Chapter 5
Exploring the Role of Epigenetics in Cereal and Leguminous Crops Exposed to Abiotic Stress

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Abstract Epigenetics affects the gene expression due to chromatin structure changes without involving the DNA sequences. Epigenetic gene expression mechanisms play an important role in abiotic stress tolerance in plants. The mechanisms such as histone modifications, DNA methylation, and noncoding (nc) RNAs are the key elements of the epigenetic regulation machinery which leads to gene activation or gene silencing. Comprehensive literature showed the role of epigenetics controlling specific loci under environmental stresses in various plants. The epigenetic effects can be perceived on various developmental stages of plants in coping with the abiotic stresses. The whole genome-wide studies have led to unveil epigenetic effects of crop plants particularly cereal and legume in the era of high-throughput and next-generation sequencing (NGS) technologies. A number of epigenetics investigations are being carried out in cereals and legumes crops for abiotic stresses such as cold, drought, heat, salinity, etc. This chapter has compiled the latest improvements made in the field of epigenetics related to abiotic stresses focusing on cereal and legume crops. Moreover, development of crop varieties tolerant to abiotic stresses such as drought, cold, heat, high temperature, etc., is essential to sustain the crop productivity.

5.1 Introduction

Cereals and legumes are the important nutritional source of human being and feed for livestock. To feed the ever increasing population particularly in the developing and underdeveloping countries besides limited resources there is a need to increase the productivity of crops. Continuous threatening from global warming and various abiotic stresses such as drought, salinity, cold, heat, etc., have endangered food security (Maiti and Satya 2014). To cope with the ever increasing population and

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R. Alvarez-Venegas et al. (eds.), *Epigenetics in Plants of Agronomic Importance: Fundamentals and Applications*, https://doi.org/10.1007/978-3-030-14760-0_5

alarming environmental stresses, it is essential to develop crop varieties with high yield and quality tolerant to various stresses. These crops suffer from various biotic and abiotic stresses at different growth stages, resulting in decrease in crop yield and quality. Abiotic stresses cause modifications in the (de)methylation pattern at the coding region of some stress-responsive genes and regulate their expression, affect plant quality, and decrease plant productivity. By activating molecular networks such as signal transduction, stress perception, metabolite production, and expressions of specific stress-related genes, plants can overcome environmental stresses.

Epigenetics is defined as heritable modification in chromatin structure which intensely influences expression of genes but does not involve change in the DNA sequence (Fujimoto et al. 2012). The term epigenetics (Waddington 1942) was derived from e*pigenesis* to capture the reasonable presumption that a layer of mechanisms exist that reside above (*epi*) the level of the *genes* during organismal development that control their output in order to specify cell fate determination (Sweatt 2013). Mirouze and Paszkowski (2011) stated the term epigenetics as heritable variation in gene regulation resulting from covalent modifications of DNA and its associated chromatin proteins without changing the underlying nucleotide sequences. Hence, the term epigenetics can also be defined as the stable heritable phenotype resulting from changes in chromosome without alterations in the DNA sequence. The key epigenetic marks which regulate different plant traits in response to biotic and abiotic stimuli are cytosine methylation, histone modifications, and small RNA accumulation. These epigenetic changes are reported to be reversible in nature and provide speedy retort mechanisms to plants to withstand pathogen and environmental stress (Hewezi et al. 2017).

The mechanism of epigenetic regulation involves the modification of histones, DNA methylation, and the action of noncoding (nc) RNAs (Fig. 5.1). The DNA methylation, histone modifications, and nc RNAs such as either long nc RNAs or small RNAs lead to open or closed chromatin states associated with gene activation or gene silencing, respectively. The small RNAs include small interfering RNAs (siRNAs) and microRNAs (miRNAs). Epigenetic changes do not alter the genetic code sequence of DNA, but modify the activation of certain genes. The noncoding structure DNA itself or the associated chromatin proteins may be modified, causing activation or silencing. RNA interference (RNAi) mediates gene silencing at post-transcriptional level in a sequence-specific manner (Yang et al. 2017). This array of processes is clearly interconnected and almost certainly acts in a complex, interactive, and redundant fashion (Berger 2007).

With the advent of high-throughput techniques, a wealth of information on epigenetic regulation in crop plants is generated and in recent years, the rapid progress in next-generation sequencing (NGS) has led to the unveiling of epigenetic landscapes at genome-wide scale (epigenomes). There is growing aspiration to understand the stability and role of epigenetic regulatory systems in plants surviving under adverse environmental conditions (Geyer et al. 2011). The high-throughput techniques and NGS have helped to study the effect of epigenetics on various developmental stages of plants under biotic and abiotic stresses. The epigenetics

