance in Populus davidiana. Front. Plant Sci. 12, 755539. https://doi.org/10.3389/fpls.2021.755539.

Li, X.-P., Björkman, O., Shih, C., Grossman, A.R., Rosenquist, M., Jansson, S., Niyogi, K. K., 2000. A pigment-binding protein essential for regulation of photosynthetic light harvesting. Nature 403, 391–395. https://doi.org/10.1038/35000131.

Li, X., Xie, X., Li, J., Cui, Y., Hou, Y., Zhai, L., Wang, X., Fu, Y., Liu, R., Bian, S., 2017. Conservation and diversification of the miR166 family in soybean and potential roles of newly identified miR166s. BMC Plant Biology 17. https://doi.org/10.1186/s12870-017-0983-9.

Li, C., Xu, J., Li, J., Li, Q., Yang, H., 2014. Involvement of Arabidopsis histone acetyltransferase HAC family genes in the ethylene signaling pathway. Plant Cell Physiol. 55, 426–435. https://doi.org/10.1093/pcp/pct180.

Li, W., Cui, X., Meng, Z., Huang, X., Xie, Q., Wu, H., Jin, H., Zhang, D., 2012. Transcriptional Regulation of Arabidopsis MIR168a and ARGONAUTE1 Homeostasis in Abscisic Acid and Abiotic Stress Responses. Plant Physiol. 158 (3), 1279–1292. https://doi.org/10.1104/pp.111.188789.

Li, J., Song, Q., Zuo, Z.-F., Liu, L., 2022a. MicroRNA398: a master regulator of plant development and stress responses. IJMS 23, 10803. https://doi.org/10.3390/ijms231810803.

Li, Y., Yang, Z., Zhang, Y., Guo, J., Liu, L., Wang, C., Wang, B., Han, G., 2022b. The roles of HD-ZIP proteins in plant abiotic stress tolerance. Front. Plant Sci. 13, 1027071. https://doi.org/10.3389/fpls.2022.1027071.

Li, Q., Wang, X., Sun, Z., Wu, Y., Malkodslo, M.M., Ge, J., Jing, Z., Zhou, Q., Cai, J., Zhong, Y., Huang, M., Jiang, D., 2023. DNA methylation levels of TaP5CS and TaBADH are associated with enhanced tolerance to PEG-induced drought stress triggered by drought priming in wheat. Plant Physiol. Biochem. 200, 107769. https://doi.org/10.1016/j.plaphy.2023.107769.

Liebsch, D., Palatnik, J.F., 2020. MicroRNA miR396, GRF transcription factors and GIF co-regulators: a conserved plant growth regulatory module with potential for breeding and biotechnology. Curr. Opin. Plant Biol. 53, 31–42. https://doi.org/10.1016/j.pbi.2019.09.008.

Lim, C.W., Baek, W., Han, S.-W., Lee, S.C., 2013. Arabidopsis PYL8 plays an important role for ABA signaling and drought stress responses. Plant Pathol. J. 29, 471–476. https://doi.org/10.5423/PPJ.NT.07.2013.0071.

Liu, D., Song, Y., Chen, Z., Yu, D., 2009. Ectopic expression of miR396 suppresses GRF target gene expression and alters leaf growth in Arabidopsis. Physiol. Plant. 136, 223–236. https://doi.org/10.1111/j.1399-3054.2009.01229.x.

Liu, C., Lu, F., Cui, X., Cao, X., 2010. Histone methylation in higher plants. Annu. Rev. Plant Biol. 61, 395–420. https://doi.org/10.1146/annurev.arplant.043008.091939.

Liu, N., Staswick, P.E., Avramova, Z., 2016. Memory responses of jasmonic acid-associated Arabidopsis genes to a repeated dehydration stress. Plant Cell Environ. 39, 2515–2529. https://doi.org/10.1111/pce.12806.

Liu, L., Cao, X., Zhai, Z., Ma, S., Tian, Y., Cheng, J., 2022. Direct evidence of drought stress memory in mulberry from a physiological perspective: antioxidative, osmotic and phytohormonal regulations. Plant Physiol. Biochem. 186, 76–87. https://doi.org/10.1016/j.plaphy.2022.07.001.

Lu, X., Wang, X., Chen, X., Shu, N., Wang, J., Wang, D., Wang, S., Fan, W., Guo, L., Guo, X., Ye, W., 2017. Single-base resolution methylomes of upland cotton (Gossypium hirsutum L.) reveal epigenome modifications in response to drought stress. BMC Genomics 18, 297. https://doi.org/10.1186/s12864-017-3681-y.

Lu, Hongchen, Chen, L., Du, M., Lu, Haiqin, Liu, J., Ye, S., Tao, B., Li, R., Zhao, L., Wen, J., Yi, B., Tu, J., Fu, T., Shen, J., 2023. miR319 and its target TCP4 involved in plant architecture regulation in Brassica napus. Plant Sci. 326, 111531. https://doi.org/10.1016/j.plantsci.2022.111531.

