Plants are always subjected to different types of biotic and abiotic stresses. To maintain optimum growth and achieve normal productivity, plants evolve transcriptional and post transcriptional mechanisms to acclimatize to stresses. In past decade, increasing interest in epigenetics has shown its role in plants in stress response and acclimatization. DNA and histone methylations, the main mechanisms behind epigenetics are environmentally induced and heritable. This intelligent behavior of plants to memorize past events in the form of epigenetic changes enables them to produce resistant progenies. Also, these changes can be promising tools for generations of stress tolerant varieties. Here, in this article we are discussing the role of epigenetics in stress tolerance in plants.

**PLANT STRESS**

Plants being immobile are continuously subjected to the frequent changes in environment that often severely limits their optimum performance. Plants are subjected to a variety of abiotic stresses including drought, flood, salinity, heat, cold, frost, UV-B etc, and the severity of the stresses are increasing on account of global climate change. Some of these environmental abnormalities which are stressful to the plants are favorable to some pathogens and pests, which in turn act as biotic stresses for the plants. For example, increase in temperature also increases the habitat range for pathogens and facilitates their spread (Bale et al. 2002). The combined effect of biotic and abiotic stresses is extremely severe on growth and development (Pandey et al. 2017). Under natural conditions, plants generally are exposed to a combination of multiple stressed simultaneously such as drought and heat, salinity and excess water, heat and high UV-B rays etc. The effect of these conditions is more severe on crops than wild plants. Abiotic stress combined with a pathogen attack can destroy the whole crop and drastically reduce the productivity (Atkinson and Urwin 2012). The effect of multiple simultaneous stresses can be additive or antagonistic. Combined effect of drought and heat is much severe than their individual effect (Rizhsky et al. 2002) But in some conditions it is beneficial to the plant like combined effect of drought and O₃ stress. Drought decreases stomatal conductance and makes the plant more tolerant to O₃ stress. Plants have evolved many strategies like avoidance, tolerance, resistance or escape to minimize the influence of these stresses on growth and productivity. All these strategies need precisely controlled gene expression. Growing interest in understanding of stress response mechanisms has found epigenetic mechanisms playing role at transcriptional and post transcriptional levels.

**EPIGENETICS**

Epigenetics means “on top of” genetics, which involves the changes in genome without any change in nucleotide sequence (Bender 2004). Despite of obvious differences in animals and plants, the organization of genome and epigenome is similar. In animals cell fate is largely determined at embryonic stage but plants grow continuously through meristem activity. This post embryonic development in plants is influenced by environmental factors. Organization of epigenome is a function in response to environmental cues which provide phenotypic plasticity to plants in a non-avoidable environment (Pikaard and Scheid 2018). Epigenome organization and their function are crucial for gene expression. Alternative epigenetic states are produced by modification in genomic DNA. These modifications produce novel epialleles which increase plant adaptability towards changing environment (Reinders et al. 2009). Epigenetic modifications are found to be operated in plants in response to stress. Plants “memorize” stress condition by conserving epigenetic changes and pass on these changes to next generation through transgenerational inheritance. Epigenetic regulations of gene expression are through either by DNA methylation, or by histone modification. Mechanisms involved in these modifications and role of epigenome to increase plant adaptability are explained further in this article.

**DNA METHYLATION**

Addition of methyl group is catalyzed by DNA Methyltransferases. Methylation at 5°carbon of cytosine...
(N5mC) residue is the most prevalent DNA modification in eukaryotes. Other modifications such as methylation at N6 position of adenine (N6mA) or N4 position of cytosine (N4mC) are also found in prokaryotes. Establishment of methylation pattern is catalyzed in three types of sequences: CpG, CpHpG and CpHpHp where H refers to A, T or C. CpG and CpHpG methylation is symmetrical in nature which is directly copied from parent DNA strand after replication while methylation in CpHpH sequence is asymmetrical in nature and has to be established de novo after replication (Karlsson et al. 2011). CpG methylation is most widespread, stable and involved in transgenerational inheritance (Saze 2012). Methylation is found at both promoter and genic regions. It regulates differential gene expression by inhibiting the interaction of DNA sequence and transcription factors. Methylation at CpG and CpHpG is mainly maintained by enzyme MET1 (Methyltransferase 1) and CMT3 (Chromomethylase 3), respectively (Dangwal et al. 2014). Mutation in MET1 leads to decrease in CpG methylation in whole genome. CMT3 is a plant specific DNA methyltransferase which is mainly responsible for methylation in centromeric repeats and transposons (Lindroth and Jacobsen 2001). De novo methylation at asymmetrical sites is catalyzed by DRM1 and DRM2 (Domain rearranged Methyltransferase). It is an RNA directed DNA methylation process in which targeted loci are transcribed by plant specific RNA pol IV. Silencing of transgenes, transposable elements and various repeats is done by this process.

