

Effect of Epigenomics on different stresses of Horticultural crops

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ABSTRACT

Horticultural Crops are affected by many environmental stresses including both biotic as well as abiotic. However, eventually, these are facing major challenges to enhance the productivity of field crops due to changes in environmental conditions. In order to cope with the fickle environments, plants are innately evolved with intricate gene signalling cascades and stress avoidance mechanisms. Epigenetic modifications are one such regulation which influences the plant stress responses under adverse environments. These epigenetic changes include the potential DNA methylation, histone modification and small RNAs coupled with the regulation of gene expression without altering the DNA sequences which eventually enhances the tolerance adoptive responses to the adverse environments. The epigenetic modifications in the genome develop a stress memory in plants which further enables them to better combat with extreme stress conditions. In this review, we attempted to recapitulate the recent progress and emphasize how the changes of DNA methylation, histone modification, and small non-coding RNA regulation alters in different growth stages of plants in response to major abiotic stresses such as salinity, drought, cold and heat. We also discuss the importance and prospects of epigenomics towards the possible improvement of plant responses to abiotic stresses for Climate resilient agriculture.

Key words : *Epigenomics, Horticultural crops, Plant stress.*

Introduction

Non coding DNA is also called as Epigenetics and it is a continuously progressing branch since the past two decades. Improvement of crop varieties with traditional breeding methods is tedious, time consuming, expensive and is unable to meet progressive living standards and demand in today's world whereas epigenetics holds great potential for the improvement of plant varieties with respect to yield and nutritional quality by creation of novel epialleles, transgenic RNAi. Studies of epigenetic responses to different stresses can increase our understanding of plant stress adaptation and mecha-

nism underlying them which can be further exploited for the development of improved crop varieties.

Epigenetics is the study of changes in the gene expression pattern occurred without active changes in the DNA sequence that intern show the alterations in the phenotype or desired phenotype which may or may not be inherited for next generations. Epigenetic regulatory mechanisms are of three types- DNA methylation, histone modification and RNA interference (RNAi). DNA methylation is a chemical modification mainly catalyzed by cytosine methyl transferases which involves addition of methyl group in DNA sequence on to the position 5 of

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pyrimidine ring in the cytosine residue. It mostly occurs in a sequence specific manner, primarily within CpG dinucleotide. The addition of methyl group in DNA sequence acts as a binding site for various protein complexes that modifies the histone scaffolds containing the DNA and as a result changes the expression level of corresponding gene. Histones undergo both post translational modifications as well as have several variants which are expressed differentially under specific conditions (Saraswat *et al.*, 2017).

Majorly, DNA methylation and histone modification play a significant changes/alteration in the genetic information and results in the alterations in the chromatin structure which further skew the access to restricted genetic information. Chemical modification of Cytosine (C) in DNA through methylation results in the alterations of various cellular process and results in the diverse functions in plants (Slotkin and Martienssen, 2007). This chemical modification of C was carried out by methyltransferase enzymes at 5' position in C by using S-adenosyl-L-methionine (SAM) as a cofactor. Methylation of C involves regulation of important process such as gene expression, transposon silencing and interaction between and among the chromosomes, which plays an important role in plants under both biotic and abiotic stresses (Lang *et al.*, 2017).

The enzymes that involve in the methylation and maintenance were can be categorized into two groups. Among them, enzymes that involve in the denovo DNA methylation were in the first group and enzymes that involve in the maintenance of established DNA methylation were grouped as second group. These enzyme activities take place at specific genomic regions/sequences in the DNA (Chen *et al.*, 1991). Majority of the research findings on DNA methylation was done in *Arabidopsis* and *Zea mays*. Further, in detailed analysis in *Arabidopsis*, mutants with no methylation in CpG or CpHpG were isolated in *Arabidopsis* (Li *et al.*, 2014; Fu *et al.*, 2018). But the information is limited and the detailed analysis is required for the understanding of developmental imbalances in DNA methylation depleted plants (Gehring and Satyaki, 2017).

