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Plant epigenetic mechanisms: role in abiotic stress and their generational heritability

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Abstract

Plants have evolved various defense mechanisms including morphological adaptations, cellular pathways, specific signalling molecules and inherent immunity to endure various abiotic stresses during different growth stages. Most of the defense mechanisms are controlled by stress-responsive genes by transcribing and translating specific genes. However, certain modifications of DNA and chromatin along with small RNA-based mechanisms have also been reported to regulate the expression of stress-responsive genes and constitute another line of defense for plants in their struggle against stresses. More recently, studies have suggested that these modifications are heritable to the future generations as well, thereby indicating their possible role in the evolutionary mechanisms related to abiotic stresses.

Keywords Abiotic stresses · Adaptations · DNA methylation · Epigenetic mechanism · Plant populations

Introduction

Abiotic stresses in crop plants constitute one of the serious threats to food security causing reduction in crop productivity leading to economic losses. The regions that faced abiotic stress (heat stress) year after year were most affected, as farmers have reduced total area under cultivation. Abiotic stresses lead to a series of complex changes at molecular, biochemical and physiological levels that culminate into morphological changes affecting crop yield and productivity (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).

Alterations in DNA sequence as a result of mutations leads to trait variation that plant breeders often use to estimate heritability and improve trait performance among the plant populations. In addition to DNA sequence variations, findings have also suggested that plant response to stresses can be attributed to the changes in chromatin states (Gehring and Henikoff 2007). The chromatin structures can be modified rapidly and reversibly by the insertion of methyl groups (Chinnusamy and Zhu 2009). Such modifications that alter expression of genes without disturbing its nucleotide sequence are referred to as epigenetic changes (Madlung and Comai 2004).

The concept of epigenetics has its roots in the ancient theory of epigenesis proposed by Aristotle to condemn the theory of perforation. However, the modern concept of epigenetics was developed in twentieth century by Waddington (1942) in the proposed model of "Epigenetics Landscape" (Tsaftaris et al. 2007). In the present context "epigenetics refers to both heritable changes in gene activity and expression (in the progeny of cells or of individuals) and also stable, long-term alterations in the transcriptional potential of a cell that are not necessarily heritable" (NIH "Roadmap Epigenomics Project 2013"). These changes are either mitotically stable or may be meiotically heritable for several future generations despite the fact that they do not cause any change in the core DNA sequences of an organism (Bird 2007; Bonasio et al. 2010). In the recent years, both genetic and biochemical studies have enhanced our knowledge of various epigenetic processes that involved DNA

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methylation, histone modification and RNA-mediated gene silencing. These processes are correlated with each other as DNA methylation is required for chromatin modifications and vice versa, while RNAi-based mechanisms regulate both the processes (Fig. 1) (Hidetoshi et al. 2012).

Epigenetic mechanisms play an essential role in gene expression regulation in response to environmental stresses in plants (Boyko and Kovalchuk 2008; Pontvianne et al. 2010). Abiotic stresses like temperature, day length, UV, water, salt, and oxidative stresses in plants cause modifications in the (de)methylation pattern at coding region of some stress-responsive genes and regulate their expression (Beck et al. 2004; Pecinka et al. 2009; Boyko et al. 2010b; Zemach et al. 2013; Fang et al. 2014; Xie and Yu 2015). Though these modifications can be specific to tissue, species, organelle or age of an organism (Bhutani et al. 2011); the mechanisms involved need to be studied thoroughly to produce plants for future that are engineered with the ability to have minimal effect of a stress. In this review, efforts have been made to discuss the recent advances and mechanisms related to epigenetics that are involved in abiotic stress and their generational heritability.

Master regulators of epigenetics at molecular level

Modifications at the genomic (DNA methylation) and chromatin (histone modifications) levels have so far been the focus of research into the mechanism of epigenetics that regulate expression of a gene. Of late, the RNA-directed DNA methylation (RdDM) has also been shown to be involved in the methylation of homologous loci in a genome. Together, all three mechanisms have been involved in the regulation of gene expression.

DNA methylation

Enzyme catalyzed transfer of a methyl moiety from S-adenosyl methionine to 5th position of the cytosine residue of DNA (converting it to 5-methylcytosine often referred as

Fig. 1 Relationship among molecular mechanisms involved in DNA modifications

^{5m}C) brings about a conserved and sometimes heritable modification that results into an epigenetic event also termed as DNA methylation. The ^{5m}C promotes transcriptional repression by preventing the activators from binding to their target sites. The transcriptional regulation of genes serves as an adaptation towards different stresses. The degree of gene regulation depends upon the intensity and duration of stress (Urano et al. 2010). These classes of plant adaption towards different stresses that occurs by modifying the DNA methylation blueprint can be termed as DNA Methylation Mediated Adaptations (DAMMS). DAMMS depends upon the degree of ^{5m}C in plants which ranges from 4 to 37 percent depending upon the species (Steward et al. 2000). The total ^{5m}C content of a plant genome correlates with the repetitive content of a genome (Bender 2004). The majority of methylated residues in plants are found in repetitive sequences harbouring heterochromatin regions, but few genes have also been reported to undergo methylation in euchromatin region (Saze et al. 2012).

