

Review

Epigenetics: A Key to Comprehending Biotic and Abiotic Stress Tolerance in Family Poaceae

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Abstract: Climate change has had a significant impact on many ecosystems around the world, prompting native population species to adapt to the current weather patterns eventually. Pre-existing genetic variation in populations explains part of this adaptation. Still, recent studies have shown that new stable phenotypes can be generated through epigenetic modifications in just a few generations, thereby contributing to the stability and survival of plants in their natural habitat as they eventually adjust to the surrounding impacts. The state of chromatin inside plant cells varies, allowing cells to fine-tune their transcriptional profiles to better adapt to stimuli from the external environment. Within a cell, chromatin state changes such as post-transcriptional histone modifications and variations, DNA methylation, and non-coding RNA activity are all examples of chromatin state alterations that may epigenetically dictate certain transcriptional outputs. Recent advances in the field of 'Omics' in major crops has made it easier to identify epigenetic changes and their impact on plant responses to environmental stresses. These epigenetic mechanisms thus play an important role in improving crop adaptation and resilience to changing environments, and this variation that has emerged can thus be exploited in crop breeding, ultimately leading to the generation of stable climate-resilient genotypes.

Keywords: epigenetics, epigenetic variation, chromatin changes, omics, climate-resilient crops

1. Introduction

Family Poaceae (formerly known as Gramineae) comprises monocotyledonous flowering plants and ranks among the top five flowering plant families. Domesticated cereal crops like wheat, corn, rice, barley, millets, and other species often used to nourish livestock and poultry, pertain to one of the most important plant families on the world. These cereal crops provide just over half (51%) of all the human dietary energy requirements [1]. Members of the Poaceae family are most vulnerable to both biotic and abiotic stresses. Insect pests, fungi, bacteria, viruses, drought, cold, heat, salinity are respectively the biotic and abiotic stresses affecting the crops [2]. Different crops respond differently

to various abiotic stresses: wheat and rice are sensitive to water scarcity and soil salinity, leading to severe yield reductions. At the same time, barley seems to have an innate drought and salinity tolerance. Stress is inevitable in the life cycle of living organisms. Plants, however, are sessile organisms that have evolved sophisticated gene regulation mechanisms to ensure their survival in the changing environment [3]. Stressful conditions generally do not occur as isolated events but as crosstalk of multiple stresses. These mechanisms entail genes linked to a number of interconnected pathways that lead to improved stress tolerance [4].

In response to stress, plants change their morphological traits, physiology, and other characteristics. They detect environmental changes and transmit the altered environment signals through a signal transduction cascade [5, 6], resulting in the accumulation of transcription factors that activate gene expression and allow the adaptation of plants to environmental challenges [7]. Depending upon whether the stress is permanent or transitory, plants respond through various short term and long-term strategies. Short term strategies include alteration in the plant homeostasis. Long-term strategies include transgenerational changes involving the development of heritable gene expression changes. This consists of creating new epigenetic marks while erasing old ones, as well as the increased expression of some genes while silencing the expression of others. Thus, epigenetic regulation is also one kind of the important mechanism for gene regulation in response to stress. Severe and prolonged stress can lead to genome alterations which may sometimes contribute towards better adaptation [8].

The DNA sequence contains the basic information that guides plant behaviour, and changes in DNA sequence caused by mutation or genetic recombination result in new alleles that may confer enhanced stress tolerance to the plant. However, the rate of formation of new gene combinations is too slow compared to the occurrence of different stresses in the environment [9]. Thus, the survival of the plant under these conditions is highly dependent on the regulation of a number of stress-responsive genes, or epigenetic mechanisms. The growing understanding of epigenetic regulation in response to environmental stimuli has sparked interest in the role of epigenetics in crop hardiness to abiotic stress, with an emphasis on the *Arabidopsis thaliana* plant species [10]. Drought also has a major impact on crop yield; however, it has been demonstrated that the severity of the stress depends on the phenological status of the plant [11, 22]. Impact of extreme heat waves has been analysed in wheat [13], rice [14] and maize [15]. Because the effects of stresses on crops are variable and complex, especially when crops are confronted with various stresses, breeding crop varieties for environmental stresses is a slow and challenging process. [16]. Recognizing this gap, this review paper provides a detailed overview of epigenetics involvement in abiotic and biotic stress tolerance in Poaceae.

2. What is Epigenetics?

Aristotle, in his book "On the Generation of Animals", first described the phenomenon of epigenetics to distinguish the unfolding development of an organism from "preformationism". The phenomenon was first studied by Conrad H. Waddington and Ernst Hadorn, and in 1942, Waddington coined the term "Epigenetics", which has been derived from two words "epi", a Greek prefix meaning "on top of"/"in addition to"/"near" and "genetics", to describe how genes interact with the environment to produce a phenotype. Epigenetics, thus, refers to the phenomenon of genetically identical cells or organisms expressing their genomes differently, resulting in phenotypic differences. It is a

modification of gene expression without a change in DNA sequence and is potentially stable and heritable [17].