Histone modification

Histone proteins play an important role in the gene regulation through post translational modification before or after converting into nucleosome with

chromatin (Roudier *et al.*, 2009). In plants, these histone modifying variants/enzymes are often coded by large gene families. Histone acetylation and deacetylation plays key role in the epigenetic mark/studies, acetylation is associated with active chromatin and transcription, this was mediated by the enzyme Histone acetyl transferase (HAT), and histone acetylase mediated the deacetylation/ remove the acetylated histones and make them to original suppressive chromatin or function less chromatin (Zoghbi and Beaudet, 2016; Seto, E. and Yoshida, 2014). HD2 or HDT family are the Plant specific histone deacetylases which play important role in gene silencing. Among these methylases, HD6 play a significant role in methylation of CG and CGH by associated/interacted with MET1 (DNA methyl transferase) which enhances the transposon and transgene silencing, nucleolar dominance and suppression of rRNA genes. On the other hand, *Arabidopsis* mutants' deficient with HDA6 results in the alteration of morpho-agronomic traits such as seed maturation and control in the flowering time. Transgenic plants with over expression or suppression of histone deacetylase 6 (HDA6) gene lines showed altered pleiotropic morphological changes in these lines, still there is confusion in the functions of these genes (Kim *et al.*, 2012). The in detailed analysis of these genes will be intricate due to their redundancy.

DNA methylation

The gene expression change in plant cell occurs because of demethylation and hypermethylation of the genomic DNA under abiotic stresses. In tobacco when abiotic stresses like aluminium, low temperature and salt stresses were induced a glycerophosphodiesterase-like protein gene (NtGPDL) was expressed. However, the NtGPDL gene neither expressed at biotic stress nor at non stress. This study reveals that due to abiotic stresses the coding region of NtGPDL gene was demethylated and transcriptional activation occurs. The non-stressed and biotic stressed plants were usually methylated and causes NtGPDL gene to be silenced but when abiotic stress induced demethylation might induce histone modification and chromatin alteration which leads to enhanced transcription (Choi and Sano, 2007). Under salt stress in the genome of the facultative halophyte *Mesembryanthemum crystallinum*, there is a shift of photosynthesis from C3 to CAM was coupled with

stress induced specific CpNpG-hypermethylation of the genome. When salt stress was induced there is two fold increase in the CCWGG sequences (W = A or T) which does not change any genome sequence but coupled with hypermethylation of satellite DNA that probably changes the chromatin structure which regulates the plants to adapt under salt stress condition also switching C3 to CAM plants (Dyachenko *et al.*, 2006).

Small RNAs in relation to epigenetic changes

Cytosine alteration and histone modification plays vital role in the epigenetic changes in switching on and off of the necessary genes to cope with the environmental imbalances or any stress mediated at the transcriptional level. Apart from these changes, epigenetic regulations were also occurring at post transcriptionally by mRNA degradation or inhibition of translation process. This kind of regulation is important and it plays key role especially during the biotic stress when the plants get infected by viruses or microbial pathogens. In RNA mediated epigenetics, siRNA, RNA polymerase (POL IV), RNA- DEPENDENT RNA POLYMERASE 2 (RDRP2) and dsRNA plays important role in the generation and cleavage of dsRNA to siRNA. Later, ARGONAUTE (AGO) proteins, mainly AGO4 and AGO6 pair with nascent transcripts derived from the activity of POL V. Then further these were subjected to DNA methylation which is mediated by RNA- DIRECTED DNA METHYLATION 1 (RDM1) and bind to single-stranded methylated DNA18 and the detailed mechanism was described (Zhang *et al.*, 2018). The POL V produces distinct ncRNA with variations in the 5' ends from the same locus and they initiate transcription independently without requirement of promoters. Recent studies on genome wide scanning were not identified promoter motifs for these transcripts (Law *et al.*, 2013; Zhang *et al.*, 2013) and some POL V generated ncRNA have 7-methylguanosine caps at the 5' ends. This suggests that POL V generated RNAs undergoes certain RNA processing activities which is mediated by POL II- transcribed mRNAs, but the ncRNA generated by POL V has no polyadenylation in 3' end and thus they are different form transcripts generated by RNA POL II.

