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Epigenetic Regulation of Drought Adaptation in Wild Grass Species

Jiong Fu
Hainan Provincial Key Laboratory for Crop Molecular Breeding, Sanya, 572025, Hainan, China
Corresponding author: Jiong.fu@hitar.org

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Abstract This study synthesizes current knowledge on the epigenetic regulation of drought adaptation in wild grass species, with emphasis on DNA methylation, RNA-directed DNA methylation, histone modifications, chromatin accessibility, non-coding RNAs, and stress memory. We argue that epigenetic regulation should be treated not as an isolated molecular layer, but as part of a molecular ecology framework in which repeat-rich grass genomes, local climatic heterogeneity, transposable element control, developmental state, and population history jointly shape drought-responsive phenotypes. Mechanistically, the strongest conserved themes are: maintenance and remodeling of CG, CHG, and CHH methylation by MET1, CMT/SUVH, and RdDM pathways; dynamic coupling between DNA methylation and heterochromatin marks such as H3K9 methylation; the involvement of active chromatin states and accessibility changes in rapid stress-responsive transcription; and the potential for within-generation and, in some cases, transgenerational stress memory. From a molecular ecology perspective, we propose that the next generation of studies in wild grasses should combine environmental gradient sampling, common gardens, reciprocal transplants, and multi-omics assays such as whole-genome bisulfite sequencing, ATAC-seq, ChIP-seq or CUT&Tag, RNA-seq, and small RNA-seq. We then develop a detailed case analysis for Setaria viridis as an ideal wild-grass model for drought epigenomics and outline a publication-ready workflow integrating WGBS, ATAC-seq, histone profiling, and transcriptomics. Finally, we discuss how epigenetic knowledge can inform conservation genomics, restoration, epibreeding, and targeted epigenome editing, while also emphasizing key limitations, including causality, tissue heterogeneity, epigenetic resetting, and the still-limited number of direct field-based studies in natural wild-grass populations. Together, the evidence supports a transition from correlative stress epigenetics to predictive eco-epigenomics for dryland conservation and climate-resilient grass improvement.

Keywords Drought adaptation; Wild grasses; Eco-epigenomics; DNA methylation; RNA-directed DNA methylation; Chromatin accessibility; Stress memory; Setaria viridis; Conservation genomics; Epibreeding

1 Introduction

Grasslands and rangelands are under escalating pressure from climate change, drought, land degradation, and woody encroachment. Recent global assessments have emphasized that large fractions of the world's rangelands are already degraded, and climate-driven drought is increasingly interacting with land-use change to alter ecosystem structure, productivity, hydrology, and biodiversity. Because grasses dominate many open biomes and frequently determine both forage production and belowground carbon dynamics, understanding the biological basis of drought resilience in wild grass species is a conservation problem as much as a plant biology problem (Fortes and Gallusci, 2017). Furthermore, the increasing frequency and intensity of extreme drought events are expected to impose strong selective pressures on natural plant populations, making the identification of adaptive mechanisms a priority for both ecosystem conservation and climate-resilient agriculture (Auge et al., 2023).

At the same time, epigenetics has become central to plant environmental biology because it offers a mechanistic framework through which plants translate external stress signals into altered patterns of gene regulation without changing their underlying DNA sequence. Reviews published over the past decade have converged on the view that plant environmental memory can involve multiple interconnected mechanisms, including DNA methylation, histone modifications, chromatin remodeling, RNA-mediated regulation, and persistent stress priming across developmental stages or even generations (Law and Jacobsen, 2010; Du et al., 2015; Crisp et al., 2016; Lämke and Bäurle, 2017; Auge et al., 2023). In plants, these mechanisms are particularly important because sessile organisms cannot escape unfavorable environmental conditions and must continuously adjust their physiology, growth, and reproductive strategies in response to environmental fluctuations. Epigenetic regulation therefore provides a potentially rapid and reversible mechanism for enhancing phenotypic plasticity and environmental responsiveness (Gutzat and Mittelsten Scheid, 2012; Springer and Schmitz, 2017).