However, sometimes such changes can even be harmful, such as the development of cancers. Epigenetic reprogramming in response to various environmental challenges contributes to phenotypic diversity as well as resistance to these challenges [18; 19]. The three important epigenetic modifications currently known for initiating and maintaining epigenetic change are DNA methylation, histone modification, and non-coding RNA (ncRNA)-associated gene silencing (Inhibition of RNA) [20]. Stress acts as a stimulus, changing genic expression levels through a variety of mechanisms including DNA methylation, histone modifications, and RNA interference [21]. Studies of epigenetic responses to various stresses can help us better to understand plant stress adaptation and the mechanisms that underpin it for betterment of crop cultivars. Some stress-induced changes are reverted to their baseline state; however, some of these changes are stable and heritable, named epigenetic “stress memory” [22- 25]. The knowledge of stress memories can increase our understanding with regard to the adaptation of plants to stresses. Thus, from the last two decades, epigenetics has become a rapidly evolving branch. The role of epigenetics in a variety of stress responses is constantly being discovered through new and ongoing research.

3. Mechanism of an Epigenetic process

The mechanism of an epigenetic process can be divided into 3 stages:

- i. Epigenator: It is a trigger (food/toxins/radiation/hormones etc.) that alters the cells’ environment to produce an epigenetic phenotype. Such signals are transient, lasting long enough in the cell environment to initiate the epigenetic process.
- ii. Epigenetic initiator: The trigger (epigenator signal) is translated to mediate the epigenetic effect on chromatin. Epigenetic initiator is primed by epigenator, and determines the location on a chromosome where epigenetic state should be established.

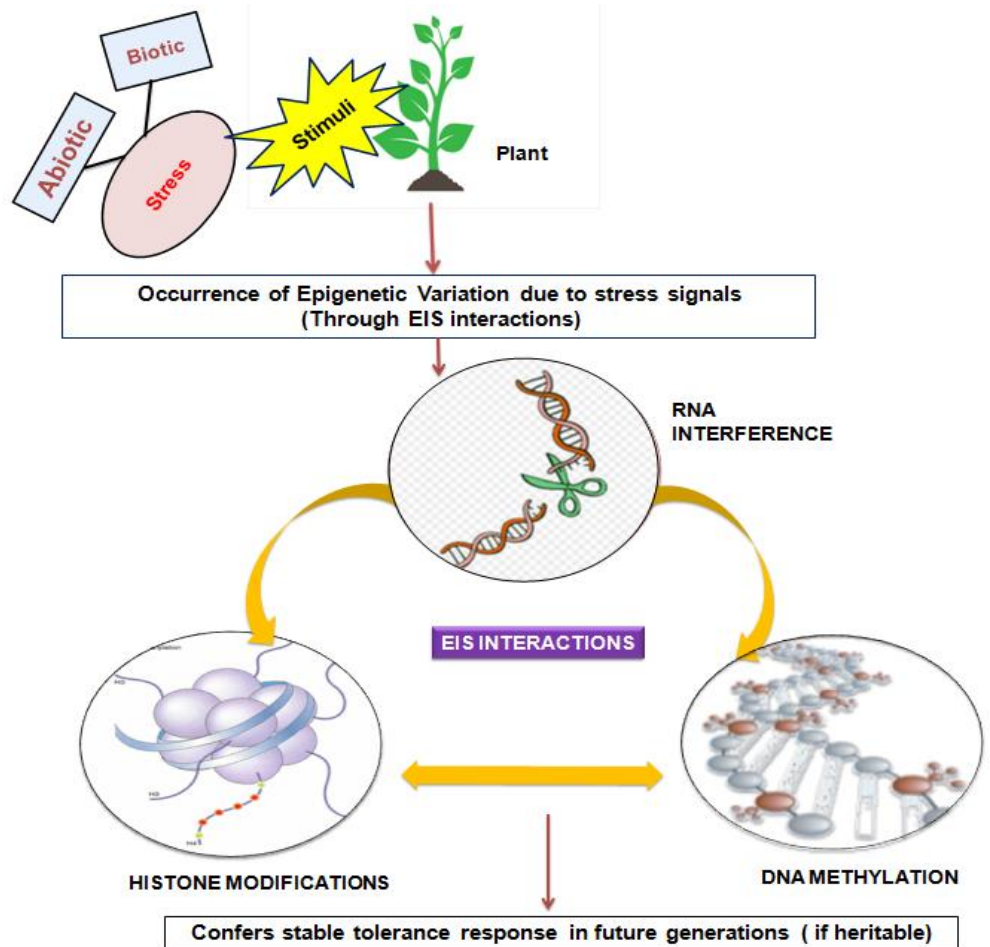


Figure 1. Schematic representation of the machinery of epigenetic regulation through EIS interactions.

iii. Epigenetic maintainer: The DNA sequence specificity of maintainers is not absolute.