RNA DIRECTED DNA METHYLATION (RDDM)

RdDM mainly directs de novo establishment of DNA methylation in asymmetric CpHpH sites. Biogenesis of siRNAs is catalysed by RNA Pol II and Pol IV. Single stranded RNAs are produced by Pol IV and then converted into double stranded by RNA dependent RNA Polymerase2 (RDR2) while RNA PolII produce dsRNAs from inverted repeats. These dsRNAs are further processed by DICER Like 3 (DCL3) proteins and then methyl transferase activity of HUA enhancer 1 (HEN1) catalyze methylation of 3' nucleotide at 2'-OH and load them on ARGANOUTE 4 (AGO4). These complexes then target chromatin associated scaffold transcripts and recruit DOMAIN REARRANGED METHYLTRANSFERASE 1 and 2 (DRM1 & 2) which catalyse methylation at asymmetric sites (Zhong et al. 2014).

HISTONE MODIFICATIONS

Chromatin is a complex structural unit which comprises of DNA strands, RNA, and histone proteins. The packaging of DNA in such complexes regulates gene expression and transcription. Histones are available in different forms termed as histone variants such as H2A.Z, H2A.X and several others (Kamakaka and Biggins 2005). A number of post-translational modifications occur in histone protein. Combination of histone variant and these modifications constitute histone code which directs functional state of chromatin. Most of transcriptionally active genes are more loosely packaged and are associated with RNA polymerases and hence referred as euchromatin. On the other hand, heterochromatin contains transcriptionally inactive genes which are tightly wrapped around histone proteins. Epigenetic alterations such as DNA methylation of cytosine and di-methylation of lysine 9 in H3 histone (H3K9me2, mark of heterochromatin) maintain the gene at silenced state (Bernatavichute et al. 2008). Trimethylation of H3K27 (H3K27me3) is also known to be responsible for reducing the gene expression (Mir et al. 2017). H2A.W, a variant of H2A is also found mainly in silenced genes (Yelagandula et al. 2015).

EPIGENETIC CHANGES DURING ABIOTIC STRESS

Regulation of gene expression through epigenetic modification helps plant system to combat various stress conditions. Several studies suggests that the components of chromatin structure are modified or altered and hence are the primary targets for transcriptional stress response. In various studies, comparison of wild type and stress treated plants showed difference in the level of methylation under stress conditions.

- Methylation sensitive amplification polymorphism study conducted in mangrove plants taken from riverside and salty habitat found hypomethylation in plants grown in salty habitat (Lira-medeiros et al. 2010).
- In tobacco cell suspension culture, DNA hypermethylation was found at two heterochromatic loci under osmotic stress. However, it reverted back under normal conditions (Kovarik et al. 1997).
- In pea genome, a specific cytosine hypermethylation (CCGG) was found in water deficient plants (Labra et al. 2002).
- Adaptation for heat stress tolerance was found to be associated with switching between DNA methylation and H3 histone acetylation in cork oak leaves of forest plants (Rodriguez et al. 2013).
- ZmMI1 identified in maize root specific tissue
under cold stress contains a putative protein coding region and a retrotransposon which remained hypomethylated under cold stress. Down regulation of MET1 is responsible for this hypomethylation (Steward et al. 2000).

- Tam3, a transposon showed alteration in methylation in CpNpN sites under cold stress in Antirrhinum majus (Hashida et al. 2006).

All these evidences indicate role of epigenetic mechanisms in stress tolerance and also provide some clues for downstream processes governed for adaptation. In soybean, 49 transcription factors having differential expression under salinity stress were examined for DNA methylation. Expression level and methylation pattern of MYB, AP2 and b-ZIP transcription factor family genes were found to be associated with stress adaptation (Song et al. 2012). In order to acclimatize under stress, plants change their physiological process like onset of reproductive phase, switch between C3- photosynthesis and CAM metabolism. Stress hormone Abscisic acid (ABA) is significantly associated with changes in gene expression due to methylation/demethylation. ABA induced accumulation of miRNA1026 and hypermethylation at CpG sites in its target gene PpbHLH in Physcometrilla patens showed integrated role of phytohormones and transcription factors to cope up with stress.

**EPIGENETIC CHANGES DURING BIOTIC STRESS**

Soil contains a repertoire of micro fauna some of which are symbionts to plants while others are pathogens. Plants interact with microbes after recognizing conserved molecular signals known as MAMPs (Microbes Associated Molecular Patterns) such as flagellin, chitin etc. Subsequently through transcriptomic reprogramming plant decides whether to promote symbiosis or activate defence against pathogen. Studies conducted on Arabidopsis showed important role of DNA methylation in defense priming. Reduction in DNA methylation increases gene expression and imparts higher resistance towards pathogens (Dowen et al. 2012). Following studies are the evidences for the role of epigenetics in defense priming.

- A key regulator of SAR (Systemic Acquired Resistance), NPR1/NIM1 was found to have effect of H3 methylation on its expression in Arabidopsis (Bowling et al. 1997).
- Genes of PR and WRKY family were found to be regulated by Chromatin Assembly Factor-1 (CAF-1). It changes nucleosome assembly around transcription start site. It also controls trimethylation of H3K9 in order to activate defence genes (Mozgová et al. 2015).
- Arabidopsis plants defective in MET1 and DDC showed a resistant phenotype against Pseudomonas syringe pv. tomato DC3000 due to higher level of gene expression (Dowen et al. 2012).
- Chemically induced demethylation in rice R gene Xa21G, showed resistant phenotype against Xanthomonas oryzae pv. Oryzae (Akimoto et al. 2007).
- Plants also utilize siRNA mediated DNA methylation against viruses by deactivating their gene expression through methylation (Yadav and Chattopadhyay 2011).