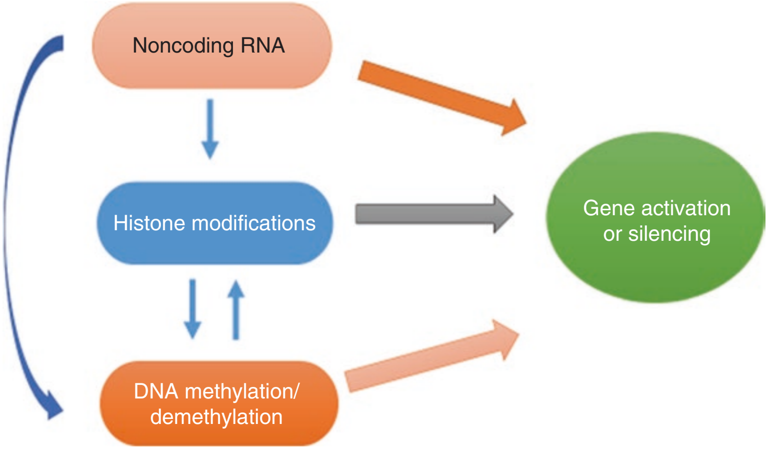

Fig. 5.1 Three epigenetic mechanisms, viz., DNA methylation, histone modifications, and noncoding (nc) long or small RNA molecules, lead to changes in chromatin structure without altering the underlying DNA sequence

also has importance in the transgenerational adaptive response to environmental stimuli of plants (Weinhold 2018). The burgeoning area of epigenetics and its role in abiotic stress is emphasized in this chapter in context of the role of chromatin regulators.

5.2 Abiotic Stresses

Various environmental stresses such as drought, cold, heat, and salinity affect growth and development of plants, which consequently hampers the plant productivity. Under environmental stresses low crop productivity results due to various changes in plants at genotypic and phenotypic levels (Asada 2006). However, plants have evolved an array of defense mechanisms to adapt to different stresses by quick and coordinated changes at transcriptional and post-transcriptional levels (Boyko and Kovalchuk 2008). The stress tolerance mechanisms have been reported to inherit over generations, though the inheritance mechanism may differ among plant species based upon intensity and duration of stress and the genetic composition of the plant species (Chen et al. 2010). Excessive abiotic stress due to drought, heat, salinity, etc., and/or limitation of an important mineral affect the genes that regulate the epigenetics mechanism (Fang et al. 2014). Bocchini et al. (2015) reported that chromatin modifications, methylation, chromatin remodeling, and RNAi mechanisms can rapidly regulate gene expression under stress. Bruce et al. (2007) reported that these modifications can be "memorized" by plant somatic cells after a stimuli to stress and further can be utilized as an epigenetic mark which can be inherited transgenerationally. When their progenies face stressful conditions, the same epigenetic alteration will occur. Moreover, female gamete is responsible for causing epigenetic changes (Wibowo et al. 2016). The key factor in the plant's response to stress and its adaptation is the plasticity that transmitted from one generation to another generation, which can have a great impact on breeding programs (Fortes and Gallusci 2017). Peng and Zhang (2009) revealed that DNA methylation levels declined with some stresses like planting density, chilling, and successive subculturing, whereas an increase was found under salt stress.

5.3 DNA Methylation

The main epigenetically mark in eukaryotes is the addition of a methyl group on the 5 °C of the cytosine base to form 5-methylcytosine. Feng et al. (2010) reported that DNA methylation usually occurs in plants in three string contexts such as CG and CHG (symmetric) and the CHH (asymmetric). Niederhuth and Schmitz (2017) reported that genome stability, regulating global gene expression, and silencing deleterious transposon insertions are some of the important roles played by methylation. DNA methylation at promoter regions is related to gene silencing, while its demethylation leads to gene activation. Cokus et al. (2008) stated that the methylation at 5′ portion (promoter) and 3′ portion hampers gene expression, while expressed genes are methylated in the transcribed region (gene-body methylation). During plant development, specific enzymes facilitate the important role in demethylation and DNA methylation (Van Oosten et al. 2014). Attenuation of gene transcription occurs preferentially at C-G dinucleotide sequences in DNA sites and cytosine demethylation also occurs which can be again reconverted to unmethylated position.

In plants, two major types of methylation activities occurred such as *de novo* and maintenance. The *de novo* methylation is a process by which previously unmethylated cytosine residues are methylated, leading to the formation of new methylation patterns, whereas maintenance methylation is the process of maintenance of pre-existing methylation patterns after DNA replication (Chen and Li 2004). The mechanism of DNA methylation is governed by preferentially two types of enzymes, i.e., methyltransferases and demethylases. *De novo* methylation is established by DRM2 (domains rearranged methyltransferase 2) in the new DNA sequences generated after DNA replication, whereas MET1 (DNA methyltransferase 1) and CMT (chromomethylase) are responsible for maintenance of CG and CNG methylation, respectively (Chen et al. 2010). DNA glycosylases catalyze the removal of methyl group from cytosine residue (Cao et al. 2000). A central dogma of the epigenetics field has depicted that once DNA methylation patterns are established upon the genome in terminally differentiated cells, those modifications are permanent and essentially immutable.

Genome-wide profiling of DNA methylation is termed methylome, while the combination of both post-translational modifications of histone tails and methylation at cytosines along the genomes is termed as epigenome. Till date, most studies of plant epigenomes have been focused on DNA methylation, which is more stable than post-translational modifications of histone tails. DNA methylation is distributed in the plant genomes, including heterochromatic and euchromatic regions (Gehring and Henikoff 2007). Higher levels of cytosine methylation are reported in the heterochromatic regions, containing transposons and other repetitive sequences, whereas comparatively lesser levels of cytosine methylation in euchromatic regions inhabiting genes and non-repetitive intergenic regions. The first report on global DNA methylation profiling of endosperm and embryo genomes demonstrated widespread reduction of DNA methylation in the endosperm, particularly at regions corresponding to transposable elements (TEs) and small RNAs (Zemach et al. 2010). DNA methylation studies at genome-wide levels are well studied in various cereal and legume crops (Zhong et al. 2013).