DNA methylation in plants can be grouped into two types: symmetrical (CG or CNG) and non-symmetrical {CNN (N = A, C or T)}. The symmetrical (CG and CNG) methylation pattern are easily-copied after DNA replication while non-symmetrical (CNN) methylation has to be established de novo after each cycle of DNA replication (Karlsson et al. 2011). In Arabidopsis, dense CG methylation clusters scattered throughout the genome have been reported (Cokus et al. 2008).

DNA methylation is catalysed by a family of conserved DNA methylases (MTases) that are categorised into two groups depending upon the establishment of DNA methylation pattern: (1) maintenance MTases, which are able to maintain and transmit stable ^{5m}C patterns through consecutive generations, and (2) de novo MTases, that can transfer methyl groups to unmethylated cytosines, include Methyltransferase 1 (MET1), Chromomethylase 3 (CMT3) and domains rearranged methylase (DRM) (Sahu et al. 2013). MET1, an homologue of the mouse Dnmt1 (DNA methyltransferases 1) most likely function as maintenance methyltransferases, but may also play a role in de novo methylation. The *Arabidopsis* MET1 gene, a member of a small multigene family, preferably methylates cytosines in CpG sequences (Zemach et al. 2010). The CMT3 methylates CpNpG sequences particularly in centromeric repeats and transposons (Henikoff and Comai 1998). These methyltransferases transmit the symmetric methylation (CpG and CpNpG) imprints on the parental DNA (Bond and Baulcombe 2014). DRM, a homologue of Dnmt1 in plants includes three types of DNA methyltransferases; DRM1, DRM2 and DRM3. DRMs catalyse de novo methylation of cytosine at asymmetrical CpNpNp sites (Cao and Jacobsen 2002; Takuno and Gaut 2012). Both DRM2 and DRM3 have been reported to controls RNA-directed DNA methylation
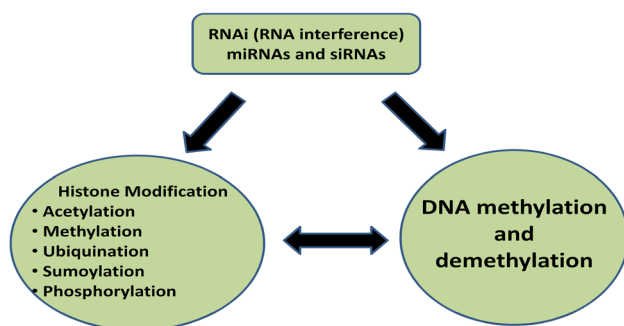
via a pathway that regulates plant-specific RNA Polymerase V in Arabidopsis (Grativol et al. 2012; Xuehua et al. 2014).

Demethylation of cytosines is equally important as it brings modified sites back to their native state and therefore affecting gene expression. The removal of methyl group from cytosines is mediated by either passive or active mechanism. Incorporation of unmodified cytosines, which may be due to the loss of activity of maintenance DNA methylases, i.e., MET1 and CMT3, during DNA replication, refers to as passive mechanism (Zhu 2009). As a result of the enzyme inactivity, there is a progressive loss of DNA methylation in the subsequent generations (Ibarra et al. 2012). Active DNA demethylation involves a base excision repair pathway undertaken by various DNA methylases which possess either only glycosylase activity (monofunctional DNA glycosylase) or both glycosylase and lyase activity (bifunctional DNA glycosylase). The ^{5m}C is removed as a free base and a single base gap left behind is filled by a non-methylated cytosine by DNA polymerase and ligase (Agius et al. 2006; Bhutani et al. 2011). The target sequences for demethylation are identified by demethylases either by sliding on the DNA molecule or as a result of interaction with the repressor of silencing (ROS) 1 complex (Ponferrada-Marin et al. 2012). Four DNA demethylases have been reported in *Arabidopsis* and these include Repressor of Silencing 1 (ROS1), DEMETER (DME), DEMETER-LIKE (DML2) and DML3 (Gong et al. 2002; Ortega-Galisteo et al. 2008). These DNA demethylases also prevent the formation of stable hypermethylated epi-alleles in plant genomes and thus maintain equilibrium between methylated and unmethylated DNA (Penterman et al. 2007).