Symbiosis and pathogenesis share similar signaling pathway, but in order to set symbiotic relation plant defence system has to be suppressed. The decision to suppress defence system for symbiosis and its activation against pathogenesis depends upon the interaction between molecules of both plant and microbe. Hypomethylation of gDNA during symbiosis provides resistance to plant against pathogens.

**INHERITANCE OF STRESS TOLERANCE**

Plants can sensitize their immune system in response to environmental stress. This phenomenon is known as defense priming in which plants gets primed in response to a stress and responds in a quicker and stronger way upon recurrence of that stress. It’s an intragenerational event and mainly acts at hormonal level, and increases the strength and range of basic resistance. Stress events can be memorized for a longer time or can be passed on to next generation. Mechanism of which are largely unknown but DNA methylation has been found to be involved. Memory of past events has been stored in the form of DNA methylation changes which provide phenotypic plasticity in future. This is known as stress memory. These changes can be passed on to next generation and provide better adaptability to the offspring under similar stress conditions. This is known as transgenerational inheritance. (Hauser et al 2011).

**CONCLUSION AND FUTURE PERSPECTIVE**

Phenotype of a plant is result of interaction between genotype and environment. Genetic variation and epigenetic regulation driven by environmental cues contribute significantly to the phenotypic plasticity in
Table 1: Summary of epigenetic reprogramming during stress response.

<table>
<thead>
<tr>
<th>SN</th>
<th>Plant</th>
<th>Genomic region</th>
<th>Stress</th>
<th>Methylation status</th>
<th>Mode of action</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>Abiotic stress</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td><em>Mesembryanthemum crystallinum</em></td>
<td>Nuclear genome</td>
<td>High salinity</td>
<td>Increase in methylation</td>
<td>CpNpG methylation</td>
<td>Bohnert, Cushman, and Buryanov 2006</td>
</tr>
<tr>
<td>2</td>
<td><em>Arabidopsis</em></td>
<td>Sodium transporter gene (AtHKT1)</td>
<td>Salt tolerance</td>
<td>Decrease in methylation</td>
<td>Loss in cytosine methylation in a putative small RNA target region</td>
<td>Baek et al. 2018</td>
</tr>
<tr>
<td>3</td>
<td>Tomato</td>
<td>Non-transposon Asr1</td>
<td>Water stress</td>
<td>Asymmetric CNN methylation</td>
<td>Drought conditions brought about higher CG methylation levels in the first exon</td>
<td>González, Ricardi, and Iusem 2011</td>
</tr>
<tr>
<td>4</td>
<td><em>Zea mays</em></td>
<td>MuDR</td>
<td>N&lt;sup&gt;+&lt;/sup&gt; implantation</td>
<td>Decrease in methylation</td>
<td>Increases the expression of mudrA and mudrB</td>
<td>Hashida et al. 2006</td>
</tr>
<tr>
<td>5</td>
<td><em>Zea mays</em></td>
<td>Ac/Ds transposon</td>
<td>Cold stress</td>
<td>Demethylation</td>
<td>Cold-induced root-specific demethylation</td>
<td>Steward, Kusano, and Sano 2000</td>
</tr>
<tr>
<td>6</td>
<td><em>Antirrhinum majus</em></td>
<td>TAM3</td>
<td>Low temperatures stress</td>
<td>Decrease in methylation</td>
<td>Methylation at CHH motifs</td>
<td>Hashida et al. 2006</td>
</tr>
<tr>
<td></td>
<td><strong>Biotic stress</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>7</td>
<td>Tobacco</td>
<td>NtAlix1</td>
<td>Tobacco mosaic virus</td>
<td>Decrease methylation</td>
<td>Altered DNA methylation</td>
<td>Wada et al. 2004</td>
</tr>
<tr>
<td>8</td>
<td><em>Arabidopsis</em></td>
<td>RMG1 promoter</td>
<td><em>Pseudomonas Syringae</em></td>
<td>Demethylation</td>
<td>RMG1 is targeted by RdDM and ROS1-Dependent DNA demethylation</td>
<td>Yu et al. 2013b</td>
</tr>
</tbody>
</table>
Figure 1: Summary of stress causing changes in epigenome. These changes can be transient or stable. Stable epigenetic changes confer adaptability in upcoming generations (Adapted from Chinnusamy and Zhu, 2009).
plants. However, plants are not able to evolve mechanisms in response to rapidly changing climate because of slow evolutionary processes. The ever increasing phenomena of global climate change are adversely affecting the growth and productivity of plants, especially crops. This is proving to be a major challenge and newer strategies must be found to meet the demand of plant derived products such as food, cloth, medicines etc. Future challenges in plant improvement must leverage our growing knowledge and understanding of epigenetics regulation of stress response to address these issues.

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