5.3.1 Methylation Under Abiotic Stress

Understanding the mechanisms of epigenetic regulation of plant growth and development could create new genetic variation for improving crop productivity as well as adaptation to stress environment. Stress can cause hypermethylation or hypomethylation of DNA. Drought-induced hypermethylation has been proposed to play a primary and direct role in reducing the metabolic activity in plant (Labra et al. 2002). They reported drought-induced hypermethylation and hypomethylation in drought-tolerant and drought-susceptible varieties of rice, respectively. Tan (2010) stated that the changed methylation level in maize exposed to osmotic and salt stress helps in stress acclimation. Stressful environment produces transgenerational epigenetic modifications leading to enhanced stress adaptability in future progenies (Ou et al. 2012). It has been reported that non-stressed progenies carrying modified methylation patterns acquired from the stressed parent rice plants exhibit enhanced stress tolerance (Kou et al. 2011). In addition to gene silencing, cytosine methylation is aimed at silencing of transposons as their activity can have disastrous effects on the plant, especially if they insert into a gene and disrupt its function. Steward et al. (2002) reported that the cold stress at seedlings stage in maize created the DNA demethylation at genome-wide level. The osmotic stress in rice was associated with a higher expression of specific genes due to proline biosynthesis, but also with a global DNA demethylation (Zhang et al. 2013), whereas in some cases, the imposition of cold stress did not necessarily related to DNA demethylation events, for example, in the case of *Medicago sativa* plant, the imposition of cold stress was associated with transcription activation of specific retrotransposons (Ivashuta et al. 2002). Several reports correlating DNA methylation dynamics with stress adaptation are available. A drought-sensitive genotype of horse gram (*Macrotyloma uniflorum*) shows higher methylation (Bhardwaj et al. 2013). Differential DNA methylation patterns were reported in Barley genotypes under drought particularly in drought related genes (Kapazoglou et al. 2013). These studies indicate that certain genomic regions may be more prone to differential methylation upon stress imposition/relief eventually corresponding to a stress adaptation process. Distinct epigenetic variations were reported due to the presence of methylome variations in the population to tolerate abiotic stresses. Methylome variations are present in natural plant populations and may help individuals to better cope with different environments. Mayer et al. (2014) stated that high methylation levels were observed due to different cold acclimation capacities in *Cannabis sativa* varieties.

The epigenetic changes in crop genomes have been studied by many research groups. For genome-wide methylation studies, one of the basic methods is methylation sensitive amplification polymorphism (MSAP). It is a potent technique for studying the whole genome cytosine methylation changes in crops. The technique has been used for this purpose in various crops like maize, rice, and wheat. The study of methylation dynamics of the regions associated with transposable elements, in response to abiotic stress, can be helpful in understanding the trend of epigenomic changes specifically targeting gene flanking regions, which may not be reflected in the whole genome cytosine methylation analysis. Another technique for high-throughput methylation studies is methyl chip-on-chip. It involves the enrichment of methylated regions by immunoprecipitation of sonicated and denatured genomic DNA with an antibody specific for methylated cytosine, followed by hybridization on to chip. Using this technique, the methylome analysis for the stress-responsive genes gives us an idea about the genes being activated or silenced under stress. Also, histone PTMs are known to show dynamic covalent changes during stress (Bruce et al. 2007).

Earlier studies showed that the DNA methylation influences the various developmental processes. DNA methylation differences were observed in tissue and organ types in soybean and sorghum (Song et al. 2013). Although they supported the association of hypomethylation with higher gene expression nearby the gene, the difference between organ methylation was very little. It is yet unclear whether these were spontaneous in nature or were developmentally controlled DMRs (differentially methylated regions). MSAP revealed lower level of sorghum tissue methylation. Similar results with insignificant methylation changes across seven tissues except for the endosperm have been reported by Zhang et al. (2011). The studies on *A. thaliana*, rice, and maize endosperm showed a genome-wide hypomethylation (Waters et al. 2011).

5.4 Histone Modifications

Another epigenetic mechanism, histone modifications have significant role in various developmental stages of plant (Forderer et al. 2016). In plants, histone modifications are the second major category of epigenetic mechanisms. The histone proteins present in the nucleus exist largely as octameric complexes, which make up the core of the chromatin particle around which most DNA is wrapped, forming a three-dimensional histone/DNA complex. Individual isoforms of histone monomers can also be swapped in and out of the octamer, a regulatory mechanism referred to as histone subunit exchange. Subunit exchange and post-translational modifications trigger either increases or decreases in transcription, depending upon the particular modification, the particular histone isoform involved, and even the context of other histone modifications in which the modification resides. A histone code concept aroused from these mechanisms, wherein modifications of histone are interpreted in situ as a combinatorial code regulating gene transcription rates at specific loci across the genome.