Histone modifications

Post-translational modifications of histones (acetylation, ubiquitination, biotinylation, methylation, sumoylation and phosphorylation) are key regulator of DNA-associated processes. The histone protein is an octamer with two copies each of histone 2A (H2A), histone 2B (H2B), histone 3 (H3) and histone 4 (H4). The amino acid residues on H3 and H4 are more prone to modifications due to the protruding end of N-terminal tail that is easily accessible to modifying enzymes. The histone tail modification is a key control point in determining chromatin structure and gene regulations (Eichten et al. 2014). While phosphorylation, acetylation and ubiquitination of histone tails are associated with gene up-regulation, the processes of de-acetylation and biotinylation are associated with gene down-regulation (Chen et al. 2010). Histone methylation is one of the most important covalent modifications, as it has been reported to affect both up- and down-regulation of gene expression (Law and Jacobsen 2010). Gene expression can be affected by site, degree and number of methyl groups that are being

added to the lysine and arginine residue (Ding et al. 2012). In *Arabidopsis,* methylation of histone H3 at K4 and K36 is associated with actively transcribed genes, whereas H3 methylation at K9 and K27 is predominant at constitutively condensed chromatin and developmentally inactive global genes (Nakayama et al. 2001; Li et al. 2012). In case of acetylation, Lys-36 in histone H3 (H3K36ac) is newly discovered to be involved in various chromatin modification in plants (Mahrez et al. 2016).

Extensive enzymatic machinery is involved in histone modifications including histone methyltransferase (HMT), histone de-methylase (HDM), histone acetyltransferase (HAT), and histone de-acetylase (HDAC) as key enzymes (Marmorstein and Trievel 2009; Grativol et al. 2012). Histone methyltransferase (HMT) catalyze the transfer of up to three methyl groups to lysine and arginine residues on histones H3 and H4. Depending upon the domain they enclose in their structure, HMT can be classified as- lysine-specific conserved SET-domain protein family and arginine-specific protein family (Wood 2004; Sawan and Herceg 2010). The lysine-specific conserved SET proteins originally identified in *Drosophila* and are referred to as suppressor of variegation (S̲u-var3-9) (Tschiersch et al. 1994), E̲nhancer of zeste (Ez) (Jones and Gelbart 1993) and T̲rithorax (Trx) (Stassen et al. 1995)—hence the name SET. These domains catalysed the histone lysine methylation (except in H3K79), and have vital effect on the formation of heterochromatin and transcriptional regulation of genes depending upon mono-, di- or tri-methylation of distinct lysine residues (Qian and Zhou 2006). So far, a total of 41 SET-domain proteins encoded by 29 active genes have been reported in *Arabidopsis* (Pontvianne et al. 2010). The identification of putative nuclear localization signals in many SET-domain proteins and crystal structures of the ternary complexes of SET-domain proteins bound to AdoHcy and histone H3 peptides have elucidated beyond doubt their role in chromatin remodelling and epigenetic control over chromatin function (Xiao et al. 2003).

Arginine-specific protein family consists of two different types of methyltransferases; the first type produces mono- and di-methylarginine (asymmetric), while the second type produces mono- and symmetric di-methylarginine. Arginine-specific protein family is also involved in many animal diseases as well (Scaramuzzino et al. 2015). HMT also causes the methylation of both heterochromatin and euchromatin, although heterochromatin is more methylated as compared to active euchromatin. Methylation of H3K9, H3K27, H3K79 and H4K20 that occurs in the heterochromatin region causes the gene silencing while methylation of H3K4 at euchromatin region causes the gene expression (Tsaftaris et al. 2007; Jacob et al. 2014). The silencing and expression of different genes occur in response to different stresses, thus constitutes an important strategy in plants to survive.

Histone demethylases (HDM) remove methyl group from histones and alter transcriptional regulation of a gene by maintaining a control on the methylation level of histones. Shi et al. (2004) reported four histone demethylases in *Arabidopsis* on the basis of conserved domain of human LSD1 (lysine-specific demethylase1). Two classes of HDM were reported to reverse the methylation pattern of lysine. The LSD1 class (lysine-specific demethylase 1) of HDM act on mono- and di-methylated lysines and the LSD2 (Jumonji C) domain de-methylates mono-, di- and tri-methylated lysine by hydroxylation (Metzger et al. 2005; Tsukada et al. 2006). These classes of demethylases are also reported to control the gene expression in the plants under stress (Shen et al. 2014). Histone acetyltransferases (HAT) acetylate conserved lysine on histone proteins by transferring an acetyl group. HAT enzymes are involved in transcriptional activation, generating binding sites for specific protein and in acetylating nuclear receptors proteins to facilitate gene expression in various plant development process (Yuan and Marmorstein 2013; Fang et al. 2014). Histone de-acetylase (HDAC) remove acetyl groups from lysine residue of histone and act in synchronization with histone acetyltransferases to regulate active and reversible histone acetylation which modifies chromatin structure and function thus, controlling multiple cellular processes (Hollender and Liu 2008; Ma et al. 2013).