Post translational modification

The histone modifications associated with two submerged genes ADH1 and PDC1 activated under submergence was studied in rice. The Lys4 residue

of histone H3 protein was trimethylated from dimethylation on 52 and 32 coding regions of the ADH1 and PDC1 genes further acetylation of H3 also occurs under submergence condition. However, the methylation and acetylation of the histone comes to normal condition under re-aeration. This study reveals the methylation and acetylation of ADH1 and PDC1 genes increase under submergence and comes to normal levels during non-stress condition (Tsuji *et al.*, 2006). Histone H3 Ser-10 phosphorylation, H3 phosphoacetylation and histone H4 acetylation, elevated drastically under high salinity and cold stress in Arabidopsis and tobacco which indicates the stress related genes were induced (Sokol *et al.*, 2007).

Epigenetic Gene Regulation in response to Abiotic Stress Tolerance at different growth stages in plants

Researchers intensively explored the potential epigenetic modifications in different plant systems under various abiotic stress conditions such as high salinity, osmotic stress, drought, extreme temperatures (heat or cold), anoxic, nutrient deprivation and UV radiation. Throughout of its life cycle, plants had to go through multitude of climatic extremities. Being a sessile organism in nature, plants were innately evolved with intricate signalling genetic mechanisms that could alleviate the stress induced damages. Numerous reports suggest the changes in DNA methylation/ demethylation patterns can occur either genome wide or at an individual loci in response to stress stimuli in plants (Zhang *et al.*, 2018).

DNA methylation alterations in response to salt and drought stress found to be specific to tissue, genotype and developmental stage dependent (Begcy *et al.*, 2018). However, compared to all other developmental stages of plant life, stress encountered at reproductive stage renders more profound and detrimental consequences on the plant growth potential and net yield productivity (Begcy *et al.*, 2018).

Role of epigenetics in vegetative growth and other development related functions

In plants RNA- directed DNA methylation (RdDM) is an authentic pathway for de-novo methylation which comprises of small interfering RNAs (siRNAs), scaffold proteins along with other proteins (Zhang *et al.*, 2018). Similarly, columella cells in

the root meristems were reportedly contain higher DNA methylation activity due to their less dense pericentromeric regions. This phenomena suggests vital RdDM activity in meristems and mutations in RdDM pathway related genes in maize (Erhard *et al.*, 2009) and rice (Moritoh *et al.*, 2012) mutants displayed strong developmental defects.

Epigenetic changes under abiotic stress at different stages of reproductive phase

Pre-fertilization events

Male or female gametophyte formation is one of the critical events of pre-fertilization process and it is known to be governed by different epigenetic factors and gene networks in plants. In rice, it was reported that while progression of meiosis, an increase in demethylation of lysine 9 of histone3 (H3K9me²) and on the other hand reduction in acetylation of lysine 9 of histone3 (H3K9) and phosphorylation of histone 3 (H3S10) is required and this epigenetic phenomenon is coordinated by the *Meiosis Arrested At Leptotene 1* (MEL1) gene. The *OsMEL1* encodes for an Argonaute protein which is specific for the germline development selectively binds on 21-nt phasiRNAs (Komiya *et al.*, 2014). In accordance to this, the *osmel1* mutant accumulates excess 21-nt phasiRNAs which results in aberrations at microspore mother cell vacuolation and tapetum formation. This further forbids the chromosomal condensation which ultimately resulted in male sterility (Nonumura *et al.*, 2007). Male fertility is also depends on the changes in the photoperiods (Ding *et al.*, 2012). Zhou *et al.* 2005 reported a study where a spontaneous mutation caused by photoperiod changes resulted in the hypermethylation eventually lead to male sterility in rice (Ding *et al.*, 2012).

In addition to the endogenous epigenomic regulation, external abiotic factors such as extreme temperatures (Cold or heat), drought, humidity and oxygen availability also has an influence in the function and proper germ line development of female and more precisely, the male gametophyte development.