In order to modify transcriptional readout of the associated gene, the modifications of histones control these structures. According to Engelhorn et al. (2014) histone modifications refer to modifications on the N-tails of nucleosomal histones which consist of ubiquitination, phosphorylation, methylation, biotinylation, sumoylation, and acetylation on specific serine, arginine, threonine, and lysine residues. DNA associated developments are controlled only by histone post-translational modifications. Li et al. (2014b) stated that the histone tail modifications were the major control point for determination of chromatin structure and gene regulations. The chromatin change occurred due to modifications of these chemicals which lead to operation of chromatin, i.e., closing and opening and ultimately transcriptional regulations (Allis and Jenuwein 2015). Different developmental stages of plants such as response to stimuli, flower initiation, and development of seed are due to modifications of histones (Gallusci et al. 2016; Banerjee and Roychoudhury 2017). Chen et al. (2010) stated that ubiquitination, acetylation, and phosphorylation of histone tails are linked with gene activation and processes of biotinylation and de-acetylation are linked with gene inactivation. According to Law and Jacobsen (2010) methylation in histones is reported to control both activation and deactivation gene expression. The transcription and regulation of gene is affected by a number of methyl groups, sites, and degrees added to arginine and lysine residue (Ding et al. 2012). For example, in *Arabidopsis,* genes are inactive when H_3 methylation occurs at K9 and K27, and methylation of histone H3 at K4 and K36 is associated with actively transcribed genes (Nakayama et al. 2001; Li et al. 2012).

5.4.1 Histone Modifications Under Stress

The histone modifications lead to chromatin accessibility particularly in the promoter region of the gene, such as methylation or acetylation (Berger 2007; Kouzarides 2007). Expression changes in stress-responsive genes are due to modifications of histones which are transient in nature and response differentially under stress conditions (Zong et al. 2013). Zong et al. (2013) correlated the modifications of histones with induction of transcription genes under water stress conditions in rice plant. Another report by Tsuji et al. (2006) stated that in rice plant under submerged conditions acetylation increase of H_3 marks was associated with stress specific genes. Hu et al. (2012) specified that the increase of H_3K9ac, a mark of histone acetylation reported in the heterochromatic chromatin knobs, was correlated with the increase in transcription, whereas H_3K9me2 was associated with the decrease in transcription. They further stated that these changes occurred with the reduction of different levels of DNA methylation.

5.5 Noncoding RNA

The opening and closing of chromatin occurred due to noncoding RNAs such as either long nc RNAs or small RNAs (siRNAs and microRNAs miRNAs) which is associated with gene silencing and activation, respectively. In general, ncRNAs function to regulate gene expression at the transcriptional and post-transcriptional level. Those ncRNAs that appear to be involved in epigenetic processes can be divided into two main groups: the short ncRNAs (<30 nts) and the long ncRNAs (>200 nts). Three major classes of short noncoding RNAs are microRNAs (miRNAs), short interfering RNAs (siRNAs), and piwi-interacting RNAs (piRNAs). Both major groups are shown to play a role in heterochromatin formation, histone modification, DNA methylation, and gene silencing. Law and Jacobsen (2010) stated that the sequence-specific methylation is caused by double stranded RNA (ds-RNA) molecules and RNA-directed DNA methylation (RdDM). RNA interference (RNAi) is interrelated with the RdDM which is involved in the methylation of cytosine (Wassenegger et al. 1994; Meister and Tuschl 2004). In eukaryotic nuclear plants, miRNAs are small noncoding RNA structures which functions in RNA silencing and post-transcriptional regulation of gene expression (Lee et al. 1993; Maxwell et al. 2012). Xu et al. (2013) stated that eukaryotic plants have distinct classes of siRNAs, such as natural antisense siRNAs, heterochromatic-siRNAs, and trans-acting siRNAs and the siRNAs are facilitating gene silencing through methylation of histone and RdDM (Mosher et al. 2008). In crop plants and *Arabidopsis* a number of small RNAs have been identified by large-scale genome-wide and gene-specific studies. It has been observed that the siRNAs and small RNAs–miRNAs played a significant role in different developmental stages of plant under various environmental stress conditions. Bologna (2014) indicated that small RNAs control the regulation of genes which could be inherited under abiotic stress conditions.

5.5.1 Noncoding RNA Under Stress

The crop plant growth and productivity are reduced under biotic and abiotic stresses such as drought, heat, cold, and infections due to fungal, bacterial, and viral disease. To survive under these stresses, plant cell utilizes multi-gene regulation systems. Emerging evidence has revealed that ncRNAs play a critical role in the regulation of gene expression in response to stress conditions. Numerous novel antisense transcripts are accumulated due to abiotic stresses which are the major source of siRNAs (Zeller et al. 2009). Hc-siRNAs (heterochromatic-siRNAs), siR441, and siR446 were found to be downregulated under abiotic stresses but show an increase in the creation of their precursors, entailing that the processing of siRNA precursors is inhibited that seems to be a mechanism of regulation due to stress responses (Yan et al. 2011).

The miRNAs play an important under abiotic stress resistance particularly under cold, heat, salinity, etc. Twenty-six new miRNAs showed upregulation or downregulation under abiotic stress in the small RNA analysis of *Arabidopsis* seedlings (Sunkar and Zhu 2004). In *Oryza sativa* under cold stress the miR319 was found to be downregulated, whereas upregulation of miRNAs was observed under cold stress in *Brachypodium* (Lv et al. 2010; Zhang et al. 2009). The salt and alkali stress tolerance enhanced due to overexpression of miR396 in rice and *Arabidopsis* (Gao et al. 2010); moreover, in these plants the miRNA concentration deviation was observed in response to stress (Gao et al. 2010).

