

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.