Epigenetics of Abiotic Stress Tolerance in Legumes

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Abstract

Epigenetic modifications are known to alter the activation pattern of some genes and not the per se DNA sequence. Stress to the plant causes epigenetic alterations in the plant either as hyper- or as hypo-methylation of certain DNA sequences. To overcome or to counter the various abiotic stress conditions, the plant's defense machinery including cellular signaling pathways gets regulated by several stress-responsive genes, which in turn are regulated by various mechanisms including DNA and chromatin modifications, and also through different small RNA-based mechanisms. There is a sudden spurt in the epigenetic studies aiming to find their role in the imposition of various types of abiotic stress tolerance in different plant species, mainly due to the quick advancements in the high-throughput NGS technologies. Many reports associating the DNA methylation response with that of various abiotic stress adaptations are available in many legume species like soybean, chickpea, pigeon pea, Medicago, lotus, peanut, and common beans using these techniques. These legumes have shown tolerance to several abiotic stresses because of unique epigenetic variations, which are present in the natural populations. Understanding the epigenetic mechanism regulating the tolerance to the abiotic stresses will help plant breeders in the development of more resilient and climate-smart varieties, giving higher yields under varied abiotic stresses. This chapter covers the current status of a novel and promising field of epigenetics in legume crops, especially for the imposition of different abiotic stress tolerance.

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Abiotic stresses · DNA methylation · Epigenetic mark · Epigenome editing · Methylation landscape

4.1 Introduction

Legumes are unique in the sense that they can enhance soil fertility through natural nitrogen fixation ability and thereby help in the overall agricultural sustainability. Several grain legumes are the staple food and the key protein source, especially for the poor residing in developing and underdeveloped countries (Mishra et al. 2021). Ironically, most of the legumes suffer heavily due to the negative impact of many abiotic stresses like heat, cold, drought (water-deficit stress), and salinity (Bhalani et al. 2019; Sarkar et al. 2014, 2016). Thus, to sustain such important crops, there is a need to opt for novel approaches like epigenetics to develop the climate-resilient and abiotic stress-tolerant varieties in the legumes. Next-generation sequencing (NGS) technologies are giving an option for rapid and cost-effective omics technologies in many legumes including chickpea, mung bean, lentils, pigeon pea, peas, soybean, Medicago, etc. for the identification of key genes and regulatory pathways involved with different abiotic stress tolerance (Dasgupta et al. 2021; Mishra et al. 2020; Nawade et al. 2018). Various studies have proved the associations between methylation levels and different abiotic stresses, suggesting the pronounced role of epigenetic mechanisms in plant adaptability (Malabarba et al. 2021; Windels et al. 2021). Thus, understanding their role in the abiotic stress tolerance mechanism is very important to have improved productivity (Ramu et al. 2016).

In general, epigenetics (meaning above genetics) is being referred to as any heritable alteration which is unable to modify the DNA sequence(s) or genetic code yet causes modified gene expression and altered phenotype. However, the concept of epigenetics is constantly changing, and its exact definition is always debated (Deans and Maggert 2015). Epigenetic change results in the modification of the chromatin structure, which in turn affects the transcription pattern of the cells. Epigenetic regulation mechanisms can be largely classified into three groups, viz., DNA methylation, histone modification, and RNA interference (RNAi) (Saraswat et al. 2017).

Plants being sessile in nature are exposed continuously to the environmental vagaries and experience stresses of different kinds such as availability of water and nutrient, temperature and light regimes, and salinity (Patel et al. 2016, 2017; Reddy et al. 2020). Adaptation to these stressors needs constant dynamic changes in the plants at both morphological and molecular levels. To overcome such environmental vagaries, plants have developed several strategies including epigenetic regulation for better survivability (Saraswat et al. 2017; Shanker and Venkateswarlu 2011). Several epigenetic mechanisms including abiotic stress responses were identified mainly from the model plants like *Arabidopsis* (Pecinka et al. 2020) and rice (La et al. 2011). The knowledge derived from these species is being used to understand the similar phenomenon in legumes too (Chinnusamy and Zhu 2009; Gutzat and Scheid 2012). Also, reports mentioning the changes in the DNA methylation pattern in different plant species are available for different stresses such as water-deficit stress (Kapazoglou et al. 2013), temperature stress (Naydenov et al. 2015), and continuous cropping (Liang et al. 2019).

The most deeply studied model legumes at the genomic levels include soybean, *Medicago truncatula*, and lotus (Cañas and Beltrán 2018; Mochida et al. 2010; Ramesh et al. 2019). Lately, a few other legumes like *Phaseolus vulgaris* (common bean), chickpea, and cowpea are also being deeply investigated at the genomic level (Lobaton et al. 2018; Mishra et al. 2021, 2022; Timko et al. 2008; Varshney et al. 2013). Recently, many legume crops like pigeon pea, lentil, mung bean, peas, beans, Medicago, lotus, peanut, chickpea, and soybean have been sequenced, and the amount of genomic sequence data is increasing with each passing year (Ahmad et al. 2020; Bosamia et al. 2020; Garg et al. 2014; Mishra et al. 2020). Further, due to the rapid increase in the relatively cheap genomic technologies (including epigenome analysis), such studies even in the non-model organism have also been possible.

Under abiotic stress, plants respond differently involving multiple mechanisms through massive differential gene expressions and nuclear organizations including epigenetic changes (Budak et al. 2015). Nevertheless, studies delineating the role of epigenetics in the imposition of abiotic stresses in legumes are not very deeply understood, to date (Niederhuth and Schmitz 2014). Epigenetic variations in the DNA have been reported in response to many abiotic stresses (Pandey et al. 2016). Yet, the precise role of various enzymes catalyzing the active DNA methylations or other modifications has not been thoroughly understood.