5.6 Epigenetical Interventions in Cereal and Legume Crops

Cultivated crop plants are frequently exposed to stresses such as drought, cold stress, temperatures, heat, salinity, light intensity, cold stress, etc. These abiotic stresses distort growth of plant and ultimately reduced crop productivity. The transcriptional and post-transcriptional levels, including the epigenetic regulation of genes changes, are involved to cope with these stresses (Singh et al. 2015). Most of the abiotic stresses such as drought tolerance, salinity tolerance, and heat tolerance are controlled by the multiple gene action. It has been observed that transcriptional and post-transcriptional control of gene expression is controlled by siRNA, chromatin modifications, and DNA methylation (Angers et al. 2010). The epigenetic variations are also showing heritable variation for controlling these complex traits (Richards 2011). Epigenetic mechanisms have been associated with the regulation of stress-associated genes (Chinnusamy and Zhu 2009). As epigenetic regulation of gene expression can influence important crop traits and the creation of stably inherited epigenetic diversity could be a very powerful tool in crop improvement. Most known epigenetic variants are associated with loss of DNA methylation and correspond to gain of function variants. No direct link for phenotypic variation due to epigenetics has been detected so far, this does not mean that they do not play a role. In crops the number of examples of epigenetically controlled traits is increasing steadily (Table 5.1). Over the last two decades, significant variations in epigenetic phenotypes in plants have been recognized. A generator of epialleles, DNA methylation, could have important implications for the cereal and legume crops improvement against abiotic stresses. The following are some of the important cereal and legume crops in which epigenetical changes play an important role in against stresses.

Table 5.1 Examples of cereal and legume crops affected by epigenetics

Plant species	Type of stress	Epigenetics effect	Observations	References
Oryza sativa	Salt	T rDNA chromatin decondensation + genome-wide DNA methylation	Reduction in crop yield	Santos et al. (2011)
	Water-deficit	T H3K4me3 regarding the dehydrin genes	Reduction in crop yield	Zong et al. (2013)
	Submergence	T H3ac regarding the ADH1 and PDC1 genes	Reduction in crop yield	Tsuji et al. (2006)
	Cold tolerance	PCF5/PCF8	Reduction in crop yield	Yang et al. (2013)
		Hypermethylated in metastable Epi-d1	Reduction in plant height	Le et al. (2014)
	Osmotic	Genome-wide DNA methylation	Reduction in crop yield	Zhang et al. (2013)
	Salt stress	Demethylation at promoter region of *OsMYB91* gene and rapid histone modifications at *OsMYB9* locus	Reduction in crop yield	Zhu et al. (2015)
Triticum aestivum	Drought tolerance	miR170 miR171 miR172	Reduction in crop yield	Zhou et al. (2010)
	Heat	T rDNA chromatin decondensation	Reduction in crop yield	Santos et al. (2011)
	Heat stress	Increased histone demethylation of the various genes	Reduction in crop yield	Wang et al. (2016)
	Salt stress	Hypermethylation of cytosines at *HKT* genes	Reduction in crop yield	Kumar et al. (2017)
Zea mays	Cold	+ Genome-wide DNA methylation; nucleosome remodeling at tandem-repeat sequences with a: + DNA methylation; T H3K9ac; + H3K9me2	Reduction in crop yield	Steward et al. (2002)
	Cold	Differentially methylated	Reduction in crop yield	Shan et al. (2013)
	Cold	Methylated in rice/differentially methylated	Reduction in crop yield	Shan et al. (2013)
	Drought tolerance	PDH, POK, MAPK, PLD	Reduction in crop yield	Wei et al. (2015)
	Drought tolerance	11 different miRNA are upregulated under drought exposure	Reduction in crop yield	Kantar et al. (2011)
Hordeum vulgare	Terminal drought	Hc-siRNA-mediated hypermethylation at *CYTOKININ-OXIDASE 2.1* promoter	Reduction in crop yield	Surdonja et al. (2017)
	Drought tolerance	NFY-A	Reduction in crop yield	Ferdous et al. (2016)

(continued)

Table 5.1 (continued)

Plant species	Type of stress	Epigenetics effect	Observations	References
Glycine max	Drought tolerance	GmNFYA3	Reduction in crop yield	Ni et al. (2013)
Phaseolus vulgaris	Drought tolerance	NAF transcription factor ARF10	Reduction in crop yield	Sosa-valencia et al. (2016)
Vicia faba	Drought tolerance	Increased demethylation of *LOX, CDPK, ABC, GH,* and *PEPC* genes	Reduction in crop yield	Abid et al. (2017)
Vigna unguiculata	Drought tolerance	Transferase family protein leucine repeat rich transmembrane protein	Reduction in crop yield	Barrera-Figueroa et al. (2011)
Cicer arietinum	Drought tolerance	BHLH23 ERF/AP2	Reduction in crop yield	Hajyzadeh et al. (2015)
Macrotyloma uniflorum	Drought	DNA methylation dynamics	Reduction in crop yield	Bhardwaj et al. (2013)
Cannabis sativa	Cold	Methylome variation (locus-specific methylation and deacclimation)		Mayer et al. (2014)