Lukić, N., Kukavica, B., Davidović-Plavšić, B., Hasanagić, D., Walter, J., 2020. Plant stress memory is linked to high levels of anti-oxidative enzymes over several weeks. Environ. Exp. Bot. 178, 104166. https://doi.org/10.1016/j.envexpbot.2020.104166.

Lukić, N., Schurr, F.M., Trifković, T., Kukavica, B., Walter, J., 2023. Transgenerational stress memory in plants is mediated by upregulation of the antioxidative system. Environ. Exp. Bot. 205, 105129. https://doi.org/10.1016/j.envexpbot.2022.105129.

Luo, M., Liu, X., Singh, P., Cui, Y., Zimmerli, L., Wu, K., 2012. Chromatin modifications and remodeling in plant abiotic stress responses. Biochim. Biophys. Acta (BBA) - Gene Regul. Mech. 1819, 129–136. https://doi.org/10.1016/j.bbagrm.2011.06.008.

Luo, C., Hajkova, P., Ecker, J.R., 2018. Dynamic DNA methylation: in the right place at the right time. Science 361, 1336–1340. https://doi.org/10.1126/science.aat6806.

Ma, S., Tang, N., Li, Xu, Xie, Y., Xiang, D., Fu, J., Shen, J., Yang, J., Tu, H., Li, Xianghua, Hu, H., Xiong, L., 2019. Reversible histone H2B monoubiquitination fine-tunes abscisic acid signaling and drought response in rice. Mol. Plant 12, 263–277. https://doi.org/10.1016/j.molp.2018.12.005.

Mantoan, L.P.B., Corrêa, C.V., Rainho, C.A., de Almeida, L.F.R., 2020. Rapid dehydration induces long-term water deficit memory in sorghum seedlings: advantages and consequences. Environ. Exp. Bot. 180, 104252. https://doi.org/10.1016/j.envexpbot.2020.104252.

Martin, L.B.B., Romero, P., Fich, E.A., Domozych, D.S., Rose, J.K.C., 2017. Cuticle biosynthesis in tomato leaves is developmentally regulated by abscisic acid. Plant Physiol. 174, 1384–1398. https://doi.org/10.1104/pp.17.00387.

Marzi, D., Brunetti, P., Saini, S.S., Yadav, G., Puglia, G.D., Dello Ioio, R., 2024. Role of transcriptional regulation in auxin-mediated response to abiotic stresses. Front. Genet. 15, 1394091. https://doi.org/10.3389/fgene.2024.1394091.

Mattei, A.L., Bailly, N., Meissner, A., 2022. DNA methylation: a historical perspective. Trends Genet. 38, 676–707. https://doi.org/10.1016/j.tig.2022.03.010.

Menezes-Silva, P.E., Sanglard, L.M.V.P., Ávila, R.T., Morais, L.E., Martins, S.C.V., Nobres, P., Patreze, C.M., Ferreira, M.A., Araújo, W.L., Fernie, A.R., DaMatta, F.M., 2017. Photosynthetic and metabolic acclimation to repeated drought events play key roles in drought tolerance in coffee. J. Exp. Bot. 68, 4309–4322. https://doi.org/10.1093/jxb/erx211.

Metz, J., Lampei, C., Bäumler, L., Bocherens, H., Dittberner, H., Henneberg, L., de Meaux, J., Tielbörger, K., 2020. Rapid adaptive evolution to drought in a subset of plant traits in a large-scale climate change experiment. Ecol. Lett. 23, 1643–1653. https://doi.org/10.1111/ele.13596.

Millar, A.A., Lohe, A., Wong, G., 2019. Biology and function of miR159 in plants. Plants 8, 255. https://doi.org/10.3390/plants8080255.

Miura, K., Tada, Y., 2014. Regulation of water, salinity, and cold stress responses by salicylic acid. Front. Plant Sci. 5. https://doi.org/10.3389/fpls.2014.00004.

Morran, S., Eini, O., Pyvovarenko, T., Parent, B., Singh, R., Ismagul, A., Eliby, S., Shirley, N., Langridge, P., Lopato, S., 2011. Improvement of stress tolerance of wheat and barley by modulation of expression of DREB/CBF factors. Plant Biotechnol. J. 9, 230–249. https://doi.org/10.1111/j.1467-7652.2010.00547.x.

Mughal, N., Shoaib, N., Chen, J., Li, Y., He, Yuhong, Fu, M., Li, X., He, Yuanyuan, Guo, J., Deng, J., Yang, W., Liu, J., 2024. Adaptive roles of cytokinins in enhancing plant resilience and yield against environmental stressors. Chemosphere 364, 143189. https://doi.org/10.1016/j.chemosphere.2024.143189.

Mukarram, M., Choudhary, S., Kurjak, D., Petek, A., Khan, M.M.A., 2021. Drought: sensing, signalling, effects and tolerance in higher plants. Physiol. Plant. 172, 1291–1300. https://doi.org/10.1111/ppl.13423.