3. Epigenetic Information Systems (EIS): Most of the epigenetic machinery of higher eukaryotes appears to be providing them with cellular and genomic immunity [17]. When stress is relieved, most of the stress-induced epigenetic modifications return to their original thresholds; however, some modifications become stable and are passed down through mitotic or even meiotic cell divisions. [26]. Such stress memories significantly improve the adaptation of plants to that stress also prepare their offspring for future environmental challenges [27; 28]. With the advancement in molecular technologies, our knowledge of the mechanisms of epigenetic responses to environmental stresses is rapidly growing [29]. EIS interactions play an important role by complementing, stabilizing and reinforcing each other through complex interdependent synergy, as shown in figure 1. RNA-RNA hybridisation between siRNA and nascent mRNA also leads to DNA methylation and histone modifications [30]. The 5 methyl Cytosine binding proteins recruit and forms complexes with Histone DeAcetylases (HDACs). In turn, HDACs and histone methyltransferases (MTases) lead to the recruitment of DNA MTases[31]. Therefore, understanding shared mechanisms contributing to one or more simultaneously occurring stresses has also become an important aspect in crop improvement [32].

3.1. DNA Methylation: It is accomplished by attaching a methyl group to the cytosine carbon in the C-p-G dinucleotide sequence [33]. The 5' methylated Cytosine frequently de-aminates to Thiamine, causing mutations. This process is catalyzed by a family of DNA methyltransferases (DNMTs). The C-p-G islands are C-p-G rich areas of 200 bp to several kilobases in length, usually located near the promoters of highly expressed genes. More than 55% of changes develop clusters. Thus, methylation of C-p-G islands in promoter regions of genes may prevent or deregulate the synthesis of gene products [34; 35]. It also plays an important role in DNA repair, recombination and replication, and regulation of gene activity [36].

Three members of the DNA methyltransferase family can produce methylation either de novo, where unmethylated cytosine residues are methylated (DNMT3a and 3b) or by maintaining the pre-existing or established methylation patterns following DNA replication (DNMT1) [37;38]. Furthermore, the level and status of DNA methylation might change under stress conditions, such as salt, drought, low temperature, heavy metal, pathogen and so on [39]. DNA methylation analogues also isolated from rice [40] and barley [41]. The methylation levels can be detected by High-Performance Capillary Electrophoresis (HPCE) which measures global methylation level through the quantification of 2'-deoxynucleosides. Detection and quantification of 5-methyl 2'-deoxycytidine in genomic DNA is performed using micellar HPCE with (UV/VIS) Spectrophotometry detection [42]. Demethylation of DNA occurs in two ways in plants: passive demethylation and active demethylation [43;44]

3.2. Histone Modifications: Each and every nucleosome is made up of an octamer of four core histones (H3, H4, H2A, and H2B), with 147 base pairs of DNA wrapped around it [45] Post translational modifications (PTMs) may also occur on the lateral surface of the nucleosome core histones that are in contact with the DNA, referred to as the nucleosome core surface [46]. They mainly occur along the N-terminal tails of the core histone, including acetylation (mainly at Lysine residue), methylation (mainly at Lysine and Arginine residues), phosphorylation (mainly at Serine and Threonine residues), ubiquitination (mainly at Lysine residue) and sumoylation (mainly at Lysine residue) [47-50]. A combination of site-specific posttranslational modifications on different residues of histone tail constitutes "histone code" [51].

The most common and well-studied type of modification is acetylation of lysine residues' amino group [52]. By adding acetyl groups to histone protein tails, the positive charge of histones is decreased, thereby weakening the bond between histone proteins and DNA. This facilitates transcription by increasing the accessibility of DNA to RNA polymerase II. Histone deacetylases (HDACs) deacetylate histone tails in order to acetylate N-terminal lysine residues, thereby increasing DNA-histone interaction and inhibiting transcription [53]. Both HATs and HDACs play important roles in regulating chromatin structures related to gene expression [54]. Additionally, both may also increase or decrease the DNA binding ability of histones resulting in DNA condensation or decondensation, thereby gene inactivation or activation [55]. Histone methyltransferases (HMTs) trimethylate histone H3 at lysine 4 (H3K4), resulting in an active transcription mark, or dimethylate histone H3 at lysine 9 (H3K9), resulting in a transcriptional silencing signal. Histone demethylation can be confirmed by Chromatin Immunoprecipitation (ChIP) assays [56]. The role of histone H2A and H2B ubiquitination in regulating transcription initiation, elongation, and silencing has been well-reviewed [57, 58]. Ubiquitin is a 76-amino-acid polypeptide that regulates a wide range of activities in the body in a multitude of ways. Depending on the attached amino acid, ubiquitylation on a histone tail can either inhibit or augment gene expression. For sumoylation, the small ubiquitin-related modifier