5.6.1 Rice

Rice (Oryza sativa L.) is one of the most important staple food crops and is a primary source of food for world's population (Wang et al. 2018). Unfortunately, it is sensitive to climate changes, which leads to significant reduction in productivity. Genetic studies have been making great efforts to improve rice ability to handle environmental stresses (Jagadish et al. 2012). Epigenetic modification is controlled by epigenetic pathways, and mutations involved in disturbing the epigenetic pathways. This may lead to significant epigenetic and/or genetic changes. Due to epigenetic mechanisms and epigenomic variations accumulated during the long history of selection contribute to adaptation during the domestication of important crops like rice. Epigenetic regulations have been dissected in great detail in A. thaliana, but are still poorly characterized in rice (Deng et al. 2016). This is especially true for rice, whose genome is rich in epigenetic modifications and transposable elements (TEs) that are generally epigenetically silenced. This genetic variation awaits to be exploited for their potentials in generating a heritable source of variation for rapid environmental adaptation, which may hold tremendous importance for rice improvement under abiotic stresses.

The productivity in rice is influenced by extreme temperature, drought, cold, salinity, etc., and at various levels gene expression is involved in abiotic stress responses in different genotypes which could explain the resistant phenotype (Garg et al. 2015). In addition, Wang et al. (2016) showed that under the influence of DNA methylation a stable methylome has been observed in a drought resistant genotype compared to a drought-sensitive genotypes. Zheng et al. (2017) stated that drought-induced epimutations are non-random and are inherited from one generation to another generation (Zheng et al. 2017). Recently, studies showed the DNA methylation patterns are affected in rice when the crop is exposed to heavy metals or pesticides in soil (Feng et al. 2016). Rice, whose genome is rich in epigenetic modifications and TEs (Chen and Zhou 2013; Song and Cao 2017), epigenetic pathways disturbance may dramatically change the epigenetic profile, and could therefore lead to phenotypic variation (Li et al. 2014a, b; Song and Cao 2017). The phenotypic impact of epigenetic changes in rice may be significantly amplified by TEs via creating both epigenetic and genetic variation (Song and Cao 2017). Now many genes involved in the pathways of establishing, maintaining, and removing DNA methylation, which is the most well-studied epigenetic marker so far, have been identified (Lanciano and Mirouze 2017).

Epigenetic pathways are relatively conserved between different plant species (Chen and Zhou 2013). In rice, *de novo* establishment of DNA methylation is carried out by the RNA-directed DNA methylation (RdDM) pathway (Lanciano and Mirouze 2017). During RdDM, small interfering RNAs (siRNA) are first produced, via several steps, from the target locus, and they then, with the help of a set of proteins, head to the target locus, where the target locus gets eventually methylated by an enzyme that is called “domain rearranged methyltransferase” (DRM) (Lanciano and Mirouze 2017). There are three DRM-encoding genes that have been identified in rice so far, *OsDRM2*, *OsDRM1a,* and *OsDRM1b*, with the last two not being expressed (Moritoh et al. 2012). The RdDM takes on two different forms in plant: canonical and non-canonical. The main difference between these two forms lies in the production of siRNA. Canonical RdDM is a proactive *de novo* methylation process, during which siRNAs production starts from the transcription of target locus by RNA polymerase IV (POL IV) (Lanciano and Mirouze 2017). Wendte and Pikaard (2017) reported that the non-canonical RdDM is a passive remedial strategy which takes action when regular transcription of the target locus has already occurred, and mRNAs produced via regular transcription processed into siRNA (Lanciano and Mirouze 2017).

Plant DNA methylation can be maintained by different mechanisms depending on the sequence context (Zhang et al. 2018). In rice, CG methylation is mainly maintained by the methyltransferase OsMET1-2 that is a possible ortholog of the mammalian DNMT1 enzyme (Lanciano and Mirouze 2017). DNMT1 recognizes hemi-methylated CG during DNA duplication and methylates the unmethylated cytosine in the newly synthesized daughter DNA strand (He et al. 2011). Apart from OsMET1-2, another methyltransferase, OsMET1-1, has also been identified in rice, and OsMET1-1 may have a minor and/or redundant role in maintaining the CG methylation (Lanciano and Mirouze 2017). The maintenance of rice CHG methylation is mostly the responsibility of the plant specific chromomethyltransferase OsCMT3a (Lanciano and Mirouze 2017). The rice chromomethyltransferase (OsCMT2) has also been identified; however, the function of OsCMT2 is still unknown (Lanciano and Mirouze 2017). Rice CHH methylation is mainly maintained by OsDRM2 (Tan et al. 2016) that is also involved in the RdDM pathways (Pang et al. 2013). The *A. thaliana* ortholog of OsDRM2, DRM2, maintains CHH methylation through RdDM at RdDM target regions that include certain transposons and repeat sequences (He et al. 2011). Two rice chromatic remodeling proteins OsDDM1a and OsDDM1b lead DNA methylation. The chromatic remodeling proteins OsDDM1a/b act at CG and CHG methylation within both euchromatins and heterochromatins (Tan et al. 2016).