Müller, L.M., Bahn, M., 2022. Drought legacies and ecosystem responses to subsequent drought. Glob. Chang. Biol. 28, 5086–5103. https://doi.org/10.1111/gcb.16270.

Munné-Bosch, S., Alegre, L., 2004. Die and let live: leaf senescence contributes to plant survival under drought stress. Funct. Plant Biol. 31, 203. https://doi.org/10.1071/FP03236.

Nazir, F., Peter, P., Gupta, R., Kumari, S., Nawaz, K., Khan, M.I.R., 2024. Plant hormone ethylene: a leading edge in conferring drought stress tolerance. Physiol. Plant. 176, e14151. https://doi.org/10.1111/ppl.14151.

Nguyen, N.H., Vu, N.T., Cheong, J.-J., 2022. Transcriptional stress memory and transgenerational inheritance of drought tolerance in plants. IJMS 23, 12918. https://doi.org/10.3390/ijms232112918.

Ost, C., Cao, H.X., Nguyen, T.L., Himmelbach, A., Mascher, M., Stein, N., Humbeck, K., 2023. Drought-stress-related reprogramming of gene expression in barley involves differential histone modifications at ABA-related genes. IJMS 24, 12065. https://doi.org/10.3390/ijms241512065.

Pant, B.D., Buhtz, A., Kehr, J., Scheible, W., 2008. MicroRNA399 is a long-distance signal for the regulation of plant phosphate homeostasis. Plant J. 53, 731–738. https://doi.org/10.1111/j.1365-313X.2007.03363.x.

Peerzada, Y.Y., Iqbal, M., 2021. Leaf senescence and ethylene signaling. In: Aftab, T., Hakeem, K.R. (Eds.), Plant Growth Regulators. Springer International Publishing, Cham, pp. 153–171. https://doi.org/10.1007/978-3-030-61153-8_7.

Pei, L.L., Zhang, L.L., Liu, X., Jiang, J., 2023. Role of microRNA miR171 in plant development. PeerJ 11, e15632. https://doi.org/10.7717/peerj.15632.

Pesacreta, T.C., Acharya, A., Hasenstein, K.H., 2021. Endogenous nutrients are concentrated in specific tissues in the Zea mays seedling. Protoplasma 258, 863–878. https://doi.org/10.1007/s00709-021-01606-4.

Petek-Petrik, A., Petrík, P., Lamarque, L.J., Cochard, H., Burlett, R., Delzon, S., 2023. Drought survival in conifer species is related to the time required to cross the stomatal safety margin. J. Exp. Bot. 74, 6847–6859. https://doi.org/10.1093/jxb/erad352.

Petek-Petrik, A., Petrík, P., Halmová, M., Plichta, R., Matoušková, M., Houšková, K., Chudomelová, M., Urban, J., Hedl, R., 2024. Comparison of morphological and physiological response to drought stress among temperate forest understory forbs and graminoids. Plant Biol. J. https://doi.org/10.1111/plb.13750 plb.13750.

Petrík, P., Petek, A., Konôpková, A., Bosela, M., Fleischer, P., Frýdl, J., Kurjak, D., 2020. Stomatal and leaf morphology response of European beech (Fagus sylvatica L.) provenances transferred to contrasting climatic conditions. Forests 11, 1359. https://doi.org/10.3390/f11121359.

Petrik, P., Petek-Petrik, A., Kurjak, D., Mukarram, M., Klein, T., Gömöry, D., Střelcová, K., Frýdl, J., Konôpková, A., 2022. Interannual adjustments in stomatal and leaf morphological traits of European beech (Fagus sylvatica L.) demonstrate its climate change acclimation potential. Plant Biol. J. 24, 1287–1296. https://doi.org/10.1111/plb.13401.

Petrík, P., Petek-Petrik, A., Mukarram, M., Schuldt, B., Lamarque, L.J., 2023. Leaf physiological and morphological constraints of water-use efficiency in C3 plants. AoB PLANTS 15. https://doi.org/10.1093/aobpla/plad047 plad047.

Petrík, P., Petek-Petrík, A., Lamarque, L.J., Link, R.M., Waite, P.-A., Ruehr, N.K., Schuldt, B., Maire, V., 2024. Linking stomatal size and density to water use efficiency and leaf carbon isotope ratio in juvenile and mature trees. Physiol. Plant. 176, e14619. https://doi.org/10.1111/ppl.14619.

Prasad, R., 2022. Cytokinin and its key role to enrich the plant nutrients and growth under adverse conditions-an update. Front. Genet. 13, 883924. https://doi.org/10.3389/fgene.2022.883924.