Legumes generally have large genome sizes, many TEs, repeat regions, and numerous high-copy-number genes, and to understand their functions, legume breeding should include novel -omics technologies including the use of epigenetic approaches while going for the development of new high-yielding and climate-resilient varieties (Bosamia et al. 2015; Mishra et al. 2015; Salgotra and Gupta 2019). With this backdrop, this chapter gives an in-depth overview of various epigenetic studies in different legume species with a detailed focus on the role of epigenetics in abiotic stress responses in legumes.

4.2 Epigenetics and Major DNA Methylation Mechanisms

The “epigenetic landscape” and “epigenetics” terms were coined by Conrad Waddington way back during the early 1940s. Gene expression can be regulated through various epigenetic mechanisms like chromatin modifications (e.g., histone acetylation, methylation, phosphorylation, and ubiquitylation) and DNA modifications (e.g., cytosine methylation) (Gibney and Nolan 2010). These epigenetic modifications are prompted by various developmental and/or environmental reasons, which then modify the chromatin architecture without changing the DNA

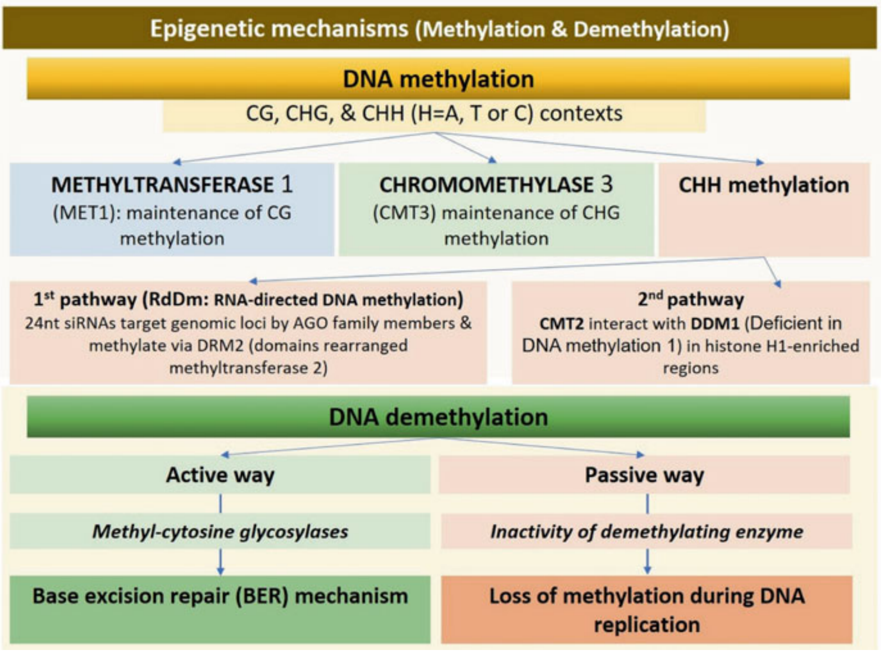

Fig. 4.1 Outline of DNA methylation and demethylation operating in the plants

sequence(s) (Chinnusamy and Zhu 2009). The detailed understanding of the role of epigenetic factors regulating various abiotic stresses is still very limited.

Among various epigenetic mechanisms, DNA methylation and posttranslational histone modifications (PHM) are the deeply studied DNA modification mechanisms. In the case of DNA methylation, a methyl group gets added from *S*-adenosyl-L-methionine to the fifth C of the cytosine ring, which results in the formation of 5-methylcytosine (5mC). In plant system, DNA methylation is reported to occur in three sequence contexts, viz., (1) symmetric CG, (2) symmetric CHG, and (3) asymmetric CHH, where H can be A, T, or C base or except G any other base (Malabarba et al. 2021). Process-wise DNA methylation can be of three types, viz., (1) de novo methylation, (2) maintenance of methylation, and (3) demethylation, which involves several enzymes (Fig. 4.1).

4.2.1 De Novo Methylation

The process uses domains rearranged methyltransferase-2 (DRM2), which gets controlled by RNA-directed DNA methylation (RdDM) pathway (Law and Jacobsen 2010; Matzke and Mosher 2014), wherein Pol IV (RNA pol IV) transcribes single-stranded RNAs (ssRNAs) which then form double-stranded RNA intermediates (dsRNAs) by RNA-dependent RNA polymerase 2 (RDR2). Afterward, DCL3

(RNase III-class DICER-LIKE 3) cleaves the dsRNAs to form 24-nt small interfering RNAs (siRNAs), which get incorporated into AGO4 (ARGONAUTE 4) and base-paired with Pol V and produce scaffold RNA and use DDR protein complex. This comprises proteins such as defective in RNA-directed DNA methylation 1 (DRD1), RNA-directed DNA methylation 1 (RDM1), and defective in meristem silencing 3 (DSM1) that stabilize the Pol V and chromatin interaction using MORC protein complex. Pol V then guides the AGO4 to the chromatin (Wierzbicki et al. 2009). These ultimately result in the DRM2 recruitment, which is followed by methylation of specific DNA base(s) (Matzke and Mosher 2014; Huiming Zhang and Zhu 2011). The precise function of the RdDM pathway indirect gene methylation and regulation is still not very clear. Rather, this pathway targets some repetitive sequences and transposable elements (TEs), which then controls the activation and repression of close-by gene(s) (Sigman and Slotkin 2016). The methylation of CHH context (de novo) of mostly heterochromatin regions especially that of TEs was regulated by the CMT2-dependent pathway (Zemach et al. 2013), which acts in a siRNA-independent way and is dependent on decreased in DNA methylation 1 (DDM1) chromatin remodeler.