5.6.2 Maize

Maize (*Zea mays* L.) is another important staple food crop besides a model plant used for genetics, genomics, and other fundamental research (Bennetzen and Hake 2009). In maize, during seed development, gene expression is under epigenetic control (Berger and Chaudhury 2009). At early seed development stages, epigenetic mechanism plays a significant role in escaping the drought (Lu et al. 2013). In comparison to *Oryza spp.* and *Arabidopsis,* maize endosperm is hypomethylated and all three plant species, i.e., rice, maize, and *Arabidopsis,* have similar pattern for CG methylation (Zemach et al. 2010a; Cokus et al. 2008). The CHG and CHH methylation had significant differences between the plant species. In maize seeds sequence differentiation occurred among the plant species due to variation in the methylation-regulated transcription (Lu et al. 2015).

Significant variations in epigenetic phenotypes in maize plants have been recognized over the last two decades. Heritable epialleles are considered as a source of polymorphism and may have significant implications in crop improvement. Data show that F1 hybrids of maize are in general less methylated than their parental inbreds. Tani et al. (2005) explained the role of methylation in the expression of maize genes and performance of hybrids under different growth conditions with maize inbreds and hybrids. Repeated selfing for the isolation of inbreds, with emphasis on combining ability of inbreds, leads to gradual accumulation of methylated sites, which get released and/or when the inbreds are crossed to generate hybrid. Stressful growth conditions result in more methylated DNA, and such stress-induced methylation and suppression of genome activity could be at the core of higher yield of the hybrid (Kumar and Bhat 2014).

5.6.3 Wheat

Wheat is one of the most important cereal crops having global production of more than 700 million tonnes which provides 20% of the daily protein requirements, and calories for 4.5 billion people globally (Arzani and Ashraf 2017). Productivity of crop plants under abiotic stress such as salt is lagging behind because of limited knowledge about epigenetic and molecular mechanisms in wheat plant. Salt stress affects metabolic processes in plants through impairment of water potential of cells, ion toxicity, membrane integrity and function, and uptake of essential mineral nutrients (Arzani and Ashraf 2016). The stress perception and signaling has been complemented with the stress-induced biochemical, physiological, and epigenetic changes (Kumar and Singh 2016; Kumar et al. 2017). The information about the biochemical, physiological, molecular, and epigenetic aspects of salt tolerance will not only be helpful in cloning of the genes involved in salt tolerance, development of transgenics, and better breeding programs, but also in screening germplasm toward breeding for saline conditions (Sairam et al. 2002).

The stress is sensed through cell membrane, transduced to various inducers to regulate structural and molecular alterations including H_2O_2 accumulation, induction of transcription factors, and molecular and epigenetic regulation of gene expression through transcriptional and/or translational reprogramming for protective defense mechanism (Kumar et al. 2017). Alleles/epialleles for the differentially expressed genes can be identified from the salt-tolerant genotype and validated in EpiRILs/mapping populations for their possible use in the stress wheat breeding program. Increasing evidences suggest the key role of genetic background and epigenetic changes in regulating expression of the stress-associated genes (Kumar et al. 2017). Expression level of HKTs regulated through genetic and epigenetic mechanisms rationalized the observed responses of wheat genotypes. Better understanding about the structural, functional, and regulatory control of HKTs may enable further improvement in salt tolerance of plants in future, and development of more salt-tolerant wheat crop varieties (Kumar et al. 2017).

5.6.4 Legumes

Legume crops play an important role in improving agricultural sustainability through increasing nitrogen use efficiency and enhancing soil fertility. Grain legumes being an important source of nutrition particularly protein for poor consumers and farmers suffers from various stresses. Hence, there is a need for novel approaches to develop improved versions of legume cultivars that are able to cope with a range of environmental stressors. Next-generation technologies are providing the tools that could enable the more rapid and cost-effective genomic and transcriptomic studies for most major legume crops, allowing the identification of key functional and regulatory genes involved in abiotic stress resistance. Therefore, it is essential to intensify legume improvement programs by using advanced breeding approaches and techniques, to develop new high-yielding legume cultivars that are able to cope with a range of environmental stresses.

5.6.4.1 Cowpea

Cowpea (*Vigna unguiculata*) is a good model crop for studying drought tolerance. Although microRNAs (miRNAs) play an important role in plant abiotic stresses in legumes like cowpea, Barrera-Figueroa et al. (2011) studied the role of miRNA and their associates in drought-tolerant genotypes. Earlier, it was not understood how miRNAs might contribute to different capacities of drought tolerance in different cowpea genotypes. The drought-associated microRNAs have been identified in cowpea genotypes (Barrera-Figueroa et al. 2011). A deep sequencing of small RNA reads was generated from two cowpea genotypes of a drought-sensitive and drought-tolerant that grew under well-watered and drought stress conditions. Barrera-Figueroa et al. (2011) reported that the miRNA expression was inconsistent in cowpea genotypes. They found that nine miRNAs were predominantly or exclusively expressed in one of the two genotypes, whereas some of the miRNAs were drought-regulated in only one genotype. They suggested that miRNAs may play important roles in drought tolerance in cowpea and may be a key factor in determining the level of drought tolerance in different cowpea genotypes.