Wild grasses are especially valuable systems for investigating drought-associated epigenetic adaptation for several reasons. First, many species occupy extensive environmental gradients characterized by substantial variation in precipitation, temperature, and soil moisture availability, resulting in pronounced local adaptation and ecological differentiation. Second, grass genomes are frequently enriched with transposable elements and repetitive DNA, making DNA methylation-mediated genome stabilization and transposon silencing particularly important components of stress adaptation (Sigman and Slotkin, 2016; Wicker et al., 2018). Because environmental stress can alter the activity of transposable elements and the chromatin landscape surrounding them, epigenetic regulation may play a disproportionately important role in grass genome responses to drought (Cavrak et al., 2014; Ito et al., 2011). Third, several wild and semi-wild grasses represent the evolutionary relatives of globally important cereal crops, providing opportunities to translate discoveries from natural systems into crop improvement strategies aimed at enhancing drought tolerance (Springer and Schmitz, 2017). Finally, a limited number of grass species, particularly Setaria viridis, offer the experimental tractability necessary to integrate ecological sampling, functional genomics, and epigenetic analyses within a single framework. As a rapidly cycling, transformable C4 grass with extensive genomic resources, S. viridis has emerged as a powerful model for elucidating the molecular and epigenetic mechanisms underlying drought adaptation in natural grass populations (Brutnell et al., 2010; Jiang et al., 2013; Sebastian et al., 2014).

This study is therefore organized around a simple proposition: drought adaptation in wild grasses emerges from the interaction of ecological selection, population history, genome architecture, and multi-layered epigenetic regulation. The manuscript emphasizes recent literature, uses a molecular ecology lens throughout, and closes with a detailed Setaria viridis case analysis and a forward-looking agenda for conservation, adaptive restoration, and epibreeding.

2 Epigenetic Architecture and Molecular Ecology Framework

2.1 DNA methylation and transposable element regulation in drought adaptation

DNA methylation represents the most extensively studied epigenetic mechanism involved in plant responses to drought stress. In plants, cytosine methylation occurs in three sequence contexts, namely CG, CHG, and CHH, which are maintained through distinct but interconnected pathways. CG methylation is primarily maintained by METHYLTRANSFERASE 1 (MET1), whereas CHG methylation is regulated through the coordinated activities of CHROMOMETHYLASE 3 (CMT3) and SUVH-mediated feedback loops. CHH methylation is largely established and maintained through CMT2 and the RNA-directed DNA methylation (RdDM) pathway, while active DNA demethylation is mediated by DNA glycosylase-dependent mechanisms (Law and Jacobsen, 2010; Du et al., 2015; Bewick et al., 2017; Parrilla-Doblas et al., 2019).

In wild grass species, DNA methylation serves functions beyond simple promoter regulation. It plays a crucial role in silencing repetitive sequences and transposable elements (TEs), thereby maintaining genome stability under environmental stress conditions (Zemach et al., 2013; Sigman and Slotkin, 2016). Because many grass genomes contain exceptionally high proportions of transposable elements, epigenetic regulation of TEs becomes particularly important during drought adaptation. For example, transposable elements account for more than 80% of the wheat genome and substantially influence genome evolution and gene regulation (Wicker et al., 2018). Environmental stresses may induce TE activation or alter chromatin states surrounding TE-adjacent genes, leading to changes in gene expression patterns (Cavrak et al., 2014; Ito et al., 2011). Consequently, drought adaptation in grasses is closely associated with the interaction between epigenetic regulation and genome architecture, highlighting the importance of methylation-mediated control of repetitive genomic regions.