Prerostova, S., Dobrev, P.I., Gaudinova, A., Knirsch, V., Körber, N., Pieruschka, R., Fiorani, F., Brzobohatý, B., Černý, M., Spichal, L., Humplik, J., Vanek, T., Schurr, U., Vankova, R., 2018. Cytokinins: their impact on molecular and growth responses to drought stress and recovery in Arabidopsis. Front. Plant Sci. 9, 655. https://doi.org/10.3389/fpls.2018.00655.

Ramírez, D.A., Rolando, J.L., Yactayo, W., Monneveux, P., Mares, V., Quiroz, R., 2015. Improving potato drought tolerance through the induction of long-term water stress memory. Plant Sci. 238, 26–32. https://doi.org/10.1016/j.plantsci.2015.05.016.

Rao, X., Yang, S., Lü, S., Yang, P., 2024. DNA methylation dynamics in response to drought stress in crops. Plants 13, 1977. https://doi.org/10.3390/plants13141977.

Rathnasamy, S.A., Kambale, R., Elangovan, A., Mohanavel, W., Shanmugavel, P., Ramasamy, G., Alagarsamy, S., Marimuthu, R., Rajagopalan, V.R., Manickam, S., Ramanathan, V., Muthurajan, R., Vellingiri, G., 2023. Altering stomatal density for manipulating transpiration and photosynthetic traits in rice through CRISPR/Cas9 mutagenesis. CIMB 45, 3801–3814. https://doi.org/10.3390/cimb45050245.

Reyes, J.L., Chua, N., 2007. ABA induction of miR159 controls transcript levels of two MYB factors during Arabidopsis seed germination. Plant J. 49, 592–606. https://doi.org/10.1111/j.1365-313X.2006.02980.x.

Rudolf, J., Tomovicova, L., Panzarova, K., Fajkus, J., Hejatko, J., Skalak, J., 2024. Epigenetics and plant hormone dynamics: a functional and methodological perspective. J. Exp. Bot. 75, 5267–5294. https://doi.org/10.1093/jxb/erae054.

Rudy, E., Tanwar, U.K., Szlachtowska, Z., Grabsztunowicz, M., Arasimowicz-Jelonek, M., Sobieszczuk-Nowicka, E., 2024. Unveiling the role of epigenetics in leaf senescence: a comparative study to identify different epigenetic regulations of senescence types in barley leaves. BMC Plant Biol. 24, 863. https://doi.org/10.1186/s12870-024-05573-9.

Rui, M., Chen, R., Jing, Y., Wu, F., Chen, Z., Tissue, D., Jiang, H., Wang, Y., 2024. Guard cell and subsidiary cell sizes are key determinants for stomatal kinetics and drought adaptation in cereal crops. New Phytol. 242, 2479–2494. https://doi.org/10.1111/nph.19757.

Sadhukhan, A., Prasad, S.S., Mitra, J., Siddiqui, N., Sahoo, L., Kobayashi, Y., Koyama, H., 2022. How do plants remember drought? Planta 256, 7. https://doi.org/10.1007/s00425-022-03924-0.

Safari, M., Mousavi-Fard, S., Rezaei Nejad, A., Sorkheh, K., Sofo, A., 2022. Exogenous salicylic acid positively affects morpho-physiological and molecular responses of impatiens walleriana plants grown under drought stress. Int. J. Environ. Sci. Technol. 19, 969–984. https://doi.org/10.1007/s13762-020-03092-2.

Sah, S.K., Reddy, K.R., Li, J., 2016. Abscisic acid and abiotic stress tolerance in crop plants. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00571.

Saibo, N.J.M., Vriezen, W.H., Beemster, G.T.S., Van Der Straeten, D., 2003. Growth and stomata development of Arabidopsis hypocotyls are controlled by gibberellins and modulated by ethylene and auxins. Plant J. 33, 989–1000. https://doi.org/10.1046/j.1365-313X.2003.01684.x.

Sajeevan, R.S., Parvathi, M.S., Nataraja, K.N., 2017. Leaf wax trait in crops for drought and biotic stress tolerance: regulators of epicuticular wax synthesis and role of small RNAs. Indian J. Plant Physiol. 22, 434–447. https://doi.org/10.1007/s40502-017-0333-9.

Santos, A.P., Serra, T., Figueiredo, D.D., Barros, P., Lourenço, T., Chander, S., Oliveira, M.M., Saibo, N.J.M., 2011. Transcription regulation of abiotic stress responses in rice: a combined action of transcription factors and epigenetic mechanisms. OMICS 15, 839–857. https://doi.org/10.1089/omi.2011.0095.

Schuster, A.-C., Burghardt, M., Riederer, M., 2017. The ecophysiology of leaf cuticular transpiration: are cuticular water permeabilities adapted to ecological conditions? J. Exp. Bot. 68, 5271–5279. https://doi.org/10.1093/jxb/erx321.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Chang. 7, 395–402. https://doi.org/10.1038/nclimate3303.

Seth, R., Iorizzo, M., Maritim, T.K., Kumar Sharma, R., 2024. Editorial: epigenetic and gene regulation underlying crosstalk in plant development and stress responses. Front. Genet. 15, 1427102. https://doi.org/10.3389/fgene.2024.1427102.