5.6.4.2 Hemp

Hemp (*Cannabis sativa*) is one of the important crops which enhance the soil fertility. But this crop also suffers from various stresses like cold, temperature, drought, etc. The capacity to tolerate cold stress for adaptation in hemp plant is controlled under the molecular and epigenetic mechanisms. The molecular mechanisms underlying cold adaptation in hemp revealed higher levels of complexity of genetic, epigenetic, and environmental factors (Meyer et al. 2013). They reported that the hemp genotypes accumulated soluble sugars under cold stress which could be maintained at higher levels under this stress. These genotypes acclimated the most efficiently accumulated transcript levels of *COR* genes involved in *de novo* DNA methylation. Furthermore, these hardy hemp genotypes displayed significant increases in methylcytosine levels at *COR* gene loci when deacclimated, suggesting a role for locus-specific DNA methylation in deacclimation (Mayer et al. 2013).

5.6.4.3 Faba Bean

Faba bean (*Vicia faba* L.) is consumed as food for humans and animals because of its high content of protein. It plays a significant role in fixation of nitrogen through symbiotic relations. Numerous workers described the significant role of epigenetic in a plant under abiotic stress response. The histone modifications, sRNAs, DNA methylation, or longer noncoding RNAs are involved in epigenetic gene regulation, including chromatin regulation mediated (Meyer 2015). Under drought conditions it showed a high degree of correlation between changes in DNA methylation and gene expression DNA methylation modifications in faba bean cultivars, suggesting a possible role of DNA methylation in faba bean in response to drought tolerance. Abid et al. (2017) stated that the expression pattern of drought stress response genes is influenced with DNA methylation. They identified potentially drought stress-related differentially methylated regions (DMRs) and provided a basis for further studies into the role of epigenetic regulation of faba bean responses to drought stress and other environmental stresses. High homology to various putative proteins has been observed which can be chosen for further characterization. Under drought stress conditions of faba bean the genome-wide epigenetic changes occurred in response to the stress (Abid et al. 2017).

5.6.4.4 Common Bean

Common bean (Phaseolus vulgaris L.) is known as grain of hope throughout the world as it is an important component of agriculture and feeds about 300 million people in tropics and 100 million people in Africa alone. It is rich in proteins, carbohydrates, micronutrients, and vitamin A and represents an important source of dietary protein for humans and animals. Micronutrient plays an important role in both animals and plants. Both iron and zinc deficiencies are the major problems faced by public health sector in the world. It is possible that common bean and other legumes may have particular strategies for gene regulation under stress conditions. It has become clear in recent years that many stress responses involve epigenetic components and we are far from understanding the mechanisms and molecular interactions. The recent description of the common bean genome (Schmutz et al. 2014; Vlasova et al. 2016) will provide invaluable knowledge for future PTGS studies. The knowledge of post-transcriptional regulation in common bean is mediated by the legume-specific miR1514a induced during drought stress (Sosa-valencia et al. 2016). miR1514a targets the transcript encoding NAC family of transcription factors, through cleavage and subsequent generation of secondary phasiRNAs. This process occurs during the exposure of adult plants to drought stress. Furthermore, based on an RNA-seq strategy downstream regulatory targets of the transcription factor NAC 700 were observed (Sosa-valencia et al. 2016). miR1514a is a legume microRNA that is induced in response to drought stress in common bean and shows differential accumulation levels in roots under drought stress conditions. The degradome analysis revealed that miR1514a targets the transcripts of two NAC transcription factors (TFs), Phvul.010g121000 and Phvul.010g120700. Furthermore, expression studies and small RNA-seq data indicate that only Phvul.010g120700 generates phasiRNAs, which also accumulate under drought conditions. They determined the functionality of NAC-derived phasiRNA associates with ARGONAUTE 1 (AGO1). In addition, a transcriptome analysis of transgenic hairy roots with reduced miR1514a levels revealed several differentially expressed transcripts involved stress responses which are regulated by the NAC TF and/or by phasiRNAs. They also demonstrated the participation of miR1514 in the regulation of a NAC transcription factor transcript through phasiRNA production during the plant response to drought stress (Sosa-valencia et al. 2016). Moreover, the manipulation of the epigenetic processes involved in abiotic stress are key points in order to improve future plant breeding and crop productivity of legumes.

5.7 Conclusions

Epigenetic changes modify the activation of certain genes, but not the genetic code sequence of DNA which causes activation or silencing of gene expression. Under drought stress conditions, the defense mechanisms of a plant such as cellular pathways, morphological adaptations, inherent immunity, and specific signaling molecules are controlled by stress-responsive genes by transcribing and translating specific genes. The regulation of the expression of stress-responsive genes due to DNA modifications, chromatin alterations, and small RNA-based mechanisms provide another defense mechanism for plants under stress conditions. The epigenetic control in response to various abiotic stresses is now available due to rapid progress in high-throughput techniques and NGS in model and crop plants. The techniques such as methyl chip-on-chip and MSAP provide wealth of information for whole genome cytosine methylation changes in crops. These techniques have been used in various crops like maize, rice, wheat, and legumes to study methylation dynamics of the regions associated with transposable elements in response to abiotic stresses. Epigenetic can constitute another genetic engineering tool to be applied for defense mechanism in plant species under various environmental stresses. In future, epigenetics may be an important and alternate tool to develop transgenic plants to combat the abiotic stresses.

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