4.2.2 Maintenance of Methylation

This is very much dependent on the sequence contexts; for example, methylation of CG context is reportedly maintained by methyltransferase 1 (MET1) and decrease in DNA methylation 1 (DDM1), whereas CHG by chromomethylase 2 and 3 (CMT2 and CMT3), and CHH by DRM2 and CMT2 (Chan et al. 2005).

4.2.3 DNA Demethylation

Demethylation can be through either active or passive ways, wherein passive demethylation denotes loss of methylation during DNA replication due to the inactivity of the demethylating enzyme (Zhu 2009). This process is being regulated by four bifunctional 5mC DNA glycosylases, viz., repressor of silencing 1 (ROS1), Demeter (DME), DME-like 2 (DML2), and DML3, which removes the 5mC using base excision repair (BER) pathway (Zhang and Zhu 2012). Due to the antagonistic effect of RdDM and ROS1 activity, some sort of coordination has been reported between DNA methylation and demethylation, which in turn stops the hypermethylation of certain loci (Tang et al. 2016). A 39-nt regulatory element or MEMS (DNA monitoring methylation sequence) is the ROS1 promoter and functions as a putative sensor of MET1 and RdDM pathway. Very high activity of MET1 and RdDM results in the hypermethylation of MEMS, which causes activation of ROS1 demethylase activity and regulates DNA methylation at the whole-genome level (Lei et al. 2015).

4.3 Methylation of Various Regions of the Gene

Gene expression also gets regulated by the methylation in the promotor region via inhibition of transcriptional activators/repressors. This may completely inhibit the tissue-based gene expression (Johnson et al. 2007; Zhang et al. 2006), or this may also regulate specific processes like gene imprinting during seed development or immune-responsive gene regulation (Matzke and Mosher 2014; Zhang et al. 2018a). However, the function of DNA methylation within the gene bodies is still not very clear, and two hypotheses have been proposed about their role, viz., (1) masking of the cryptic transcription sites, which will assist in its isoform splicing (Neri et al. 2017), and (2) reduction in the gene expression variations via exclusion of H2A.Z from the nucleosome (Zilberman et al. 2008). The function of methylation in the TE activity regulations is thoroughly studied, wherein it mainly functions as either TE silencing or a repressor of the transposition by hypermethylation of all the sequence contexts (Sigman and Slotkin 2016).

4.3.1 Histone Modifications

Chromatin accessibility in the gene's promotor region is observed through histone modifications, especially through methylation or acetylation (Berger 2007; Kouzarides 2007) (Fig. 4.2). A nucleosome consists of eight histone proteins (two copies each of H2A, H2B, H3, and H4 proteins), which are wrapped by 147 bp DNA (Peterson and Laniel 2004) and function through epigenetic modification of various genes by controlling the access and binding of regulatory elements (Berger 2007). Modification of the amino acids present at the N-terminal tails of histone proteins (H3 and H4) is reported, which can either activate the genes via acetylation, phosphorylation, and ubiquitination or repress the genes mainly via methylation (with some exceptions) (Zhao et al. 2019). Even though histones are considered as highly conserved proteins, plants do possess structurally and functionally discrete classes of H2A (H2A.X, H2A.Z) and H3 (H3.3) forms (Deal and Henikoff 2011). Increased H3K9ac (in the heterochromatic chromatin knobs) was found to be associated with an increase in the transcription, while increased H3K9me2 was found to be correlated with a decrease in the transcription of certain stress-responsive genes (Yong Hu et al. 2012). The stress-responsive genes in the plants show transient modifications in the histones under varied stress conditions (Zong et al. 2013).

4.3.2 Noncoding RNAs and Epigenetic Regulation Under Abiotic Stress

Noncoding RNAs (long ncRNA or small ncRNAs) regulate the opening and closing of the chromatin and are associated with both gene silencing and activation at both transcriptional and posttranscriptional levels. The ncRNAs which are associated

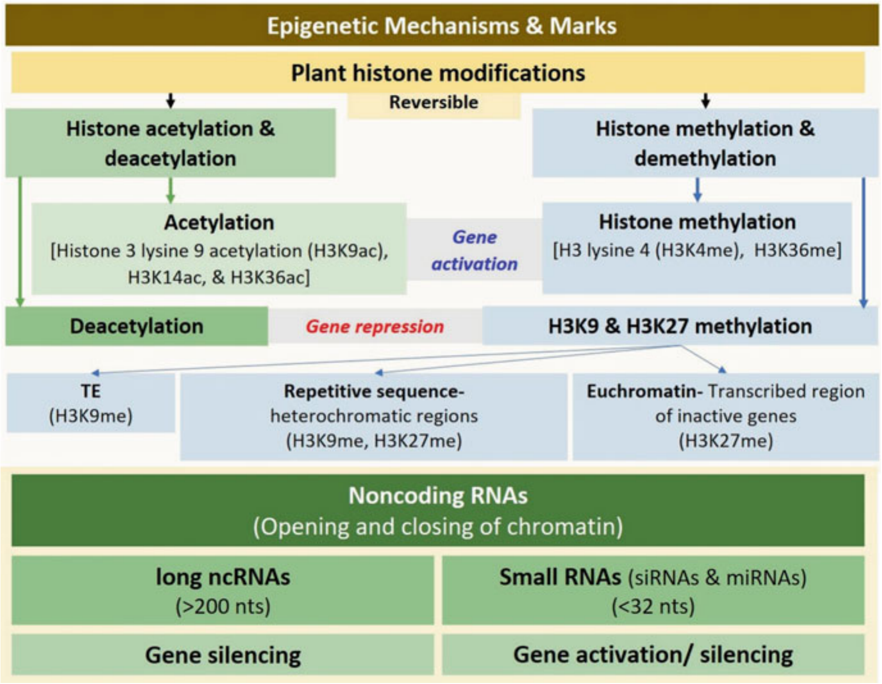

Fig. 4.2 Schematic representation of epigenetic mechanism and marks operating in plants