(SUMO) family of proteins modifies histone H4, which are around 100 amino acids long and inhibits euchromatic transcription by recruiting histone deacetylase and heterochromatin proteins [59]. Thus, histone modifications may regulate gene expression by regulating chromatin dynamics directly influenced by post-translational modifications of the amino-terminal tails of the histones [60] and result in malfunctions of chromatin structure modifiers [61]. Almost all cellular processes, including transcription, replication, repair, recombination, and chromosome segregation, rely on the precise organization of chromatin. Histone-DNA interactions results in the altered accessibility of specific DNA regions to transcription machinery [62]. Chromatin remodelling factor (CHR), including the SWI/SNF ATPases, the imitation switch (ISWI) ATPases, and the chromodomain and helicase-like domain (CHD) ATPases subfamilies, may play a role in mediating either ATP-dependent chromatin remodelling or post-translational histone modifications. [63]. The ATP-dependent chromatin remodelling complexes could alter nucleosome composition and positioning and thus regulate DNA accessibility and gene expression. Posttranslational histone modifications, on the other hand, may affect nucleosome interactions and thus chromatin compactness and structure [64].

3.3. RNAi (RNA Interference): Andrew fire & Craig c. Mello shared in 2006 for the discovery of RNAi in *Caenorhabditis elegans*. The mechanism by which particular segments of double-stranded RNA may prevent the expression of a certain gene with a similar sequence to a dsRNA that is orthologous to the gene is about to be expressed. Non-coding RNAs (ncRNAs) are critical epigenetic components of plants because they regulate a variety of functions such as growth, development, and responses to environmental stresses. Non-coding RNAs are classified based on their length into two categories: short chain non-coding RNAs and long chain non-coding transcripts [65, 66]. Short-chain non-coding RNAs, such as microRNAs (miRNAs) and small interfering RNAs (siRNAs), regulate gene expression at both the transcriptional and post-transcriptional levels, according to substantial literature conducted in animals and plants over the last few decades [67]. Both these are small RNAs with an average length of 18-24 nucleotides (nt) (sRNA) [68]. Long non-coding RNAs (lncRNAs) are non-coding RNAs with lengths greater than 200 nucleotides (nt) and are found in a wide variety of species [69]. RNA interference (RNAi) is a technique for post-transcriptional gene silencing that makes use of double-stranded RNA to silence genes following transcription [70]. It's a popular choice for gene function analysis because of the assay's high specificity and efficiency. Whereas, small interfering RNAs (siRNAs) can travel through plants using different carrier proteins (non-cell-autonomous travel), whereas miRNAs travel lesser distances.

4. Tolerance to abiotic and biotic Stresses in members of Family Poaceae: The role of Epigenetic Machinery

Abiotic and biotic stresses such as salinity, drought, heat, cold, submergence, heavy metal toxicity, weed/insect infestations and pathogen infections seriously threaten the growth and yield of important cereal crops such as rice, wheat, maize and barley [71]. Numerous research findings have led to new crop breeding programs for enhancing their resistance to such stresses. Recent years have seen an increase in evidence that plants use complex epigenetic processes to fine-tune their response to environmental stressors, which is consistent with known studies [72]. Here as necessary consequence, epigenetics has become one of the most popular research topics in plant functional genomics, as it appears to be particularly promising in terms of knowing plant species ability to adapt to environmental stress. Understanding the persistent and heritable characteristics of epigenetic marks and epigenetic regulatory systems has now become incredibly valuable for breeding capabilities. [73].

There's a growing body of evidence that methylation of DNA in response to stress causes phenotypic variation. This process has been linked to transposon mobility, siRNA-mediated methylation, and host methyl transferase activation. For example, the overall level of DNA methylation in a plant at the same developmental stage is lower in roots than in leaves, implying that both roots and leaves play a role in the plant's response to drought stress [74]. Drought, heat, and heavy metal toxicity all contribute to an increase in demethylation. Further, epigenetic mechanisms also play an active role in response of plants to biotic stresses, such as diseases caused by bacteria, viruses, fungi, parasites as well as insect and weed infestations, by controlling the expression of several resistance genes [28]. This immune memory state of plants is mediated by DNA methylation, RNA interference mechanisms, and histone modifications, and it is passed down to the next generation in few cases. Therefore, identifying of different mechanisms and studying their differential expressions in various tissues play a major role in research related to epigenetics [75]. Epigenetic mechanisms allow for alternative phenotypes with the same genetic sequence, which has resulted in a paradigm shift in genetics and ramifications across a wide range of disciplines. As a result, much effort has gone into deciphering epigenetic mechanisms, biological roles, and natural variation. Acquired knowledge about epigenetic responses in model plants can be transferred to cereal crops and used to increase phenotypic variation for breeding purposes due to recent advances in genome sequencing, bioinformatics tools, and associated techniques ChIPseq, FAIRE-seq, Chromosome Conformation Capture, or small RNA analysis.