Abiotic stresses effects pollen development

Both drought and cold stress induction showed similar type of sterility in rice (*Oryza sativa*). The levels of ABA in cold-sensitive and cold-tolerance rice seedlings were similar at first 8h of cold induction whereas in tolerant lines after 8h of cold induction

ABA levels reduced until 16h of our study. The ABA biosynthesis gene encoding 9-cis-epoxycarotenoid dioxygenase in anthers is mainly expressed in parenchyma cells surrounding the vascular bundle of the anther. Under cold stress, the TaABA8'OH1 gene with OsG6B tapetum-specific promoter produces lower levels of ABA in anthers of wheat transgenic lines. The cold stress tolerant transgenic lines showed that anther sink strength (OsINV4) was maintained and improved. This study suggests that ABA and ABA 8'-hydroxylase play an important role in controlling anther ABA homeostasis and reproductive stage abiotic stress tolerance in cereals (Ji *et al.*, 2011).

Abiotic stresses during embryo sac development

The drought induction elevated ABA concentration in ovaries of maize before fertilization. In this study the watered controls are with normal levels of ABA whereas the drought induced maize ovaries produced high ABA which leads to abortion in ovaries of female flowers (Asch *et al.*, 2001).

Effects of abiotic stress on fertilization and early seed development

Water deficit condition can perturb the fertilization by reducing the ability of stigma receptivity in maize and increase the unwanted antipodal cell number in embryo sac. Elevated ABA levels under drought stress could be one of the possible reasons for poor fertility and flower abortion. The ABA elevation under stress could be a result of reduced DNA methylation of hormone related gene transcription (Begcy and Dresselhaus, 2018).

Effect of abiotic stresses influence on fertilization mechanisms

The reduction in fertility is common in both male and female gametes under drought, cold and heat stress due to higher accumulation of ABA (Ji *et al.*, 2011). These studies suggested that abiotic stresses raise the levels of ABA which aborts the male and female gametes

Abiotic stresses effect on early seed development

Stress at reproductive stage in cereals lead to the limited endosperm development which affects the seed size (Li *et al.*, 2015). Under heat and drought stress losses in barley was noticed and the reduction of 60% both grain weight and seed size were observed in wheat (Ejaz and von Korff, 2017). Particu-

larly, environmental stresses delay developmental transition from syncytial to cellularization stage of endosperm development. In contrast to transcriptional inactivation some methylations lead to transcriptional activation H3K27me³, which is associated with gene silencing whereas H3K4me³ makes transcriptional activation (Zhang *et al.*, 2007).

Effect of abiotic stress on seed maturation

Maturation and development of seed is an important stage in which several critical events such as complete embryo growth development and storage products get accumulated. In addition to this, the seed also gets desiccation tolerance with dormancy activation (Begcy and Dresselhaus, 2018). In a very recent report, it was revealed that during seed maturation and differentiation there is a strong elevation of acetylation of proteins in rice. On gene ontology studies, these acetylated proteins were belonging to the biological processes including starch and sucrose metabolism, glycolysis/gluconeogenesis and tricarboxylic acid cycle (Wang *et al.*, 2017). Similarly, hyper acetylation at histone regions along with cell cycle prolongation and growth inhibition was found in maize during and after in maize. Together, this denotes that apart from DNA methylation and histone modification the acetylation also has some unknown function in seed development.

Epigenetic changes in crops against different abiotic stresses

Due to the unpredictable climate change, crop plants are frequently exposed to a variety of abiotic stresses resulting in reduced crop productivity. Analysis of the stress-associated genes and their regulation in response to the stress can be utilized to enhance understanding of the plant's ability to adapt under changing climatic conditions. DNA methylation and/or histone modifications are influenced by abiotic/biotic factors resulting in the better adaptability of the plants to the adverse environmental conditions. Such epigenetic modifications provide a mechanistic basis for stress memory, which enables plants to respond more effectively and efficiently to the recurring stress as well as to prepare the offspring for potential future assaults.