with epigenetic regulation (i.e., heterochromatin formation, histone modification, DNA methylation, and gene silencing) are of two major types, viz., the short ncRNAs (<30 nts) and the long ncRNAs (>200 nts). The short ncRNAs are grouped into three major types: (1) microRNAs (miRNAs), (2) short interfering RNAs (siRNAs), and (3) piwi-interacting RNAs (piRNAs) (Salgotra and Gupta 2019). Sequence-specific methylation is known to be caused by ds-RNA and RdDM (Law and Jacobsen 2010), while RNAi was reportedly associated with the RdDM causing cytosine methylation (Meister and Tuschl 2004; Wassenegger et al. 1994). In plants, miRNAs are known to cause RNA silencing and posttranscriptional gene regulation (Lee et al. 1993; Maxwell et al. 2012). Various classes of siRNAs (i.e., antisense siRNAs, heterochromatic siRNAs, trans-acting siRNAs) were known to enable gene silencing through methylation of histone and RdDM (Mosher et al. 2008; Xu et al. 2013).

Several reports have proved the role of ncRNAs in the regulation of gene expression under abiotic stress conditions. Zeller et al. (2009) reported the accumulation of various novel antisense transcripts under abiotic stress situations in the plants, which were the source of siRNAs. Downregulation of certain siRNAs such as Hc-siRNAs (heterochromatic siRNAs), siR441, and siR446 has been reported under abiotic stress situations, which seems essential for the gene regulation, especially under stress conditions (Yan et al. 2011). The miRNAs are known to have a major role under different abiotic stress-like conditions, especially under cold, heat, salinity, etc. (Salgotra and Gupta 2019).

In mung bean, among different sequence contexts, the proportion of mCHH DNA methylation was very high, while in soybean (Schmitz et al. 2013), mCG is the most commonly methylated sequence context. Both mung bean and common bean had maximum cytosine methylation in the CHH sequence context (Do Kim et al. 2015). These two species were known to have diverged nearly 8.0 Ma (million years ago), whereas soybean is considered to have diverged from the mung bean nearly 19.2 Ma (Lavin et al. 2005). Thus, the traces of mCHH-enriched DNA methylation in both mung bean and common bean might have come from their common ancestor (Kang et al. 2017).

The role of the RdDM pathway has been observed regulating the seed parameters (size and weight) in chickpea during the seed development stage, which showed a gradual increase in the methylation of CHH context of TEs along with increased frequency of small RNAs in hypermethylated TEs (Rajkumar et al. 2020). Kurdyukov et al. (2014) have studied a 2HA seed line of *Medicago truncatula* which was highly embryogenic, and microarray showed downregulation of an ethylene insensitive 3-like gene in 2HA callus. Ethylene is reportedly linked with several developmental processes such as somatic embryogenesis (SE) and various types of stress responses. The *Medicago truncatula EIL1* gene (MtEIL1) was found to be epigenetically silenced in the 2HA line, which could be due to the increased level of miRNA targeting its 3′UTR and also due to the methylation of *MtEIL1* (Kurdyukov et al. 2014). A plant-specific gene *MutS HOMOLOG1* (*MSH1*) has been used for the RNAi suppression in several plant species including soybean for the production of developmental changes including abiotic stress response along with methylome repatterning. Therefore, RNAi can be a direct means of exploitation of epigenetic variations associated with abiotic stress tolerance in plants (Raju et al. 2018).

4.4 Epigenetics and Abiotic Stress Tolerance in Legumes

4.4.1 Temperature-Stress Tolerance

Climate change induced by various factors including excessive greenhouse gas (GHG) emission has caused many negative impacts on crop plants primarily in the form of heat stress due to global warming. The mean temperature of the earth is reportedly increased to the tune of 0.35 °C from 1979 to 2003 (Venterea 2014; Walther et al. 2002). An increase in the temperature or heat stress is known to cause early flowering (Peñuelas et al. 2009), modified plant architecture (Wahid et al. 2007), poor seed development, decreased dormancy, reduced size, and poor grain yield (Folsom et al. 2014; Long and Ort 2010), and shifting of plant establishment to higher altitudes (Pauli et al. 2012). For the transcriptional machinery, chromatin conformation plays a major role by allowing the access of DNA sequences (Li et al. 2008). Several studies have proved the role of histone acetylation and methylation in the plant's response to abiotic stresses (Stępiński 2012). In the root meristem of the soybean, changes were recorded for the DNA methylation, histone methylation, and histone acetylation when grown under different temperature regimes.

4.4.1.1 Heat Stress

In response to abiotic stress like heat, the heat-stress factors (HSF) and secondary metabolites have been found to have a great role in managing such stress response (McClung and Davis 2010). In addition, even by the transcriptional reprogramming like by upregulation of kinases and various transcription factors (TF) and downregulation of growth-related genes, such stresses were also managed (Popova et al. 2013). ROS1 was reported to be demethylating all the DNA methylation contexts as in the ros1 mutants all the DNA methylation contexts get hypermethylated (Tang et al. 2016). Heat stress is also known to affect DNA methylation in different plant species as increased global methylation and homologous recombination frequency (Boyko et al. 2010).

Various methylation process proteins [e.g., DRM2, nuclear RNA polymerase D1 (NRPD1)] also show upregulation upon high-temperature stress and increased DNA methylation (Naydenov et al. 2015). The RdDM pathway is also reported to partially regulate the transcriptional response to high-temperature stress (Popova et al. 2013). Interestingly, global DNA methylation induced by heat stress is species and tissue specific. In addition, the result of the impact of heat stress on transgenerational memory was recorded as phenotypic changes over generations by different researchers (Migicovsky et al. 2014; Suter and Widmer 2013). During repeated heat-stress conditions, methylation of histone H3K4 was found to be associated with the persistent expression and hyper-induction of high temperature-responsive genes (Lämke et al. 2016).