4.1 Epigenetic modifications for adaptation to abiotic stress tolerance

Since the Green Revolution (1960s), rice (*Oryza sativa* L.) has been the world's most significant food crop, supplying staple food for almost half of the world's population and accounting for around 51% of human calorie consumption [76]. A 50% reduction in biomass, 39% reduction in grain yield and 28% reduction in straw yield of rice has been attributed to abiotic stresses [77]. In terms of area and global food supply, wheat (*Triticum aestivum* L.) outperforms all other cereals [76]. It is farmed in a broad array of geographic regions across the globe, requiring the adaptation of its physiological responses to abiotic and biotic challenges [78]. It provides substantially more protein per gram (12–15%) than rice or maize (2–3%), making it a superior grain [79], but despite this, its output is much lower than those of rice and corn [80]. Extreme abiotic stresses such as drought, high temperature, and salinity, among others, will reduce wheat output by 20%–30%, especially in developing countries [81]. Wheat yields are negatively impacted by stress throughout the reproductive stage of the plant [82]. Dubbed the queen of grains, maize (*Zea mays* L.) is cultivated in over 166 nations for various uses. Abiotic stresses such as moisture, high/low temperature, salt, and nutrition stress, in maize, have resulted in 17–60% of yield losses in various countries [83]. Although the crop possesses inherent resistance to severe conditions, abiotic stresses hamper its performance, corresponding to about 10–15% yield losses [84].

Wang et al. were the first to establish a link between abiotic stress responses and stress-induced epigenetic variation in rice by demonstrating that drought-tolerant and drought-susceptible rice cultivars displayed genotype- and tissue-specific differential DNA methylation upon imposing drought stress during the tillering stage [85]. Recent research employing the '-omics' technology has demonstrated a relationship between changed DNA methylation patterns and varied gene expression throughout the genome of three rice cultivars with variable susceptibilities to increasing salt and drought stress [86]. It has also been revealed that many HAT genes actively express in rice under heat and water stress. Elevated expression of HvTX1 in barley under drought stress suggests

that it plays an active role in drought tolerance. Few other examples of epigenetic regulation for various abiotic stresses in different cereals are mentioned in Table 1.

4.1.1 Salt-induced stress

Salt accumulation in soil reduces the absorption of water and nutrients, leading to osmotic stress, ion toxicity, nutrient imbalance, and even water deficit [87;88]. DNA methylation alterations in salt-sensitive and salt-tolerant rice genotypes were observed in response to increasing salinity [85]. DNA methylation of retrotransposons, stress-responsive genes, and chromatin modification genes was found on several rice chromosomes [89]. The cytosine methylation and gene expression differences at these selected Methylation Sensitive Amplification Polymorphic (MSAP) sites were found independent of the salt tolerance of the rice genotype. Methylation of the gene body may be crucial for organ- and genotype-specific regulation of gene expression under salt stress. Ferreira et al. investigated a sequence of differentially methylated regions (DMRs) between control and salt-exposed plants [90], and a general trend towards demethylation was detected, similar to some earlier studies (85, 91). Overexpression of miR156 was reported to boost rice tolerance to salt stress while decreasing the expression of transcription factor target genes, which are primarily involved in forms of development [92]. These studies identified novel epigenetic mechanisms and target genes associated with rice genotypes' responses to salt stress, as well as new avenues for improving the crop's salt stress resistance.

Salt stress-induced reactions have activated few genes that are associated with the cell wall in maize roots, such as expansin 2 (ZmEXPB2) and xyloglucan endo trans glucosylase (ZmXET1). The upregulation of these genes' transcription has been linked to increased H3K9ac in their promoters and open reading frames. Subsequent research established that two HAT genes (ZmHATB and ZmGCN5) are responsible for the active acetylation of salt-responsive genes in maize [93]. In wheat, Singh et al. demonstrated that the root tissues of salt-tolerant (Kharchia-65) genotype were 30-40% more methylated compared to shoot tissues. Due to the fact that roots are the first to encounter salt stress, they must limit access of Na⁺ into root cells; thus, increased methylation in the root tissues of the salt-tolerant genotype (Kharchia-65) helped reduce Na⁺ absorption from the soil. This suggested that the genes implicated in salt tolerance may be epigenetically controlled, with hypermethylation possibly inhibiting their expression, especially the high-affinity potassium transporters (HKTs). Additionally, they identified differences in HKT gene expression between salt-tolerant and salt-sensitive bread wheat genotypes in root and shoot tissues [94]. Also, distinct epigenetic alterations in particular genes such as HKTs in shoots and roots of wheat genotypes possessing variable degrees of vulnerability to salt stress was observed [95].