RNA-directed DNA methylation

Double stranded RNA (ds-RNA) molecules induced sequence-specific methylation to cause de novo methylation, called as RNA-directed DNA methylation (RdDM). In plants, dsRNA structures are generated as intermediates of viral replication intermediates, products of the endogenous RNA-directed RNA polymerase or through transcribed inverted repeats (Law and Jacobsen 2010). RdDM is interrelated with the RNA interference (RNAi) suggesting that small RNAs have a role in eliciting and guiding cytosine methylation (Wassenegger et al. 1994; Meister and Tuschl 2004). Small RNAs are a class of RNAs that do not code for proteins and their function depends on their structure. In plants, small RNAs are classified into- micro RNA (miRNA) and small interfering RNA (siRNA) based on their origin, structure and pathways they regulate. MicroRNAs are small (21–24 nucleotides long) non-coding RNA structures, encoded by eukaryotic nuclear DNA in plants and functions in RNA silencing and post-transcriptional regulation of gene expression (Lee et al. 1993; Maxwell et al. 2012).

Small interfering RNAs are 20–25 nucleotide (nt) long ds-stranded RNA structures that also regulates gene expression at the transcriptional (RNA silencing) and post-transcriptional levels. Plants have distinct classes of endogenous siRNAs, such as: trans-acting siRNAs, natural antisense siRNAs, and heterochromatic-siRNAs (Xu et al. 2013). The siRNAs are responsible for mediating gene silencing through RdDM and histone methylation (Mosher et al. 2008). The RdDM mechanism initiated with the production of single stranded RNAs (ssRNAs) requires as CLASSY1 (CLSY1), a potential chromatin remodelling protein, and DNA-directed RNA Polymerases IV; the ssRNAs are generated from transposons or repeats containing regions (Havecker et al. 2010) by DdR Pol IV a with the help of SHH1 (Sawadee Homeodomain Homolog1) (Law et al. 2013) and DTF1 (DNA-binding Transcriptional Factor1) (Zhang et al. 2013). These ssRNAs are later converted into double stranded RNA (dsRNA) by RDR2 (Fig. 2).

The dsRNAs processed by DICER-LIKE3 (DCL3) and HUA-ENCHANCER1 (HEN1) after methylation of 3′ terminal ends with the help of methyltransferase, are loaded onto the effector protein called Argonaut4 (AGO4). A complex of AGO4 (containing guide RNA strand) and Nuclear RNA Polymerase E1 (NRPE1) subunit of Pol V target guide strand RNA to base pair with gene transcript to be silenced (Law and Jacobsen 2010). The siRNA and associated proteins recruits DNA methyltransferase to catalyze de novo CpNpN-type asymmetric DNA methylation in the promoter regions of PolV transcript (Bologna 2014). These RdDM pathways are biologically important since they control adaptation responses in different stress (biotic and abiotic), maintain genome stability and regulate development (Xie and Yu 2015). However, recent studies also confirmed that RdDM is not always related with the accumulation of corresponding siRNAs (Dalakouras et al. 2015). In the absence of RdDM, asymmetric methylation is lost, while CHG methylation is efficiently maintained by the Maintenance Methyltransferase1 (MET1) and Chromomethyltransferase3 (CMT3), respectively (Dalakouras and Wassenegger 2013).

Though being different, the mode of action exhibited by both miRNA and siRNAs in inhibiting the translation of DNA sequence suggested some kind of relatedness in their biogenesis and mechanism (Carthew and Sontheimer 2009). Both small RNAs—miRNAs and siRNAs play an important role in plant development and the adaptation responses to various biotic and abiotic stresses. Moreover, the gene regulation that are control by these small RNAs could be inherited, thus have gained much consideration as epigenetic processes that are involved in plant stress responses (Bologna 2014).