In the changing environmental scenario, an increase in the temperature is a major focus of various studies that are involved in unfolding the temperature-dependent genes and pathways (Arya et al. 2017). Temperature is a key factor affecting significantly the flowering in the plant system. Genome annotation has identified four copies of the *PIF4* gene in soybean, which were found expressing abundantly under short-day conditions (Wong et al. 2013). Also, eight copies of the *SVP* gene were identified in soybean, of which high expression of *Glyma01G02880*.1 and *Glyma02G04710*.1 has been recorded in shoot apical meristem during the floral transition phase (Wong et al. 2013). In soybean, miRNA 156 and miRNA 172 have shown upregulation during the floral transition stage, when plants were exposed to high temperatures (Li et al. 2015). H3K56ac and H3K4me3 methylation marks are usually recorded in class 3 SDGs, which showed differential expression in shoot apical meristem (SAM) in soybean, during the floral transition (Liew et al. 2013). Besides, several RNAi genes like RNA pol, dsRNA binding (DRB), Dicer-like, AGO, DNA methyltransferase, and DNA glycosylase were upregulated in SAM during the floral transition (Liew et al. 2013).

4.4.1.2 Chilling Stress

More of 5mC and H3K9me2 were recorded through immunostaining in the heterochromatin region of the soybean genome during chilling stress than during the recovery phase. However, indicators of permissive chromatin (i.e., H3K9ac, H4K12ac, and H3K4me) showed weak labeling in the euchromatin region (under stress) over recovered plants (Stępiński 2012). Ivashuta et al. (2002) reported transcriptional activation of specific retrotransposons in *Medicago sativa* under cold-stress conditions. Hypermethylation was recorded in *Cannabis sativa* genotypes when exposed to different levels of cold acclimation (Mayer et al. 2015). Epigenetic factors are known to regulate cold-stress tolerance in hemp. Under cold-stress conditions, soluble sugars are found to accumulate and be maintained in higher concentrations in the tolerant hemp genotypes. These genotypes expressed more of *COR* gene transcripts, which is associated with the de novo DNA methylation. Also, significantly higher methylcytosine levels at *COR* gene loci were recorded in the tolerant genotypes when deacclimated, thereby confirming the function of locus-specific DNA methylation (Mayer et al. 2015). Relatively more methylation over demethylation was recorded in the cold stress-tolerant genotypes over susceptible chickpea genotype. This could be due to the comparatively higher activation of cold stress-responsive genes in the tolerant genotypes (Rakei et al. 2016).

4.4.2 Drought-Stress Tolerance

Overall increased DNA methylation or hypermethylation has been recorded in both tolerant and sensitive genotypes of faba bean (Abid et al. 2017) and pea (Labra et al. 2002) under drought or water-deficit stress situations. In groundnut, the regulation of the *AhDREB1* gene (of AP2/ERF family TF) through acetylation of H3 helped in the positive regulation of water-deficit stress tolerance genes when exposed to the PEG-induced water-deficit stress conditions. Higher *AhDREB1* gene expression was recorded when an inhibitor of histone deacetylase (HDAC), i.e., trichostatin (TSA), was used, which then showed water-deficit stress tolerance in the peanut plant (Zhang et al. 2018b). In chickpea, drought stress was able to induce the *CaHDZ12* (an HD-Zip TF) activation, and its expression was found to be correlated with that of H3K9ac acetylation in the promoter region (Sen et al. 2017). Cytosine hypomethylation has been reported in the soybean roots under heat-stress conditions (Hossain et al. 2017). Reduced metabolic activity has been recorded in pea plants due to the drought-induced hyper-methylation of some key genes (Labra et al. 2002; Salgotra and Gupta 2019), while higher methylation was recorded in the drought-sensitive horse gram (*Macrotyloma uniflorum*) genotype than the tolerant genotype (Bhardwaj et al. 2013).

Epigenetic changes such as histone modifications, sRNAs, methylation of DNA, and lncRNAs were known to be associated with gene regulation in faba beans (Meyer 2015). A high degree of association between DNA methylation and gene expression under drought conditions in faba bean suggests the involvement of DNA methylation in the imposition of drought-stress tolerance (Abid et al. 2017). Several water-deficit stress-associated differentially methylated regions (DMRs) were identified by Abid et al. (2017), which became the basis for further understanding the epigenetic regulation of drought stress in faba bean.

In addition, a number of drought-responsive miRNAs are identified in various legumes (Mantri et al. 2013). Under drought and salinity stress, 259 differentially expressed miRNAs have been identified from the root tip tissue of chickpea. Many of these were found to have auxin and other abiotic stress-responsive cis-elements in their promoter region, which in turn imparted abiotic stress tolerance through various phytohormone syntheses (Khandal et al. 2017). In chickpea, under water-deficit stress, *miR408* was found to be accumulated (Hajyzadeh et al. 2015), while similar results were also reported for Medicago (Trindade et al. 2010). Interestingly, 24 novel miRNA families have been reported in water-deficit stress-tolerant and -sensitive cowpea genotype (Barrera-Figueroa et al. 2012), and of these, 22 families were reported from soybean too (Kulcheski et al. 2011). Most of the iso-miRNAs showed upregulation during water-deficit stress in sensitive genotypes, while downregulation in tolerant genotypes. miRNAs were known to play a key role in the abiotic stress tolerance in cowpea, and much water-deficit stress-associated microRNAs have been identified (Barrera-Figueroa et al. 2011). Inconsistent miRNA expression was reported in the studied cowpea genotypes and nine recorded predominant or exclusive expression in one of the two studied genotypes, while a few were found regulated under water-deficit stress in only one genotype (Barrera-Figueroa et al. 2011).