2.2 Histone modifications and chromatin state remodeling under drought stress

Histone modifications constitute a second major layer of epigenetic regulation involved in plant drought responses. Various histone marks influence chromatin structure and accessibility, thereby affecting the transcriptional activity of stress-responsive genes. Among these modifications, H3K9 methylation is commonly associated with heterochromatin formation and transcriptional repression, whereas H3K4 trimethylation (H3K4me3) is generally linked to active gene expression. In contrast, H3K27 trimethylation (H3K27me3) functions as a repressive mark involved in developmental regulation and gene silencing (Du et al., 2015; Zhao et al., 2019).

Under drought conditions, dynamic changes in histone modifications contribute to the regulation of genes involved in abscisic acid (ABA) signaling, osmotic adjustment, antioxidant defense, and developmental transitions. Importantly, histone modifications do not function independently but interact extensively with DNA methylation pathways. The reciprocal reinforcement between DNA methylation and H3K9 methylation enables coordinated chromatin remodeling at stress-responsive loci (Du et al., 2015; Enke et al., 2011). Therefore, drought adaptation is increasingly viewed as the outcome of integrated epigenetic reprogramming rather than the action of individual epigenetic marks. Recent evidence further suggests that chromatin remodeling complexes contribute significantly to the maintenance and reconfiguration of epigenetic states during environmental stress responses (Yang et al., 2018).

2.3 Chromatin accessibility and non-coding RNA-mediated regulation

Recent advances in high-throughput sequencing technologies have facilitated comprehensive investigations of chromatin dynamics during plant stress responses. Techniques such as ATAC-seq allow the identification of open chromatin regions, whereas ChIP-seq and CUT&Tag enable genome-wide profiling of histone modifications. These approaches provide valuable insights into the regulatory landscapes that govern gene expression under drought stress.

Chromatin accessibility is particularly relevant because it reflects the readiness of genes to respond to environmental stimuli. While transcriptomic analyses reveal changes in gene expression, chromatin accessibility and histone modification profiles offer information about regulatory potential, transcriptional preparedness, and stress memory (Lämke and Bäurle, 2017; Zhao et al., 2019). Consequently, integrating chromatin-level information with transcriptional data is essential for understanding drought-responsive regulatory networks.

In addition to chromatin remodeling, non-coding RNAs play pivotal roles in drought adaptation. Small RNAs, including siRNAs and miRNAs, participate in gene regulation through the RdDM pathway, guiding sequence-specific DNA methylation and transcriptional silencing (Matzke and Mosher, 2014; Erdmann and Lafontaine Picard, 2020). This pathway contributes not only to transposable element repression and genome stability but also to responses to drought, heat, salinity, nutrient deficiency, and other environmental stresses (Popova et al., 2013; Tricker et al., 2012; Xu et al., 2015). Furthermore, studies have demonstrated that mobile small RNAs can regulate genome-wide methylation patterns and contribute to environmental adaptation (Tamiru et al., 2018). For wild grasses, small RNA populations may therefore represent critical regulators of drought adaptation, providing regulatory information that cannot be detected through conventional protein-coding transcriptome analyses (Zhao and Chen, 2014).

2.4 Stress memory and the molecular ecology framework of drought adaptation

Stress memory has emerged as an important concept in plant environmental adaptation. Plants exposed to a previous drought event often exhibit enhanced responses during subsequent stress episodes, a phenomenon known as drought stress memory. This adaptive response may involve persistent DNA methylation patterns, stable histone modifications, or prolonged chromatin accessibility changes that facilitate faster reactivation of stress-responsive genes (Crisp et al., 2016; Lämke and Bäurle, 2017; Auge et al., 2023).

Although several studies have reported transgenerational inheritance of stress-induced epigenetic states, the stability and ecological significance of such inheritance remain subjects of ongoing debate (Hauser et al., 2011; Blevins et al., 2014; Gutzat and Mittelsten Scheid, 2012). Therefore, drought memory in wild grasses should be considered as a continuum encompassing immediate stress responses, recovery processes, repeated-stress priming, and potential progeny effects rather than as a single phenomenon.