Epigenetic mechanisms and abiotic stress

The plants have evolved highly regulated yet interdependent mechanisms to adapt and survive under changing environments. The discovery of functional small RNAs (smRNAs), and their role in chromatin remodelling and RNA-directed DNA methylation (RdDM) have allowed for
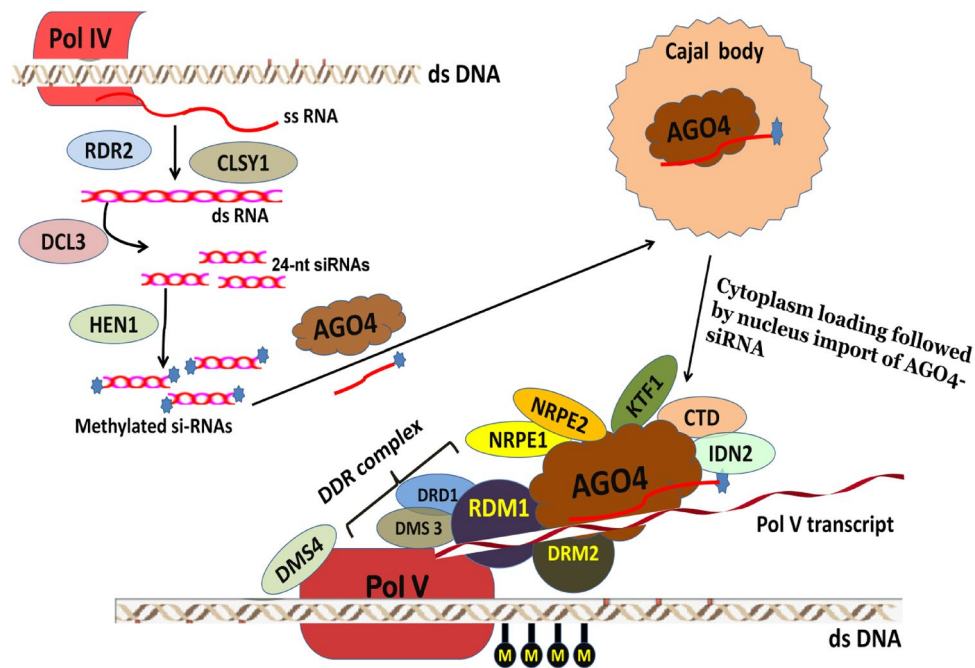
Fig. 2 Schematic illustration of RNA-directed DNA methylation. RNA-directed DNA methylation is initiated by RNA polymerases IV (Pol IV). The single stranded RNA transcript (ss RNA) transcribed by Pol IV is then copied into double stranded RNA (ds RNA) with the help of RNA-DEPENDENT RNA POLYMERASE 2 (RDR2). CLASSY 1 (CLSY1) also termed as CHR38, is a putative chromatin remodeller or helicase that helps in recruiting Pol IV to chromatin or aid in ssRNA transcript processing. DICER-LIKE 3 (DCL3) process the dsRNA into 24-nucleotide small interfering RNA (siRNA) duplexes which are later methylated by HUA-ENCHANCER 1 (HEN1) at their 3′ ends. In the presence of ARGONAUTE 4 (AGO4), ds siRNA dissociates to form ssRNA which associates with AGO4 to form an RNA-induced silencing complex (RISC). AGO4 localizes to Cajal bodies, that seems to be necessary for wild type levels of RdDM33. Independently of siRNA synthesis, Pol V transcrip-tion is assisted by the DDR complex, comprising of DEFECTIVE IN RNA-DIRECTED DNA METHYLATION (DRD1), DEFEC-TIVE IN MERISTEM SILENCING 3 (DMS3), REQUIRED FOR DNA METHYLATION (RDM1) and DMS4. AGO4 binds Pol V transcripts through pairing with the siRNA and is become stable by AGO4 interaction with the NUCLEAR RNA POLYMERASE E1 (NRPE1), NRPE2, carboxy-terminal domain (CTD) and KOW DOMAIN-CONTAINING TRANSCRIPTION FACTOR (KTF1) which also binds RNA. INVOLVED IN DE NOVO 2 (IDN2) is supposed to assist in stabilizing the pairing between Pol V transcript and siRNA. The RDM1 protein of the DDR complex and de novo cytosine methyltransferase DOMAINS REARRANGED METHYL-TRANSFERASE 2 (DRM2) binds to AGO4, bringing them close to Pol V transcribed regions and that results in DNA methylation

a better understanding of the regulatory networks triggered in response to abiotic stresses in plants (Hirayama and Shinozaki 2010).

DNA methylation pattern during abiotic stresses

In response to the abiotic stresses, DNA methylation regulates the gene expression by hindering/suppressing transcription. Changes in DNA methylation contribute significantly to the plants' ability to respond to stresses (Boyko and Kovalchuk 2008). The level of DNA methylation increases (hypermethylation) or decreases (demethylation) in response to a stress. However, the changes in methylation patterns depend on the type of stress response (Bonasio et al. 2010). Mangrove and rice plants grown under high salinity conditions show hypermethylation when compared to plants grown under normal soil conditions (Lira-Medeiros et al. 2010; Karan et al. 2012). Rice genotypes grown under drought condition were predominantly hypermethylated while drought tolerant genotypes were hypomethylated (Gayacharan 2013). In case of tobacco under biotic stress (infection with tobacco mosaic virus (TMV), the hypomethylation results in specific expression of 31 genes, which are related to stress response (Wada et al. 2004). The methylation of CG, CNG and CNN mediated by CMT3 and DRM2 also play differential role in stress conditions. In rice, CG methylation is a feature of genic regions, while non-CG methylation (CHG and CHH) is mostly found in transposable elements (Zemach et al. 2010). As such, tobacco plants when exposed to salt and cold stress in presence of aluminium and paraquat reported CG demethylation in the coding region of NtGPDL (glycerophosphodiesterase-like protein) gene (Choi and Sano 2007). Recently, a new study also supports that modification in various checkpoints of DNA also confers tolerance to Aluminium toxicity (Eekhout et al. 2017). Water deficit condition led to CG hypermethylation