The genome sequencing of common bean has generated a lot of information that can provide the much-needed evidence about future PTGS studies (Vlasova et al. 2016). Posttranscriptional regulation in common bean under water-deficit stress is reportedly regulated via a legume-specific miR1514a, which targets the NAC family of TF and generates secondary phasiRNAs (Sosa-Valencia et al. 2017b). The miR1514a showed differential expression levels in the roots of the common bean when exposed to water-deficit stress conditions. In addition, an RNA-seq study has also identified the role of NAC 700 TF in the water-deficit stress, while degradome analysis revealed the two NAC TFs (Phvul.010g121000 and Phvul.010g120700) as the target of miR1514a. In addition, small RNA-seq data indicate the role of only Phvul.010g120700 in the generation and accumulation of phasiRNAs under water-deficit stress conditions (Sosa-Valencia et al. 2017b).

4.4.3 Salinity-Stress Tolerance

In the pigeon pea shoot tissues, a global decline in the methylation levels of DNA has been reported under salinity-stress conditions (Awana et al. 2019). Similarly, imposition of continuous stress for a relatively longer duration has resulted in an increase in the overall DNA demethylation in soybean, mainly in the tolerant genotypes, and this increase corresponded well with that of increased expression of various DNA demethylases (e.g., DML and ROS1). Further, different demethylation studies could identify that the regulatory genes having CG and CHG contexts were more crucial than the CHH for their adaptation to salinity stress (Liang et al. 2019). The salinity stress in *Medicago truncatula* revealed variations to the tune of 77% in CHH, while CHG and CG showed 9.1% and 13.9% changes, respectively.

Interestingly, no such correlation has been recorded between DNA methylation pattern and level of transcripts for other salinity-stress tolerance-associated key genes, which means that these genes might be regulated by other epigenetics processes (Yaish et al. 2018). On the contrary, four TFs showed induced response under salinity stress in soybean, and of these three showed demethylations in CG and non-CG contexts and also active enrichment of histone marks (H3K4me3 and H3K9ac) along with a reduction in the repressive mark H3K9me2. Thus, the possible interplay was recorded between methylation of DNA and histone modifications when exposed to salinity stress (Song et al. 2012). In the plants of salinity-stressed soybean, cross talk has been reported between histone methylation and acetylation (Liu et al. 2010; Stępiński 2012). The soybean plants under salt-stress condition showed the binding of GmPHD5 (a homeodomain TF) with H3K4me2 marks (salt-induced), which then recruits a complex associated with gene activation having GmISWI (a type of nonhistone proteins and a chromatin remodeling factor) and GmGNAT1 (an acetyltransferase), which selectively acetylates H3K14 for the activated expression of salinity-induced genes (Wu et al. 2011).

The methylation-sensitive amplified polymorphism (MSAP) and enzyme-linked immunosorbent assay (ELISA) showed significantly more methylation in mCG under salinity stress in *M. truncatula* (Al-Lawati et al. 2016; Yaish et al. 2014). A comparative whole-genome bisulfite sequencing (WGBS) on the DNA isolated from the root tissues of *Medicago truncatula* under salinity stress and control has revealed higher methylation levels in all sequence contexts, ranging from 3.8% to 10.2%. However, qPCR-based gene expression studies did not find any stable association between mCG methylation levels and transcript abundance of some key genes involved in the imposition of salinity tolerance. Thus, it seems that some other epigenetic controllers are regulating the gene expression under salinity stress (Yaish et al. 2018).

The role of MTases regulating different aspects of plant development including different abiotic stress responses has been unfolded in different legume species using expression analysis. Garg et al. (2014) have identified 16 members of the DNMT2 family in several legume species, and increased expression of DNMT (CaDNMT2) was observed in chickpea shoots under both salt- and drought-stress conditions, suggesting the role of DNMT in abiotic stress response. Overall, under abiotic stress, more transcript was recorded for CMT and DRM genes, signifying the role of stress-induced methylation in chickpea (Garg et al. 2014). In chickpea, salinity stress was found inducing the *CaHDZ12*, which also showed a correlation with that of H3K9ac acetylation in the promoter region (Sen et al. 2017). Preferential transmission of salinity tolerance and DNA methylation was reported through the female germline. However, paternal *dme* mutants recorded restoration of paternal memory, indicating that the active DNA methylation in male gametes is essential for the inhibition of paternal inheritance of hyperosmotic priming response (Wibowo et al. 2016). The details of epigenetic response in various legumes during abiotic stress-associated processes are presented in Table 4.1.

4.4.4 Abiotic Stress Tolerance and DNA Demethylation

Several reports are aimed to analyze the changes which occur in the DNA demethylase gene when exposed to various abiotic stresses, and only some mentioning the detailed analysis involving loss-of-function mutations are available (Parrilla-Doblas et al. 2019). Interestingly, some recent studies showed the function of active demethylation of DNA in the inter-generational transmission of “stress memory” helping rapid adaptation to short-term environmental variations called “priming” (Parrilla-Doblas et al. 2019). In addition, the response of a plant to abscisic acid (ABA) has also shown active demethylation of DNA under abiotic stress conditions. Still, various factors regulating such demethylation during abiotic stress response are superficially known to the scientific community. Additionally, miRNAs are now found to have some role in the active demethylation of DNA of certain genes (Parrilla-Doblas et al. 2019). This has been generally observed during gametophyte development (Slotkin et al. 2009). However, active demethylation of DNA considers enzyme-based elimination of methylated cytosine, by a family of DNA glycosylases (such as DME, ROS1, DML2, and DML3), which was followed by the base excision repair (BER)-dependent process (Penterman et al. 2007; Zhu 2009). This does not only alter genome-wide epigenetics, but also regulate locus-specific genes with abiotic stress tolerance (Hsieh et al. 2009).