Epigenetic modifications in response to drought

Drought stress conditions generally tend to increase demethylation. It is also observed that DNA methylation shows tissue specificity. In *Oryza sativa*

drought induced a total of 12.1% methylation differences accounted across different tissues, genotype and developmental stages. The overall DNA methylation level at the same developmental stage was lesser in roots than in leaves indicating significant role of roots under water insufficiency (Suji and John, 2010).

Under stress conditions, accumulation of transcripts of stress responsive genes was positively correlated with histone modifications H3K9ac and H3K4me³ as both are marks of an active state of gene expression (van Dijk *et al.*, 2010). Overexpression of an Arabidopsis histone deacetylase homolog, AtHD2C, in transgenic Arabidopsis plants resulted in ABA insensitivity and enhanced tolerance to salt and drought stresses (Sridha and Wu 2006).

Epigenetic modifications in response to cold and freezing temperatures

Upon imposition of cold stress HDACs are upregulated that results into deacetylation of H3 and H4 and successively heterochromatic tandem repeats get activated (Ding *et al.*, 2012; Zhu *et al.*, 2008). This results into reduction of DNA methylation and histone (H3K9me²) methylation at the targeted region of maize genome (Hu *et al.*, 2012). Even after 7 days of recovery, cold induced hypomethylation was not reverted back. In a similar study conducted by Saraswat *et al.*, 2017. A recent study in apple highlighted the importance of epigenetic changes in response to dormancy caused by low temperature. High chilling conditions decreased total methylation that lead to reinitiation of active growth and subsequent fruit set in apple (Saraswat *et al.*, 2017).

Salt-induced epigenetic changes in crop plants

During salt stress the promoter and gene-body methylation plays important role in regulating gene expression in genotype and organ specific manner. The olive plants under salt stress were studied for physiological, epigenetic and genetic changes. Some of the rice genotypes Bengal, IR29 and Nipponbare plants were dead while Pokkali, Nonabokra, and Geumgangbyeon survived but showed salinity injury after 15 days of salt stress. These genotypes were analysed for methylation by using MSAP sequencing technique. Salinity stress effects methylation changes majorly in shoots of Bengal, Nonabokra, Pokkali and Geumgangbyeon and in roots of IR29

and Nipponbare genotype suggesting that many methylation changes are not “directed” (Karan *et al.*, 2012). The contrasting nature of the HAT and HDAC controls histone acetylation, which acts as a positive signal for transcriptional activation. The cell wall related genes *expansin* $\beta 2$ (*ZmEXPB2*) and xyloglucan endotransglucosylase (*ZmXET1*) in the roots of *Zea mays* were upregulated during high salt induction. The transcriptional up regulation of these genes has been correlated with increased H3K9ac in the promoter and the open reading frames (ORFs). Further studies indicated that two HAT genes (*ZmHATB* and *ZmGCN5*) are responsible for such activated acetylation in the salt-responsive genes in maize (Li *et al.*, 2014).

Heat induced epigenetic changes in crop plants

Naydenov, (2015) reported that upregulated epigenetic modulators like DRM2, nuclear RNA polymerase D1 (NRPD1) and NRPE1 may be responsible for increased genome methylation in *Arabidopsis thaliana* under heat stress conditions. Heat stress related study in rice showed reduction in seed size which is controlled by OsFIE1 (fertilization independent endosperm). Folsom and coworkers (2014), in their study reported that DNA methylation and histone (H3K9me²) methylation are the two major factors governing the expression of OsFIE1. It was found that under heat stress both DNA methylation as well as histone methylation showed a decline (DNA methylation declined by 8.8% and 6.6% with respect to CH and CHG context). Reduced methylation levels resulted into lower expression of OsFIE1 and lead to reduction in rice seed size. Histone modifications like acetylation have also been reported to occur under heat stress conditions. At high temperatures, a histone variant H2A.Z causes transcriptional changes in stress responsive genes (Kim *et al.*, 2015).