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in pea genome (Labra et al. 2002) while it induced CHG hypermethylation of satellite DNA in halophyte leading to the shifting of the carbon assimilation mechanism form C3 to CAM (crassulacean acid metabolism) (Dyachenko et al. 2006). In certain cases, the hypermethylation got reversed after removal of stress. Kovarik et al. (1997) showed that tobacco cell-suspension cultures under osmotic and salt stress show CHG hypermethylation. However, the hypermethylation was reversed when the cell culture were re-inoculated onto non-stress media. This is contradictory in case of maize where the demethylation pattern did not get reversed when the chilling condition was removed (Steward et al. 2002). The incidence of methylation and demethylation at the genic or non-genic regions also produce a wide variety of affects on the produced transcript. Methylation of promoter and 3′ region of the gene including flanking sequence may inhibit gene expression (Zilberman et al. 2007). The methylation in promoter region is associated with down-regulation of genes; the methylation of genic region exhibits a parabolic relationship with transcription. The methylation is most likely to occur in the genes that are least expressed and the most expressed genes are least likely to be methylated (Zemach et al. 2010).

Transposable elements exhibit different methylation patterns that are involved in the process of providing different adaptations to plants (Cantu et al. 2010). A retrotransposon-like sequence (*Zm*MI1) showed demethylation patterns under cold stress in maize roots (Steward et al. 2000). Severe cold stress led to decrease in methylation status and increased the excision rate of a specific transposon, *Tam3* in *Antirrhinum majus* (Hashida et al. 2006). In earlier studies, stress mediated induction of transposons was reported for *Tos*17 (rice) (Hirochika et al. 1996), *Tnt*1 (tobacco) (Beguiristain et al. 2001) and BARE-1 (barley) (Kalendar et al. 2000). The recent studies have also confirmed that some retrotransposons (*ONSEN*, an LTR-copia type retrotransposon in *Arabidopsis thaliana*) employ demethylation strategies for their activation under heat stress (Cavrak et al. 2014). Thus, apart from methylation and demethylation pattern which genes followed during stress (Deleris et al. 2016), the role of transposable elements is also imperative in providing defense mechanism.

Histone modifications associated with abiotic stress

Histone modifications play a decisive role in both plant development and their responses to stress. Among different modifications, de-acetylation and biotinylation cause repression of genes while acetylation, phosphorylation, and ubiquitination activate transcription of genes (Chen et al. 2010). There are several cases on dynamic alterations of histone tail modifications in response to abiotic stresses in plants. Tobacco plant cells when exposed to salinity, cold

and abscisic acid (ABA) resulted in the phosphorylation, phospho-acetylation and acetylation of H3 Ser10, H3 Ser10 and H4 lys14, respectively (Sokol et al. 2007). This histone modification causes the up-regulation of stress specific genes. In *Arabidopsis,* an increase in acetylation of H3K4 and H3K9 on the coding regions of dehydration responsive genes (Rd29A, RD29B, RD20 and RAP2.4) resulting their activation (Kim et al. 2009). Exposure to UV-B also caused an increase in the acetylation of H3K9/K14 on the promoter of *ELIP*1 in *Arabidopsis* and wheat (Cloix and Jenkins 2008). Chen et al. (2010) also showed that gene expression induced by ABA and salt stress is associated with the induction of gene activation marks, such as H3K9/K14ac and H3K4me3, and the reduction of gene repression marks, such as H3K9me2, at ABA and abiotic stress-responsive genes. *Arabidopsis* plants when exposed to different levels of salt stress showed hypermethylation in the progeny of stressed plants (Boyko et al. 2010b).

Non-coding RNA and abiotic stresses in plants

Apart from the several alterations in histone and DNA due to abiotic stresses, there is plethora of gene regulation instances dependent on small RNA population. These gene regulations serve as an adaptation of plants to various stress mechanisms. Two classes of non-coding RNA; miRNA and siRNA are reported to be often actively involved in the epigenetic modifications when plants are exposed to stress conditions (Chinnusamy and Zhu 2009).

Abiotic stresses induce the accumulation of various novel antisense transcripts, a source of siRNAs and thus implying their role under stress (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). Besides, these siRNA classes, nat-siRNAs (Natural antisense short interfering RNA (nat-siRNA) and ta-siRNAs (Trans-acting siRNA) were also shown to be directly involved in stress response. Under salt stress in *Arabidopsis*, the nat-siRNAs are generated from double strand of overlapping antisense transcription of the gene P5CDH (DELTA-1-PYRROLINE-5-CARBOXYLATE DEHYDROGENASE) that leads to the accumulation of proline (Borsani et al. 2005). The proline is considered as an important metabolite involved in tolerance to salt stress. The ta-siRNAs are involved in the regulation of plant growth under stressful environment (Schwab et al. 2009). Moreover, as siRNA are involved in RdDM they are able to control one-third methylation of genomic loci (Lister et al. 2008). SlAGO4, an important orthologue of AGO4 (core factor of RdDM) also plays an important role under salt and drought stress in

tomato (Huang et al. 2016). iTRAQ analysis in tobacco also confirmed that RdDM has key role in plant defense mechanism against geminivirus infection (Zhong et al. 2017).