4.4.5 Abiotic Stress Tolerance and Epigenetics-Based Breeding Strategies in Legumes

Till now, we have compiled several ways that can be used for the enhancement of abiotic stress tolerance in various legumes. The use of epigenetics and epigenomics in improving the adaptation to abiotic stresses needs a combination of technical and biological innovations so that the breeders can go for the targeted gene-specific modifications of the epigenome for the desired trait improvement. Besides positive impact, stress-based memory may also have a negative impact on yield (Chinnusamy and Zhu 2009). Thus, care must be taken while going for an epigenetic-based approach for the abiotic stress improvement of the crops. We can use the impact prediction models for the epigenetic variations on a plant’s phenotype and performance (Colicchio et al. 2015; Yaodong Hu et al. 2015). Identification of epialleles having an impact on the abiotic stress tolerance traits can result in epigenetic-based breeding of crop plants like the use of mutant lines, recurrent epi-selection, epigenomic selection, and editing (Greaves et al. 2014; Hauben et al. 2009; Lämke and Bäurle 2017; Oakey et al. 2016; Yang et al. 2015).

Table 4.1 Epigenetic response during various abiotic stress-associated processes in legumes

S. No.	Abiotic stress	Gene(s)/tissue/outcome	Crop species	Epigenetic response	Reference
1.	Cold	Reduced yield	*Cannabis sativa*	Methylome variation (locus-specific methylation and deacclimation)	Mayer et al. (2015)
2.	Drought	Reduced yield	Soybean	miR1514a modulation of a NAC TF transcript	Sosa-Valencia et al. (2017a, b)
3.	Drought	Reduced yield	Soybean	Up-regulation of isomiRNAs	Kulcheski et al. (2011)
4.	Drought	Reduced yield	Pea	Hypermethylation of cytosine residues	Labra et al. (2002)
5.	Drought	Reduced yield	Chickpea	Accumulation of miR408 transcripts; BHLH23 ERF/AP2	Hajyzadeh et al. (2015)
6.	Drought	Root	Chickpea	Accumulation of miRNAs at root apex	Khandal et al. (2017)
7.	Drought	Reduced yield	Cowpea	Very low vun-miR5021 and vun-miR156b-3p expression, while higher P5CS transcript level	Shui et al. (2013)
8.	Drought	Reduced yield	Faba bean (*Vicia faba*)	miR398a and miR2119 in dicistronic arrangement	De la Rosa et al. (2019)
9.	Drought	Reduced yield	Faba bean	Higher demethylation of *LOX*, *CDPK*, *ABC*, *GH*, and *PEPC* genes	Abid et al. (2017)
10.	Drought	Reduced yield	*Glycine max*	GmNFYA3	Ni et al. (2013)
11.	Drought	Reduced yield	*Phaseolus vulgaris*	NAF TF ARF10	Sosa-Valencia et al. (2017b)
12.	Drought	Reduced yield	*Vigna unguiculata*	Transferase family protein leucine repeat-rich transmembrane protein	Barrera-Figueroa et al. (2011)
13.	Drought	Reduced yield	*Macrotyloma uniflorum*	DNA methylation dynamics	Bhardwaj et al. (2013)
14.	Drought	DNMT	Chickpea	Increased expression of DNMT (CaDNMT2)	Garg et al. (2014)
15.	Heat	Roots	*Glycine max*	Hypomethylation of cytosine	Hossain et al. (2017)

16.	Salinity	Shoots	Pigeon pea	Reduction in the DNA methylation in shoots	Awana et al. (2019)
17.	Salinity	Root	Chickpea	Accumulation of miRNAs at root apex	Khandal et al. (2017)
18.	Salinity	Glyma11g02400	Soybean	Demethylation	Song et al. (2012)
19.	Salinity	Glyma16g27950, Glyma20g30840	Soybean	Hypomethylation	Song et al. (2012)
20.	Salinity	DNMT	Chickpea	Increased expression of DNMT (CaDNMT2)	Garg et al. (2014)
21.	Seed development	Cotyledon (*WOX*, *CUC*, *CLAVATA*, *PIN1* genes)	Soybean	DNA methylation	An et al. (2017), Lin et al. (2017)
22.	Flower development	Expressed in shoot apical meristem (SAM)	Soybean	124 histone modifiers	Liew et al. (2013)
23.	Flowering time regulation	Flower development	Peanuts	Methylation of the *FWA* promoter region	Chan et al. (2006)
24.	Flower and pod initiation	Flower development	Peanuts	Differential expression of various methylation genes (DRM2, MET1 DNA methylases, *DMS3*, *DRD1*, *MORC1*, and *IDN2*)	Wang et al. (2018)

In soybean, Raju et al. (2018) have proposed a breeding strategy using the *MSH1* gene system for the improvement of yield and stability by inducing epigenetic variations. The soybean memory lines (wild type and *msh1* acquired) were crossed to develop the epi-lines having wide variations for various yield-related traits. The identified epi-types showed low epi-type × environment (e × E) interactions and thus more stability under varied environments expressing different abiotic stresses (Varotto et al. 2020). The novel epigenetic variations induced by the *MSH1* suppression were found to be inherited for at least three generations and can be used for enhancement and stabilization of the overall yield of soybean crops. In addition, several metabolic pathway genes regulating improved adaptation and plasticity (across generations) of the plant are also identified (Fujimoto et al. 2012; Raju et al. 2018; Robertson and Wolf 2012).