From a molecular ecology perspective, understanding drought adaptation requires moving beyond experiments involving individual genotypes under controlled conditions. Instead, ecologically meaningful investigations should integrate natural population sampling, environmental gradient analyses, common garden experiments, and repeated drought treatments with multi-omics profiling. Such approaches enable researchers to distinguish environmentally induced epigenetic variation from genetically determined differences and to evaluate how epigenetic mechanisms contribute to plant performance and fitness under drought conditions (Fortes and Gallusci, 2017; Springer and Schmitz, 2017). Population epigenomics, methylation-expression association studies, methylQTL analyses, and genotype-by-environment interaction models collectively provide powerful tools for linking epigenetic variation to ecological adaptation and evolutionary processes in wild grass species.

3 Case Analysis in Setaria viridis

3.1 Ecological significance and model value of setaria viridis

Setaria viridis has emerged as one of the most promising model species for investigating epigenetic mechanisms underlying drought adaptation in wild grasses. As a wild C4 grass closely related to several economically important cereal crops, including foxtail millet and other drought-tolerant grasses, S. viridis occupies a unique position at the intersection of ecological adaptation, crop evolution, and molecular genetics. Its short life cycle, relatively small genome, ease of transformation, and well-established crossing protocols make it particularly suitable for integrative molecular ecology studies (Brutnell et al., 2010; Jiang et al., 2013; Sebastian et al., 2014).

Unlike many cultivated crop species that have undergone extensive artificial selection, S. viridis populations retain substantial natural genetic and ecological variation. This diversity provides an excellent opportunity to investigate how wild grass populations adapt to contrasting environmental conditions and whether epigenetic mechanisms contribute to drought resilience. Consequently, S. viridis represents an ideal system for examining the relative contributions of phenotypic plasticity, genetic variation, and epigenetic regulation in shaping adaptive responses to water limitation.

3.2 Experimental framework for investigating drought-induced epigenetic variation

A robust molecular ecology framework for studying drought adaptation in S. viridis should incorporate both ecological sampling and multi-omics analyses. Natural accessions collected across aridity gradients can be grown under controlled conditions and subjected to multiple water regimes, including well-watered controls, progressive drought stress, and repeated drought-recovery cycles. Such experimental designs enable researchers to distinguish immediate stress responses from persistent adaptive changes.

Comprehensive epigenomic analyses should include whole-genome bisulfite sequencing (WGBS) to characterize DNA methylation dynamics, RNA sequencing (RNA-seq) to quantify transcriptional responses, ATAC-seq to assess chromatin accessibility, and ChIP-seq or CUT&Tag approaches to examine histone modifications such as H3K4me3 and H3K27me3 (Law and Jacobsen, 2010; Du et al., 2015; Lämke and Bäurle, 2017). The incorporation of small RNA sequencing would further facilitate the identification of RdDM-associated regulatory pathways involved in drought adaptation (Matzke and Mosher, 2014; Erdmann and Lafontaine Picard, 2020). Physiological traits including leaf water potential, stomatal conductance, abscisic acid accumulation, root architecture, and biomass allocation should also be evaluated to establish links between epigenetic variation and adaptive performance.

3.3 Drought-responsive regulatory networks and epigenetic memory

Current knowledge from plant stress epigenetics suggests that drought adaptation in S. viridis is likely mediated through coordinated changes in multiple regulatory layers. Immediate responses to water deficit are expected to involve rapid transcriptional activation of genes associated with ABA signaling, osmotic adjustment, reactive oxygen species detoxification, and stomatal regulation. These transcriptional responses are often accompanied by increased chromatin accessibility at stress-responsive loci and dynamic alterations in histone modification patterns (Crisp et al., 2016; Lämke and Bäurle, 2017).