Many researchers also reported the involvement of miR-NAs and their role in plant responses to different stresses such as salinity, heat, cold and pathogens. The small RNA analysis of *Arabidopsis* seedlings revealed 26 new miRNAs, either upregulated or downregulated by abiotic stresses (Sunkar and Zhu 2004). The miR319 was found to be downregulated under cold stress in rice (Lv et al. 2010), while several families of miRNAs were upregulated under cold stress conditions in Brachypodium, (Zhang et al. 2009). The over expression of miR396 in rice and *Arabidopsis* plants enhanced tolerance to alkali and salt stress (Gao et al. 2010). These deviations in miRNA concentration correspond to an important regulation of miRNA targets that response to stress tolerance in these plants. A summary of recent research reports indicating the role of different epigenetic mechanisms including DNA methylation, histone modification and RNA-directed DNA methylation involved in various abiotic stresses is given in Table 1.

Heritability of epigenetic mechanisms

Exposure of plants to stress causes formation of epi-alleles that constitutes either transient or stable epigenetic stress memory (Molinier et al. 2006). The transient memory can be reversed upon release of stress, but the stable memory- after the stress has ceased, is maintained during remaining cycles of plant development or inherited to future plant generations contributing to adaptation and evolution of plant (Fig. 3). Moreover, transfer of epigenetic patterns through cell cycles requires rapid reestablishment of epi-alleles after twofold dilution due to replication (Jiang and Berger 2017). Unlike animals, plants establish their germ-line late during development; therefore they could sense stresses during their life and memorize them perhaps by epigenetic mechanisms in cell lineages that later form the germ-line and pass them into their progeny (Lang-Mladek et al. 2010).

The stability of stress memories and the degree and duration of stress that leads to the formation of heritable epi-alleles is still a matter of debate. Rice plants grown under water submergence conditions resulted in an increase in enrichment level of H3K4me3 and decrease in enrichment level of H3K4me2 in the coding region of submergence inducible genes. These alterations in histone were transient and resort to basal levels during re-aeration (Tsuji et al. 2006). *Arabidopsis* when exposed to cold stress, showed a decrease in enrichment level of H3K27me3 mark. This decrease was maintained for up to 3 days after returning to optimum temperature (Kwon et al. 2009). These alterations at the histone levels could not be able to inherit to

Table 1 Epigenetic mechanisms involved in abiotic stresses in different crops

S. no.	Crop species	Abiotic stress	Epigenetic mechanism(s)	References
1.	Barley	Terminal drought stress	Hc-siRNA-mediated hyper- methylation at *CYTOKININ-OXIDASE 2.1* promoter	Surdonja et al. (2017)
2.	Wheat	Salt stress	Hypermethylation of cytosines at *HKT* genes	Kumar et al. (2017)
3.	*Populas*	Drought stress	Hypermethylation of CG and CHG sites than CHH	Liang et al. (2014)
4.	*Beta vulgaris*	Salt stress	Elevated acetylation of H3K9 and H3K27 led to activation of *POX* gene	Yolcu et al. (2016)
5.	Rice	Salt stress	Demethylation at promoter region of *OsMYB91* gene and rapid histone modifications at *OsMYB9* locus	Zhu et al. (2015)
6.	*Arabidopsis*	Salt and drought Stress	Higher histone acetylation (H3K9) in promoter regions of 14 genes	Zheng et al. (2016)
7.	*Arabidopsis*	High salinity stress	Increased acetylation of histone H4 at *AtSOS1* due to inhibition of de-acetylase	Sako et al. (2015)
8.	Tomato	Salt and drought stress	*SlAGO₄A, an ortholog of AtAGO4* plays negative role through modulation of DNA methylation and RNAi pathway	Huang et al. (2016)
9.	*Vicia faba*	Drought stress	Increased demethylation of *LOX, CDPK, ABC, GH* and *PEPC* genes	Abid et al. (2017)
10.	Wheat	Heat stress (High Temperature Stress)	Increased histone demethylation of the various genes	Wang et al. (2016)
11.	*Hydrilla verticillata*	Metal (copper) stress	Hypermethylation caused over-expression of *DRM, CMT* and *SUVH6* gene	Shi et al. (2017)
12.	*Arabidopsis*	Cold stress	Non-CG hypermethylation under cold and low light stress	Raju et al. (2018)
13.	*Arabidopsis*	Drought stress	Histone methylation (H4R3sme2) in the promoter region of *ANACo55* gene	Fu et al. (2017)
14.	*Arabidopsis*	Salinity and abscisic acid	Hypomethylation at *DRM2* gene under salinity conditions	Arikan et al. (2018)