Shaffique, S., Hussain, S., Kang, S.-M., Imran, M., Injamum-Ul-Hoque, Md., Khan, M.A., Lee, I.-J., 2023. Phytohormonal modulation of the drought stress in soybean: outlook, research progress, and cross-talk. Front. Plant Sci. 14, 1237295. https://doi.org/10.3389/fpls.2023.1237295.

Shao, R., Wang, K., Shangguan, Z., 2010. Cytokinin-induced photosynthetic adaptability of Zea mays L. to drought stress associated with nitric oxide signal: probed by ESR spectroscopy and fast OJIP fluorescence rise. J. Plant Physiol. 167, 472–479. https://doi.org/10.1016/j.jplph.2009.10.020.

Sharma, M., Kumar, P., Verma, V., Sharma, R., Bhargava, B., Irfan, M., 2022. Understanding plant stress memory response for abiotic stress resilience: molecular insights and prospects. Plant Physiol. Biochem. 179, 10–24. https://doi.org/10.1016/j.plaphy.2022.03.004.

Shriti, S., Bhar, A., Roy, A., 2024. Unveiling the role of epigenetic mechanisms and redox signaling in alleviating multiple abiotic stress in plants. Front. Plant Sci. 15, 1456414. https://doi.org/10.3389/fpls.2024.1456414.

Singroha, G., Sharma, P., Sunkur, R., 2021. Current status of microRNA -mediated regulation of drought stress responses in cereals. Physiol. Plant. 172, 1808–1821. https://doi.org/10.1111/ppl.13451.

Sintaha, M., Man, C.-K., Yung, W.-S., Duan, S., Li, M.-W., Lam, H.-M., 2022. Drought stress priming improved the drought tolerance of soybean. Plants 11, 2954. https://doi.org/10.3390/plants11212954.

Sircaik, S., Dhiman, K., Gambhir, G., Kumar, P., Srivastava, D.K., 2021. Transgenic implications for biotic and abiotic stress tolerance in agricultural crops. In: Kumar Srivastava, D., Kumar Thakur, A., Kumar, P. (Eds.), Agricultural Biotechnology: Latest Research and Trends. Springer Nature Singapore, Singapore, pp. 185–221. https://doi.org/10.1007/978-981-16-2339-4_9.

Slot, M., Nardwattanawong, T., Hernández, G.G., Bueno, A., Riederer, M., Winter, K., 2021. Large differences in leaf cuticle conductance and its temperature response among 24 tropical tree species from across a rainfall gradient. New Phytol. 232, 1618–1631. https://doi.org/10.1111/nph.17626.

Smith, W.K., Geller, G.N., 1980. Leaf and environmental parameters influencing transpiration: theory and field measurements. Oecologia 46, 308–313. https://doi.org/10.1007/BF00346257.

Spieß, N., Oufir, M., Matušíková, I., Stierschneider, M., Kopecky, D., Homolka, A., Burg, K., Fluch, S., Hausman, J.-F., Wilhelm, E., 2012. Ecophysiological and transcriptomic responses of oak (Quercus robur) to long-term drought exposure and rewatering. Environ. Exp. Bot. 77, 117–126. https://doi.org/10.1016/j.envexpbot.2011.11.010.

Stojnić, S., Orlović, S., Miljković, D., Galić, Z., Kebert, M., von Wuehlisch, G., 2015. Provenance plasticity of European beech leaf traits under differing environmental conditions at two Serbian common garden sites. Eur. J. Forest Res. 134, 1109–1125. https://doi.org/10.1007/s10342-015-0914-y.

Střelcová, K., Kurjak, D., Leštianska, A., Kovalčíková, D., Ditmarová, Ľ., Škvarenina, J., Ahmed, Y.A.-R., 2013. Differences in transpiration of Norway spruce drought stressed trees and trees well supplied with water. Biologia 68, 1118–1122. https://doi.org/10.2478/s11756-013-0257-4.

Su, S., Tang, P., Zuo, R., Chen, H., Zhao, T., Yang, S., Yang, J., 2023. Exogenous Jasmonic acid alleviates blast resistance reduction caused by LOX3 knockout in rice. Biomolecules 13, 1197.

Sun, R.-Z., Liu, J., Wang, Y.-Y., Deng, X., 2021. DNA methylation-mediated modulation of rapid desiccation tolerance acquisition and dehydration stress memory in the resurrection plant Boea hygrometrica. PLoS Genet. 17, e1009549. https://doi.org/10.1371/journal.pgen.1009549.

Sussmilch, F., McAdam, S., 2017. Surviving a dry future: abscisic acid (ABA)-mediated plant mechanisms for conserving water under low humidity. Plants 6, 54. https://doi.org/10.3390/plants6040054.