DNA methylation changes are predicted to occur more selectively, particularly within transposable element-rich regions and promoter-adjacent regulatory sequences. Repeated drought exposure may induce persistent epigenetic modifications that remain detectable after recovery, thereby contributing to drought stress memory. Such memory-associated loci may exhibit sustained chromatin accessibility or retention of active histone marks, allowing more rapid and robust transcriptional responses during subsequent drought events (Auge et al., 2023). These observations support the hypothesis that epigenetic memory functions as an adaptive mechanism enabling wild grasses to cope with fluctuating environmental conditions.

3.4 Adaptive interpretation and implications for grassland resilience

The interpretation of epigenetic variation in natural populations requires careful distinction between environmentally induced responses and genuinely adaptive modifications. Not all drought-induced epigenetic changes necessarily contribute to improved fitness. Therefore, adaptive significance should only be inferred when epigenetic features are consistently associated with drought tolerance across multiple accessions, persist following stress recovery, reappear during repeated stress cycles, correlate with environmental conditions at collection sites, or are experimentally validated through functional analyses (Springer and Schmitz, 2017; Fortes and Gallusci, 2017).

Several candidate regulatory modules are expected to play central roles in drought adaptation in S. viridis. These include ABA biosynthesis and signaling pathways, aquaporin-mediated water transport systems, late embryogenesis abundant (LEA) proteins, reactive oxygen species scavenging enzymes, and developmental regulators controlling flowering and reproductive success under water limitation. In addition, epigenetic regulators such as MET1, CMT2, CMT3, DRM2, AGO4, DDM1, and ROS1-like demethylases may directly influence the establishment and maintenance of adaptive chromatin states (Du et al., 2015; Zemach et al., 2013). Collectively, these findings highlight the potential of S. viridis as a powerful model for understanding how epigenetic mechanisms contribute to ecological resilience and drought adaptation in wild grass species.

4 Conservation, Epibreeding, and Future Directions

The conservation implications of drought epigenomics in wild grasses are substantial. If wild populations contain adaptive combinations of genotype and epigenotype shaped by local drought regimes, then conservation units should not be defined solely by neutral genetic structure. Instead, sampling strategies should deliberately capture climatic heterogeneity, especially along rainfall, aridity, and disturbance gradients. For seed banking and restoration, this means recording source moisture conditions, maternal environment, and regeneration procedures, because one practical risk is that ex situ propagation under benign conditions may erase or dilute ecologically relevant epigenetic states even when DNA sequence diversity is retained. In degraded drylands and encroached grasslands, restoration success may therefore depend not only on selecting locally adapted genotypes, but also on preserving environmentally calibrated regulatory states.

Epibreeding is the translational extension of this logic. In wild and semi-wild grasses, epibreeding should not be framed as replacing conventional breeding, but as adding a regulatory dimension to it. Three routes look most promising. The first is selection on stable natural epialleles that co-segregate with drought performance. The second is the deliberate use of stress priming, recurrent drought selection, or synthetic epigenetic populations to enrich favorable regulatory states before introgression or deployment. The third is epigenomic prediction, in which methylation and accessibility profiles are incorporated into models of drought performance alongside genotype and climate-of-origin data. This is especially attractive in complex, TE-rich grass genomes where many adaptive effects may be regulatory rather than coding.

Targeted epigenome editing offers a more direct future route. The RdDM literature now makes clear that locus-specific methylation can be induced in plants by engineered RNAs, hairpin constructs, or direct tethering of methylation machinery to specific loci, including CRISPR-based approaches. This is conceptually important for drought adaptation because it allows researchers to test whether methylation at a candidate promoter, enhancer, or TE actually changes phenotype without altering the underlying DNA sequence. For wild-grass research, that means moving from association to causality at candidate drought loci. In breeding terms, epigenome editing is especially appealing where reversible or regulatory tuning is desired and where sequence modification is either unnecessary or undesirable.