Metal stress effects chromatin modification in plants

The heavy metal pollution in the environment was increased with cadmium (Cd), chromium (Cr), copper (Cu), mercury (Hg), and zinc (Zn) which becomes a global problem, affecting about 235 million hectares of the arable land worldwide (Bermudez *et al.*, 2012). These heavy metals obstruct many biological processes in plants i.e., photosynthesis, water relations, and nutrient uptake, resulting in reduced plant growth, stunting, and in some instances, death

(Mayor *et al.*, 2013). Heavy metals usually involve in the DNA methylation process of Epigenetics. DNA methylation produced heritable changes in rice for two successive generations when heavy metal stress is induced. Heavy metals like Cu⁺², Cd⁺², Cr⁺³, and Hg⁺² when induced to rice plants the two genomic copies of Tos17 at 5' and 3' regions in CNG sites were hypomethylated which was confirmed with previous results i.e., the heavy metal induction mostly results in hypomethylation and also transgenerational pattern of epigenetic changes (Cong *et al.*, 2019).

Stress memory

Increasing number of reports in the recent times emphasise that the persistent stress is required for the formation of DNA methylation dependent stress memory in plants. In *A. thaliana* prolonged submission to salt stress induces changes in DNA methylation and it can be transmitted to offspring partially. This phenomenon selectively occurs through female germ line. The inherited DNA methylation status would gradually become reset to pre-stressed state, in case of the offspring is withdrawn from the stress (Wibowo *et al.*, 2016). This pattern was in accordance with the case of *Arabidopsis thaliana* SUPPRESSOR OF DRM1 DRM2 CMT3 (SDC) gene which gets silenced through promoter demethylation in the vegetative tissues if in case the plants does not get exposed to heat stress (Sanchez *et al.*, 2014). The DECREASED DNA METHYLATION 1 (DDM1) and MORPHEUS MOLECULE1 (MOM1) genes acts as positive regulators of stress induced epigenetic memory removal in *A. thaliana* (Zhang *et al.*, 2018) but they act in redundant manner. In some cases, the stress induced epigenetic memory can be erased independently, without DDM1 or MOM1 gene intervention. Overall, the stress memory erasure is a passive process which could occur when the plant grew under normal conditions without any strong stress stimulus.

Epigenetics in Rootstock and scion interactions:

The Involvement of Epigenetics in Rootstock-Scion Interactions will be drawn on the relation between vegetable grafting, epigenetics, and the changes in morphology and quality of the products and also changes in molecular interactions between rootstock and scion. It is now evidenced that genetic exchange is happening across grafting junctions between rootstock and scion, potentially affecting grafting-medi-

ated effects already recorded in grafted plants. Gene expression changes recorded in grafted plants and how these are related to the phenotypic changes observed. Epigenetic changes in grafted fruits and vegetables stimulate more research on grafting in the future. In a future where sustainable agricultural production is the way forward, grafting could play an important role to develop products of higher yield and quality in a safe and “green” way (Ionna *et al.*, 2021).

Conclusion

The key challenge that agriculture faces in the 21st century is to increase crop production by speeding up the breeding of resilient crop species which is the key challenge of agriculture epigenetics provides fundamental molecular information with potential direct applications in crop enhancement, tolerance, and adaptation within the context of climate change.

Epigenetic-knowledge-based technologies provide a promising toolbox for breeders. Indeed, epigenetic diversity (natural or induced by different ways) can be exploited as a source of phenotypic diversity or priming, for the creation of new varieties acclimated to climate changes, or as molecular epi-markers for selecting elite individuals or for the identification of new candidate genes. The transfer of the knowledge on epigenetic signatures associated with stress tolerance/resistance in crops is still at the beginning. There are typically hundreds of molecular markers already mapped in crop genomes associated with important traits, including tolerance to environmental stresses. Epigenetic analysis will enable the discovery of new epi-alleles involved in tolerance/resistance to those biotic stresses regulated by single genes. The standardisation and normalisation of epigenetic pipelines, methods will allow the development of methodologies and approaches which could be used by breeders for molecular-marker-assisted selection. Epi-genotyping will allow us to identify epi-alleles from genetic ones for the discovery of spontaneous epi-alleles (Ionna *et al.*, 2021).

Conflict of Interest: None

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