Tan, S., Sha, Y., Sun, L., Li, Z., 2023. Abiotic stress-induced leaf senescence: regulatory mechanisms and application. IJMS 24, 11996. https://doi.org/10.3390/ijms241511996.

Teale, W.D., Paponov, I.A., Palme, K., 2006. Auxin in action: signalling, transport and the control of plant growth and development. Nat. Rev. Mol. Cell Biol. 7, 847–859. https://doi.org/10.1038/nrm2020.

Tian, Z., Li, K., Sun, Y., Chen, B., Pan, Z., Wang, Z., Pang, B., He, S., Miao, Y., Du, X., 2024. Physiological and transcriptional analyses reveal formation of memory under recurring drought stresses in seedlings of cotton (Gossypium hirsutum). Plant Sci. 338, 111920. https://doi.org/10.1016/j.plantsci.2023.111920.

Torii, K.U., 2021. Stomatal development in the context of epidermal tissues. Ann. Bot. 128, 137–148. https://doi.org/10.1093/aob/mcab052.

Torun, H., Cetin, B., Stojnic, S., Petrík, P., 2024. Salicylic acid alleviates the effects of cadmium and drought stress by regulating water status, ions, and antioxidant defense in Pterocarya fraxinifolia. Front. Plant Sci. 14, 1339201. https://doi.org/10.3389/fpls.2023.1339201.

Touche, J., Calvaruso, C., De Donato, P., Turpault, Mp, 2022. Five successive years of rainfall exclusion induce nutritional stress in a mature beech stand. For. Ecol. Manag. 507, 119987. https://doi.org/10.1016/j.foreco.2021.119987.

Touche, J., Calvaruso, C., De Donato, P., Turpault, M.-P., 2024. Drought events influence nutrient canopy exchanges and green leaf partitioning during senescence in a deciduous forest. Forest Ecosyst. 11, 100173. https://doi.org/10.1016/j.fecs.2024.100173.

Ullah, A., Tariq, A., Zeng, F., Asghar, M.A., Sardans, J., Graciano, C., Ali, I., Peñuelas, J., 2024. Drought priming improves tolerance of Alhagi sparsifolia to subsequent drought: a coordinated interplay of phytohormones, osmolytes, and antioxidant potential. Plant Stress 12, 100469. https://doi.org/10.1016/j.stress.2024.100469.

VanderWeide, J., Yan, Y., Zandberg, W.F., Castellarin, S.D., 2022. Modulation of grape cuticular wax composition following multiple heatwaves influences grape transpiration. Environ. Exp. Bot. 202, 105036. https://doi.org/10.1016/j.envexpbot.2022.105036.

Vankova, R., 2014. Cytokinin regulation of plant growth and stress responses. In: Tran, L.-S.P., Pal, S. (Eds.), Phytohormones: A Window to Metabolism, Signaling and Biotechnological Applications. Springer, New York, New York, NY, pp. 55–79. https://doi.org/10.1007/978-1-4939-0491-4_3.

Verma, S., Negi, N.P., Pareek, S., Mudgal, G., Kumar, D., 2022. Auxin response factors in plant adaptation to drought and salinity stress. Physiol. Plant. 174, e13714. https://doi.org/10.1111/ppl.13714.

Vicente-Serrano, S.M., Peña-Angulo, D., Beguería, S., Domínguez-Castro, F., Tomás-Burguera, M., Noguera, I., Gimeno-Sotelo, L., El Kenawy, A., 2022. Global drought trends and future projections. Phil. Trans. R. Soc. A 380, 20210285. https://doi.org/10.1098/rsta.2021.0285.

Virlouvet, L., Fromm, M., 2015. Physiological and transcriptional memory in guard cells during repetitive dehydration stress. New Phytol. 205, 596–607. https://doi.org/10.1111/nph.13080.

Virlouvet, L., Avenson, T.J., Du, Q., Zhang, C., Liu, N., Fromm, M., Avramova, Z., Russo, S.E., 2018. Dehydration stress memory: gene networks linked to physiological responses during repeated stresses of Zea mays. Front. Plant Sci. 9, 1058. https://doi.org/10.3389/fpls.2018.01058.

Vuković, R., Čamagajevac, I.Š., Vuković, A., Šunić, K., Begović, L., Mlinarić, S., Sekulić, R., Sabo, N., Španić, V., 2022. Physiological, biochemical and molecular response of different Winter wheat varieties under drought stress at germination and seedling growth stage. Antioxidants 11, 693. https://doi.org/10.3390/antiox11040693.

Vuksanović, V., Kovačević, B., Kebert, M., Pavlović, L., Kesić, L., Čukanović, J., Orlović, S., 2023. In vitro selection of drought-tolerant white poplar clones based on antioxidant activities and osmoprotectant content. Front. Plant Sci. 14, 1280794. https://doi.org/10.3389/fpls.2023.1280794.