Fig. 3 The conceptualization model of heritable epigenetic characters
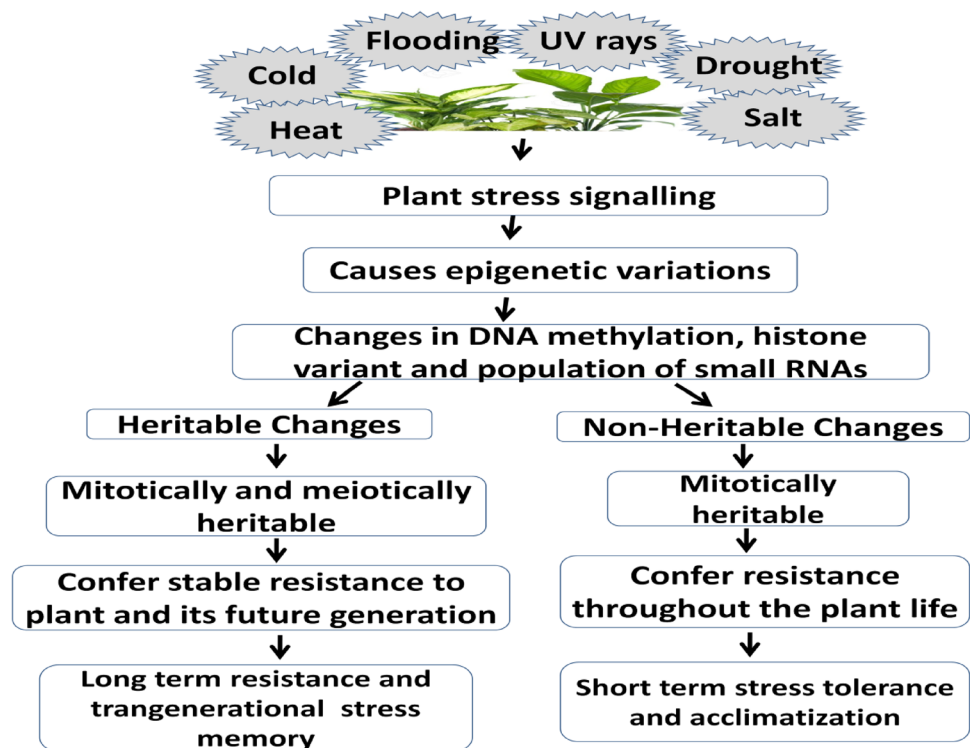
next generations as they seem to form transient epi-alleles that diminish their affect after the stress was removed. Similarly, earlier reports also confirmed that exposure of *Arabidopsis* plants to temperature stress resulted in the release of transcriptional gene silencing at several heterochromatin regions and this destabilized status was also verified at the genome-wide level by transcriptomic analyses (Pecinka et al. 2010). This transcriptional activation was transient and silencing was re-established a few days after removing the stress. Pecinka et al. (2010) also determined that the transient release of silencing and its restoration was related to temporary changes in nucleosome density. Recently, transcriptional repressive mark H3K27me3 was shown to be restored in daughter plant cells through DNA replication-coupled modification of histone variant H3.1 (Jiang and Berger 2017).

Therefore, most of the stress-induced epigenetic modifications are transient and restore to initial levels when the stress is removed, however, some of the modifications might be stable and inherited across mitotic or even meiotic cell divisions.

However, those epigenetic changes that occur swiftly and irreversibly with a prospective to sustain the "acquired stress memory" through several generations via cell divisions could be a potential mechanism for elucidating the flexibility of plant response to environment conditions. There are several reports on epigenetic mediated stress memory that helps in imparting instantaneous response towards stress which later led to the long-term adaption.

Blodner et al. 2007 reports that exposure of plants to cold stress during flowering and seed development resulted in improved photosynthetic yield recovery in their progeny in response to chilling conditions. Further, *Arabidopsis* plants grown in heat stress conditions for two generations (parent and F_1) showed an increased seed production efficiency to high temperature in the non-stressed F_3 generation, even though the F_2 generation was raised in a normal temperature (Whittle et al. 2009). Verhoeven et al. (2010) also observed that variation in DNA methylation level at several loci in a population of dandelion, upon exposure to abiotic stresses, were transmitted to the offspring of these plants.

Arabidopsis exposed to UV-C stimulated the inheritance of stress tolerance even to the untreated progeny via increased homologous frequency and global genome methylation (Boyko et al. 2010a). Rice genotypes under salt and alkaline stress treatments showed the persistence of altered DNA methylation levels in the selfed progenies (Fang et al. 2014). However, the molecular mechanism that underlies the formation of stress memory and provokes the adaptive responses over one unexposed generation has still to be figured out.

Future outlook

Epigenetics mechanism constitutes another line of defense against environmental stresses. Although a plethora of genes seems to be involved in various mechanisms of stresses that induced DNA methylation, histone alterations and

RNA-directed DNA methylation; it is still a matter of suspense that how much degree of stress may be epigenetic in nature as their mitotic and meiotic heritability behaviour is still unclear. Research have paid a way to the better understanding of transmission of epigenetic stress memory but there is still a long way to go in deepen our understanding of how these stress memory regulates gene expression and controls plant development and stress tolerance in future progenies. Epigenetics can constitute another genetic engineering tools to be applied in crop stress tolerance breeding.

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