4.1.2 Drought-induced stress

Wang et al. elucidated that of the overall alterations in genome-wide DNA methylation in rice, around 12% accounted for drought-induced site-specific methylation across genotypes, tissues and developmental stages; of these, roughly 70% were reversed upon recovery while 29% remained preserved. Furthermore, drought tended to elicit DNA demethylation processes in the two cultivars studied, which were more severe during the tillering stage and varied across tissues and stages of physical growth [78]. When drought was applied at the panicle initiation stage in rice, hypomethylation was more evident in a drought-tolerant genotype than in a drought-susceptible genotype, according to another study using Methyl-Sensitive Amplification Polymorphism (MSAP)

[96]. Since the past few years, much effort has been directed towards understanding the role of miRNAs in imparting tolerance to abiotic stresses in rice [97-103]. MiR159 was thought to function as a cellular regulator, guiding developmental or stress responses to external adverse situations [104]. Silencing the RINGfinger E3 ligase gene in rice, OsDSG1, improved drought tolerance [105]. Zhang et al. silenced the miR166 that boosted drought tolerance in transgenic rice lines, and was accompanied by morphological alterations associated with the plants' natural stress responses [106]. It has been discovered that a significant proportion of drought-induced epi-mutations (DNA methylation) in rice retained their altered methylation pattern across successive generations when exposed to drought, from tillering to the grain filling, implying drought-induced epi-marks being heritable [107]. Santos et al. [108] demonstrated that rice's epigenetic processes and transcription factor activity cooperate to regulate abiotic stress responses.

Transcriptomic and genome-wide chromatin data were merged to determine how maize adjusts its response to and recovery from drought stress [109]. This work confirmed the presence of various chromatin-mediated levels of transcriptional regulation in response to osmotic stress [110, 111] as well as the dynamics of histone modifications related to H3K4me3 and H3K9ac [109]. Long non-coding RNA collections, encoding for drought stress-responsive maize transcripts expressed in a range of tissues, were uncovered in a genome-wide screen [112]. These lncRNAs were classified as sRNA precursors or other non-coding RNAs after being aligned with other sRNA databases. Xu et al. [113] discovered that natural antisense transcripts (NATs), were also present in two recombinant inbred lines, generated from these two parental lines and fixed for combination of drought tolerance loci that conferred high or low tolerance. While the function of NATs is unclear in plants, they also discovered that NATs related to stress reactions were considerably hypomethylated and included less transposons than non-NAT genes. Using genome-wide association study in maize, Mao et al. discovered that a miniature inverted repeat transposable element (MITE) that affect gene expression via RNA-directed DNA methylation (RdDM) and accumulation of H3K9me2, resulting in drought tolerance [114].

Appels et al. investigated the whole wheat genome expression pattern utilizing 850 RNAseq samples from 32 tissues collected at different developmental stages by subjecting them to different stress treatments and found that poorly expressed genes on an average had a higher methylation status. Also, the distribution of the restrictive histone mark H3K27me3 (trimethylated histone H3 lysine 27) and the active histone mark H3K36me3 and H3K9ac (acetylated H3K9) were associated with the expression range patterns [115]. Gardiner et al. found that methylation patterns in wheat [116] in response to drought are not uniform throughout the A, B, and D subgenomes [117,118].

Terminal drought stress during grain filling is a primary abiotic factor limiting crop output in barley. In barley, the cytokinin-oxidase 2.1 (HvCKX 2.1) gene was noticed in their promoter regions of caryopsis when exposed to terminal drought, which is a stress-specific heterochromatic siRNA (hc-siRNA) of 24mer length [119]. Interestingly, seeds generated from drought-stressed mother plants showed a faster rate of shoot emergence, perhaps owing to an overabundance of cytokinin ribosides. When exposed to drought, multiple differentially methylated sites are activated in leaves of the barley plant rather than in roots [120,121]. It was also observed that barley exhibited a more significant amount of DNA methylation than other crops such as rice and maize, maybe because the barley genome has a large percentage of duplicated sequences [122]. Drought-stressed barley plants had more compact nucleosome packing, and HSP17 was identified as a drought-responsive gene [123].