Wahab, A., Batool, F., Muhammad, M., Zaman, W., Mikhlef, R.M., Naeem, M., 2023. Current knowledge, research progress, and future prospects of phyto-synthesized nanoparticles interactions with food crops under induced drought stress. Sustainability 15, 14792. https://doi.org/10.3390/su152014792.

Wang, W.-S., Pan, Y.-J., Zhao, X.-Q., Dwivedi, D., Zhu, L.-H., Ali, J., Fu, B.-Y., Li, Z.-K., 2011. Drought-induced site-specific DNA methylation and its association with drought tolerance in rice (Oryza sativa L.). J. Exp. Bot. 62, 1951–1960. https://doi.org/10.1093/jxb/erq391.

Wang, W., Qin, Q., Sun, F., Wang, Y., Xu, D., Li, Z., Fu, B., 2016. Genome-wide differences in DNA methylation changes in two contrasting rice genotypes in response to drought conditions. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.01675.

Wang, X., Mao, Z., Zhang, J., Hemat, M., Huang, M., Cai, J., Zhou, Q., Dai, T., Jiang, D., 2019. Osmolyte accumulation plays important roles in the drought priming induced tolerance to post-anthesis drought stress in winter wheat (Triticum aestivum L.). Environ. Exp. Bot. 166, 103804. https://doi.org/10.1016/j.envexpbot.2019.103804.

Wang, X., Li, Q., Xie, J., Huang, M., Cai, J., Zhou, Q., Dai, T., Jiang, D., 2021. Abscisic acid and jasmonic acid are involved in drought priming-induced tolerance to drought in wheat. Crop J. 9, 120–132. https://doi.org/10.1016/j.cj.2020.06.002.

Wang, J.-L., Di, D.-W., Luo, P., Zhang, L., Li, X.-F., Guo, G.-Q., Wu, L., 2022a. The roles of epigenetic modifications in the regulation of auxin biosynthesis. Front. Plant Sci. 13, 959053. https://doi.org/10.3389/fpls.2022.959053.

Wang, N., Yu, Y., Zhang, D., Zhang, Z., Wang, Z., Xun, H., Li, G., Liu, B., Zhang, J., 2022b. Modification of gene expression, DNA methylation and small RNAs expression in rice plants under in vitro culture. Agronomy 12, 1675. https://doi.org/10.3390/agronomy12071675.

Wang, S., Hoch, G., Grun, G., Kahmen, A., 2024a. Water loss after stomatal closure: quantifying leaf minimum conductance and minimal water use in nine temperate European tree species during a severe drought. Tree Physiol. 44, tpae027. https://doi.org/10.1093/treephys/tpae027.

Wang, F., Li, C.-H., Liu, Y., He, L.-F., Li, P., Guo, J.-X., Zhang, N., Zhao, B., Guo, Y.-D., 2024b. Plant responses to abiotic stress regulated by histone acetylation. Front. Plant Sci. 15, 1404977. https://doi.org/10.3389/fpls.2024.1404977.

Weithmann, G., Schuldt, B., Link, R.M., Heil, D., Hoeber, S., John, H., Müller-Haubold, H., Schüller, L.-M., Schumann, K., Leuschner, C., 2022. Leaf trait modification in European beech trees in response to climatic and edaphic drought. Plant Biol. J. 24, 1272–1286. https://doi.org/10.1111/plb.13366.

Wojtyla, Ł., Paluch-Lubawa, E., Sobieszczuk-Nowicka, E., Garnczarska, M., 2020. Drought stress memory and subsequent drought stress tolerance in plants. In: Priming-Mediated Stress and Cross-Stress Tolerance in Crop Plants. Elsevier, pp. 115–131. https://doi.org/10.1016/B978-0-12-817892-8.00007-6.

Xu, Z., Zhou, G., Shimizu, H., 2010. Plant responses to drought and rewatering. Plant Signal. Behav. 5, 649–654. https://doi.org/10.4161/psb.5.6.11398.

Yadav, A., Kumar, S., Verma, R., Narayan, S., Gupta, U., Lata, C., Rai, S.P., Sanyal, I., 2024. Overexpression of miR166 in response to root rhizobacteria enhances drought adaptive efficacy by targeting HD-ZIP III family genes in chickpea. J. Soil Sci. Plant Nutr. 24, 6024–6039.

Yamamoto, H., Shikanai, T., 2019. PGR5-dependent cyclic electron flow protects photosystem I under fluctuating light at donor and acceptor sides. Plant Physiol. 179, 588–600. https://doi.org/10.1104/pp.18.01343.

Yang, M., He, J., Sun, Z., Li, Q., Cai, J., Zhou, Q., Wollenweber, B., Jiang, D., Wang, X., 2023. Drought priming mechanisms in wheat elucidated by in-situ determination of dynamic stomatal behavior. Front. Plant Sci. 14, 1138494. https://doi.org/10.3389/fpls.2023.1138494.