In association with classical genetic approaches, the novel sequencing technologies have helped in understanding the epigenetic process at the whole-genome level. Epigenome profiling and epigenome editing will help in the creation of novel epiallelic variants through DNA methylation and chromatin modifications (Springer and Schmitz 2017). Breeders are now preferring to use the mapping of epigenetic marks at genome-wide level (epigenomics), and also identification of epigenetic targets to modify the plants' epigenomic variability to make them more resilient and climate smart (Lane et al. 2014). There is a need to do large-scale cross-species generation and comparison of epigenetic data in legumes, especially in response to abiotic stresses (Lane et al. 2014). Epigenetic modifications can be attempted either globally or at a specific locus using emerging techniques like CRISPR/Cas9 and dCas (Hilton et al. 2015; Moradpour and Abdulah 2020). The knowledge about the activation and repression of specific chromatin regions (using DNA-binding domains like Zn fingers, TALEs, dCas9) under specific abiotic stress can be used for the gene-specific activation or repression as per the need for the imposition of abiotic stress tolerance in crop plants (Bilichak and Kovalchuk 2016). In addition, a sound prediction model about the impact of epigenetic variations on the plant's overall performance is needed (Colicchio et al. 2015; Yaodong Hu et al. 2015).

4.5 Conclusions and Future Prospects

In legumes, the epigenetic studies are still in infancy and are mainly targeting the identification of key epigenetic factors in the plant's developmental and stress-related processes. A major reason for this could be the poor annotation of most of the legume genomes, which are incidentally full of numerous high-copy-number genes having overlapping or distinct functions (Windels et al. 2021). However, in times to come, we expect tremendous growth in legume epigenetic studies for various traits including abiotic stress tolerance. Stably inherited natural or induced epigenetic variations can be used to create climate-smart crops (Vriet et al. 2015). Otherwise, most stress-induced epigenetic modifications show reversion once there is no stress. Still, some of the modifications do show stable inheritance as epigenetic-mediated stress memory does result in long-term adaptations (Sudan et al. 2018). However, detailed studies are needed to find the factors regulating the epiallele stability in crop plants for their further use in a breeding program (Hofmeister et al. 2017). There is a need to develop various mathematical models for the identification of heritable epigenetic phenotypes, for the enhanced efficiency of the breeding program (Tal et al. 2010). Besides, epi-genotyping procedures can be developed for the identification of newly formed epialleles and their inheritance pattern (Hofmeister et al. 2017). Also, more precise epi-mutagenesis and targeted epigenome editing are needed for targeted epigenome editing (Johnson et al. 2014; Springer and Schmitz 2017).

The regions associated with the transposable elements are more prone to methylation under abiotic stress situations. Thus, these regions should be targeted to understand the trend of epigenetic changes at the whole-genome level through cytosine methylation studies (Bruce et al. 2007). Differential DNA methylation has been recorded in different tissues of the soybean (Song et al. 2013), but it is unclear whether the differences were spontaneous or developmentally controlled by differentially methylated regions (DMRs) (Salgotra and Gupta 2019). We expect an increase in the functional studies of various key epigenetic factors that can be enhanced by the recent developments in the CRISPER technologies via the generation of several epigenetic mutants at least in major legume crops. Thus, a better understanding generated about the epigenetic mechanism along with the identification of epialleles will potentially boost the plant's ability to cope with various abiotic stresses.

There is a need to modify the active DNA demethylation through CRISPER/Cas9 technology to the genes involved in the demethylation pathway. In the future, we need very precise control on the DNA methylation and demethylation of specific genes as epigenome engineering, for targeted abiotic stress tolerance breeding in the legumes (Springer and Schmitz 2017; Stricker et al. 2017). In soybean, most of the DNA methyltransferase genes were found to be expressed at low levels in seed and seem to contribute to the silencing of certain mC genes in the seed tissues. There is a need to do deep analysis about the mC pattern in different tissues under various abiotic stresses to gain an insight into the role of gene methylation, resulting in novel epigenetic gene regulation (Garg et al. 2014). The details of abiotic stress management strategies in legumes using epigenetic approaches are presented in Fig. 4.3.

Although several legume crops (viz., mung bean, lentil, peanut, chickpea, cowpea, pea, Medicago, pigeon pea, lotus, soybean, beans, etc.) have been sequenced, epigenetic studies concerning abiotic stress tolerance are limited to a few species like soybean, chickpea, pigeon pea, cowpea, and beans. There is an urgent need to study more legumes for abiotic stress tolerance using epigenetic approaches. For this, a joint research platform may be developed by various national and international organizations like the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, India), the International Center for Agriculture Research in the Dry Areas (ICARDA, Lebanon), the International Center for Tropical Agriculture which is an international research and development organization (CIAT, Colombia), and Indian Agricultural Research Institute (IARI, India), working for the

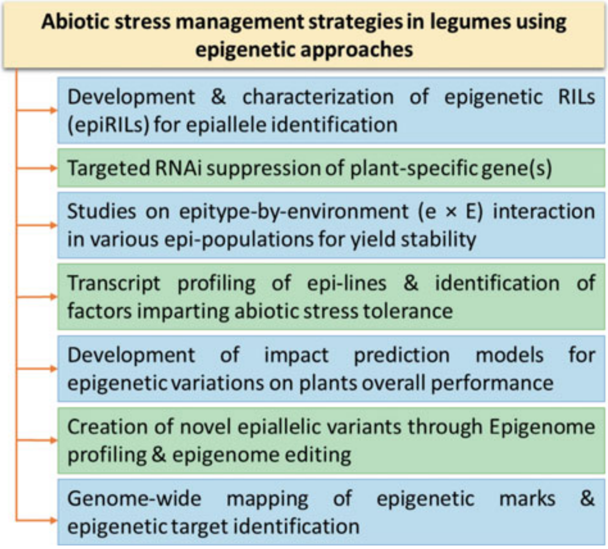

Fig. 4.3 Comprehensive abiotic stress management strategies in legumes using epigenetic approaches

improvement of various legume crops for targeted improvement using epigenetic approaches. In the initial stage, crops like mung bean, lentil, peanut, and pea can be targeted, and at a later stage depending on the availability of whole-genome information, more legumes can be added.

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