4.1.3 Cold-induced stress

Plant metabolism and the transcriptome are affected by cold stress, with key metabolic enzymes directly inhibited and gene expression reprogrammed [124]. Yang et al. observed overexpressed two miRNAs from the miR319 family, OSA-mir319a and OSA-mir319b, resulting in morphological changes [125]. Research revealed that increased acetylation of H3K9 in the upstream promoter regions of a rice gene OsDREB1 was related to cold-stress resistance through means of ChIP analysis [126]. Under cold temperatures, significant alterations in the expression of miR319 were detected in rice and sugarcane [127]. Hu et al. [128] observed that pretreatment of maize with the histone deacetylase (HDAC) inhibitor trichostatin A strongly reduces the induction of cold-stress responsive genes ZmDREB1 and ZmCOR413 in maize. These results demonstrated that HDACs activate the ZmDREB1 gene in response to cold exposure through histone modifications and chromatin structural changes and that this activation was both gene and location-specific [128,129]. A further comprehensive examination of individual genomic repeats demonstrated that cold stress selectively and transiently un-silenced tandem repetitive regions, resulting in an increase in H3K9ac and reduced DNA methylation and H3K9me2. The tandem repeat genomic areas also underwent nucleosome remodelling [130]. Numerous transposable elements have also been reported that contribute towards the adaptability of a plant to environmental stress and a retro transposon-like motif that stays demethylated under cold stress [131]. While cold stress enhanced genome-wide DNA methylation in maize root tissues, genome sequencing showed that this 1.8 kb section, identified as ZmMI1, was demethylated after chilling treatment. Under normal circumstances, the same tract had a methylation percentage of roughly 38%, double that of other locations. This gene segment encodes a fragment of a hypothetical protein-coding gene, hinting that it is involved in chilling tolerance [129].

4.1.4 Heat-induced stress

Plants exposed to high temperature (heat stress, HS), significant abiotic stress due to increased global warming, suffer from severe, and sometimes lethal, adverse effects. Plants have evolved complex mechanisms to respond to this kind of stress in order to cope with such conditions [132]. Another study on rice and heat stress found that OsFIE1 facilitated seed size reduction (fertilization-independent endosperm). DNA methylation and H3K9me2 methylation were shown to be two variables that influence OsFIE1 expression. Further investigation found that both DNA and histone methylation reduced under heat stress situations (DNA methylation dropped by 8.8 and 6.6 percent, respectively, in the CH and CHG contexts) [133]. Histone acetyltransferases (HATs) carried out acetylation of OsHAG702, OsHAG704, OsHAC701 and OsHAC704 loci in turn promoted heat stress tolerance in rice [134]. The modification of histone H3 lysine 4 (H3K4) me1/2 in wheat up-regulated the gene encoding the lysine-specific histone demethylase 1 (LSD1), which was involved in histone demethylation and promoted heat stress tolerance [135]. Ni et al. [136] found that the histone acetyltransferase TaGCN5 gene in wheat is up regulated under heat stress and that it functions similarly to GCN5 in Arabidopsis and noticed the H3K9 and H3K14 acetylation levels in the promoters of TaHSF1, TaHSF4, TaMBF1c, TaHSP17.4, and TaHSP101 that were significantly increased [137].

It was also observed that few miRNA families were also involved in heat stress response. Among them miR156, miR167, miR168 and miR398 were down-regulated in rice [138], both up and down regulation was seen in miR160 [137], upregulation of miR167, miR156 and miR398 was studied in wheat [139] and in barley upregulation of miR160 and miR167 was identified [140]. Heat stress

slows the development of maize and drastically affects crop production. By raising histone acetylation and reducing H3K9me3 levels, heat stress has been demonstrated to trigger programmed cell death and modify chromatin structure [141]. Additionally, short-term heat stress generates dynamic H3K4me2 and H3K9ac modifications in the promoter regions of maize seedlings, which are related with enhanced heat stress factor (Hsf) and rRNA gene expression, as well as membrane disturbances and an increase in reactive oxygen species [142]. It is observed that Histone deacetylases (HDAC gene) were downregulated under heat stress, and immune blotting results demonstrated that histones H3K9ac and H4K5ac levels were increased under heat stress in maize [143].

4.1.5 Submergence-induced stress

On the one hand, the world is currently facing difficulty as a consequence of global temperature increase, which has resulted in severe drought; on the other hand, the unexpected and regular occurrence of floods has become devastating across the world. Submergence induces a cocktail of stressors on the plant, including nutritional deprivation, hypoxia, infection, and low light, all of which are averse to the plant's output and life. Increased expression of two rice submergence-induced genes—alcohol dehydrogenase 1 (ADH1) and pyruvate decarboxylase 1 (PDC1)—was shown to be connected with reversible histone modifications, H3 acetylation and H3K4 trimethylation, respectively, from H3K4 dimethylation [144].