Yang, Y., Xu, L., Hao, C., Wan, M., Tao, Y., Zhuang, Y., Su, Y., Li, L., 2024. The microRNA408–plantacyanin module balances plant growth and drought resistance by regulating reactive oxygen species homeostasis in guard cells. Plant Cell 36, 4338–4355. https://doi.org/10.1093/plcell/koae144.

Yao, G., Nie, Z., Turner, N.C., Li, F., Gao, T., Fang, X., Scoffoni, C., 2021. Combined high leaf hydraulic safety and efficiency provides drought tolerance in Caragana species adapted to low mean annual precipitation. New Phytol. 229, 230–244. https://doi.org/10.1111/nph.16845.

Yu, Y., Qi, Y., Xu, J., Dai, X., Chen, J., Dong, C., Xiang, F., 2021. Arabidopsis WRKY71 regulates ethylene-mediated leaf senescence by directly activating EIN2, ORE1 and ACS2 genes. Plant J. 107, 1819–1836. https://doi.org/10.1111/tpj.15433.

Yuan, W., Suo, J., Shi, B., Zhou, C., Bai, B., Bian, H., Zhu, M., Han, N., 2019. The barley miR393 has multiple roles in regulation of seedling growth, stomatal density, and drought stress tolerance. Plant Physiol. Biochem. 142, 303–311. https://doi.org/10.1016/j.plaphy.2019.07.021.

Zavadilová, I., Szatniewska, J., Petrík, P., Mauer, O., Pokorný, R., Stojanović, M., 2023. Sap flow and growth response of Norway spruce under long-term partial rainfall exclusion at low altitude. Front. Plant Sci. 14, 1089706. https://doi.org/10.3389/fpls.2023.1089706.

Zhang, Yaxi, Xu, S., Ding, P., Wang, D., Cheng, Y.T., He, J., Gao, M., Xu, F., Li, Y., Zhu, Z., Li, X., Zhang, Yuelin, 2010. Control of salicylic acid synthesis and systemic acquired resistance by two members of a plant-specific family of transcription factors. Proc. Natl. Acad. Sci. USA 107, 18220–18225. https://doi.org/10.1073/pnas.1005225107.

Zhang, C., Zhang, W., Ren, G., Li, D., Cahoon, R.E., Chen, M., Zhou, Y., Yu, B., Cahoon, E. B., 2015. Chlorophyll synthase under epigenetic surveillance is critical for vitamin E synthesis, and altered expression affects tocopherol levels in Arabidopsis. Plant Physiol. 168, 1503–1511. https://doi.org/10.1104/pp.15.00594.

Zhang, J.-P., Yu, Y., Feng, Y.-Z., Zhou, Y.-F., Zhang, F., Yang, Y.-W., Lei, M.-Q., Zhang, Y.-C., Chen, Y.-Q., 2017. MiR408 regulates grain yield and photosynthesis via a phytocyanin protein. Plant Physiol. 175, 1175–1185. https://doi.org/10.1104/pp.17.01169.

Zhang, H., Lang, Z., Zhu, J.-K., 2018. Dynamics and function of DNA methylation in plants. Nat. Rev. Mol. Cell Biol. 19, 489–506. https://doi.org/10.1038/s41580-018-0016-z.

Zhang, H., Zhang, X., Xiao, J., 2023. Epigenetic regulation of nitrogen signaling and adaptation in plants. Plants 12, 2725. https://doi.org/10.3390/plants12142725.

Zhong, S., Gao, Y., Lu, J., Ding, C., Su, X., Zhang, B., 2021. Production of an epigenetic mutant population of Populus nigra: DNA methylation and phenotype analyses. J. Plant Biochem. Biotechnol. 30, 354–363. https://doi.org/10.1007/s13562-020-00600-w.

Zhou, S.-X., Medlyn, B.E., Prentice, I.C., 2016. Long-term water stress leads to acclimation of drought sensitivity of photosynthetic capacity in xeric but not riparian Eucalyptus species. Ann. Bot. 117, 133–144. https://doi.org/10.1093/aob/mcv161.

Zhu, J., Park, J.-H., Lee, S., Lee, J.H., Hwang, D., Kwak, J.M., Kim, Y.J., 2020. Regulation of stomatal development by stomatal lineage miRNAs. Proc. Natl. Acad. Sci. USA 117, 6237–6245. https://doi.org/10.1073/pnas.1919722117.

Zi, N., Ren, W., Guo, H., Yuan, F., Liu, Y., Fry, E., 2024. DNA methylation participates in drought stress memory and response to drought in Medicago ruthenica. Genes 15, 1286. https://doi.org/10.3390/genes15101286.

Ziegler, C., Cochard, H., Stahl, C., Foltzer, L., Gérard, B., Goret, J.-Y., Heuret, P., Levionnois, S., Maillard, P., Bonal, D., Coste, S., 2024. Residual water losses mediate the trade-off between growth and drought survival across saplings of 12 tropical rainforest tree species with contrasting hydraulic strategies. J. Exp. Bot. https://doi.org/10.1093/jxb/erae159 erae159.