Several challenges remain. Causality is still the central bottleneck. Many epigenetic marks mirror altered transcription instead of driving it. Tissue heterogeneity can blur signal, especially in leaves and meristems. Developmental stage strongly conditions the methylome and chromatin landscape, making time-resolved sampling essential. In grasses, repetitive DNA complicates mapping and interpretation. Population structure can also produce false adaptive signals if methylation is analyzed without genetics. Finally, transgenerational claims require particular caution because many stress-associated marks are reset, diluted, or contingent on repeated exposure. A rigorous field will therefore require pangenome-aware references, repeated-stress designs, recovery sampling, and explicit modeling of genotype, environment, and life history.

The most productive research agenda for 2026 and beyond is, in my view, clear. It should combine wild-population sampling across eco-climatic mosaics, long-read or pangenome-enabled methylome mapping, accessibility and histone profiling in stress time series, small-RNA analysis, fitness-linked common gardens, and targeted validation in tractable model grasses such as Setaria. That agenda is sufficiently mechanistic for molecular ecology, sufficiently ecological for conservation biology, and sufficiently translational for epibreeding.

Figure 1 showing how epigenetic information can inform seed collection, drought-resilient restoration, conservation prioritization, adaptive management, and regulatory breeding pipelines.

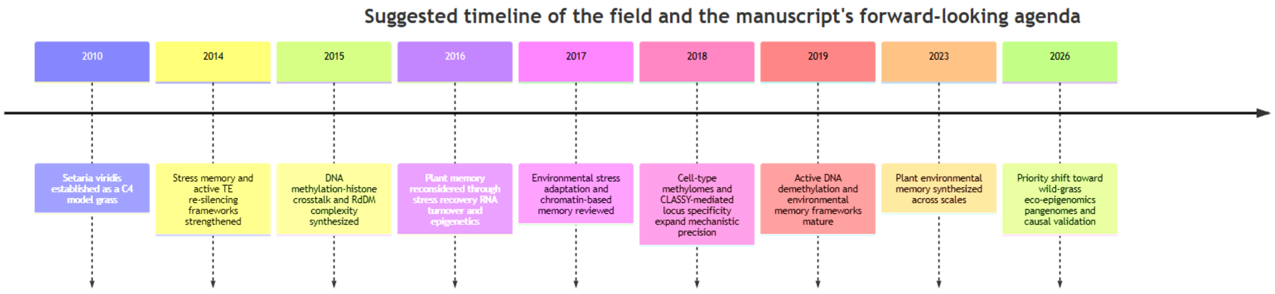

Figure 1 Conservation and epibreeding decision framework

5 Conclusions and Open Questions

Drought adaptation in wild grasses is not explained adequately by DNA sequence variation alone. The literature now supports a layered model in which drought cues are filtered through methylation pathways, histone-state transitions, accessibility changes, and small-RNA systems that collectively shape transcription, physiology, and potentially stress memory. This is especially relevant in grasses because of their ecological dominance in drylands and the regulatory importance of TE-rich genomes. The most secure mechanistic conclusions concern methylation pathway architecture, RdDM-mediated TE and stress regulation, and coupling between heterochromatin marks and gene control.

The main limitation of the current evidence base is taxonomic unevenness. Direct, multi-layer drought epigenomic datasets remain denser in model plants and crop systems than in truly wild grass populations, and integrated WGBS–ATAC–histone–RNA drought atlases are still rare for wild grasses. For that reason, Setaria viridis emerges as the most practical near-term organism for deriving causal, ecologically relevant insight that can later be transferred to less tractable taxa.

The most pressing open questions are these: Which epigenetic changes in wild grasses are adaptive rather than reactive? How stable are drought-associated states across development, dormancy, and seed regeneration? What fraction of field-relevant variation is controlled by cis-acting genetic differences versus environmentally induced epigenetic plasticity? How important are TE-adjacent regulatory changes in repeat-rich grass genomes? And can conservation and breeding programs deliberately preserve or induce beneficial regulatory states without unacceptable instability or off-target effects? Those questions define the next phase of research at the boundary of molecular ecology, conservation, and climate adaptation.

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