4.1.6 Heavy metal-induced stress

Concentrations of heavy metals over a particular level may have cytotoxic, genotoxic, and mutagenic effects on plants, resulting in abiotic stress situations [145]. Cadmium (Cd) could hinder antioxidant enzyme activity, impede regular cell division, and lessen photosynthesis in soils at low concentrations (0.3–0.8 mg kg⁻¹) [146, 147]. Lead (Pb) accumulation is likely driven by Cd pollution in all major wheat-growing areas, posing a serious threat to crop yields and well-being [68]. Aluminium (Al) ions disrupt root development by reducing water and nutrient absorption in acid soils, resulting in lower crop yields [148]. DNA methylation is a critical epigenetic process in wheat and barley that regulates the plants' responses to environmental stresses such as salt and heavy metals [149, 150]. Wheat varieties than in heavy metal-sensitive varieties exposure to the heavy metal stresses. Suggesting that DNA methylation is associated with metal stress tolerance in wheat [150]. Meanwhile, low-level expression of HvAACT1 was found associated with a higher degree of DNA methylation in Multi Retrotransposon like MRL segments, suggesting that DNA methylation controls the expression of HvAACT1, the gene responsible for Aluminium stress tolerance in barley [151]. In the case of rice, the researchers discovered specific differentially methylated regions after Cd treatment, along with methylation patterns, and discovered that most epigenetically regulated genes were transcriptionally activated under Cd stress [152]. According to a report, heavy-metal stress caused locus-specific hypomethylation in treated rice seedling plants in somatic cells [153]. Ertuk et al. [154] identified excessive accumulation of zinc that reduced the activity of methyltransferases and caused hypomethylation of certain specific gene regions. Shafiq et al. [155] proposed that heavy metals alter the DNA methylation and histone acetylation levels through the activity of DNA methyltransferases and histone deacetylases mainly at ZIP transporters in the case of maize. Therefore in view of this prospect epigenetic modifications could be regarded as a valuable means for abiotic stress tolerance imposition.

Table 1. Examples of abiotic Stress tolerance through epigenetic regulation crop plants of family Poaceae.

1

Species	Type of Epigenetic mechanism	Locus/loci / element involved	Stress to which tolerant	Biological evidence	Reference
Rice	Histone acetylation	OsHAG702 OsHAG704 OsHAC701 OsHAC704	Heat	Histone acetyl transferases (HATs) mediated acetylation of these rice loci promoted heat stress tolerance	Liu et al 2012 [156]
		OsHAG703 OsHAM701 OsHAC703 OsHAF701	Drought	Histone acetyl transferases (HATs) mediated acetylation of these rice loci promoted drought tolerance	Fang et al. 2014 [157] Liu et al. 2012 [156]
	DNA methylation	Genome wide	Drought	Hypomethylation of cytosine residues observed in drought tolerant genotypes	Gayacharan and Joel 2013 [96]
				Genotype dependent differential site-specific DNA methylation observed in genotypes	Wang et al. 2011 [74]
				Difference in DNA methylation patterns observed in drought-tolerant and susceptible genotypes	Zheng et al. 2017 [107]
		OsMYB91	Salinity	Demethylation at the promoter region of, and rapid histone modifications at, OsMYB91 locus	Zhu et al. 2015 [43]
		Genome-wide		A set of differentially methylated regions (DMRs) identified between control and stress samples	Ferreira et al. 2019 [90]
				DNA methylation under salt stress in rice	Karan et al. 2012 [89]
		Metal transporters,	Heavy metal	Due to differential demethylated regions, epigenetically regulated genes were transcriptionally activated under Cd stress.	Feng et al. 2016 [152]

		transcription factors				
	RNA interference	miR170	Drought	Down regulation of miR170 expression	Zhou et al 2010 [158]	
		miR171		Up and down regulation of miR171 expression		
		miR172		Down regulation of miR172 expression		
		miR408		Up-regulation of miR408 expression	Muttum et al. 2013 [159]	
		miR319	Cold	Over expression of OsPCF5/PCF8 loci due to miR319	Yang et al. 2013 [125]	
Barley	DNA methylation	HvDME	Drought	Expression of HvDME was induced by drought stress, which was correlated with differential DNA methylation patterns within the gene	Kapazoglou et al. 2013 [41]	
		HvTX1		Expression of HvTX1 was induced during seed development under drought stress		Papaefthimiou and Tsaftaris 2012 [160]
		HvCKX2.1		Hyper-methylation of CYTOKININ-OXIDASE promoter 2.1 by Hv-siRNA		Surdonja et al. 2017 [119]
		HvAACT1	Heavy metal	Decreased expression of HvAACT1 was found associated with a higher degree of DNA methylation in Multi Retrotransposon like MRL segments responsible for Al stress tolerance	Kashino et al. 2018 [151]	
	Histone modification	H3K4me3H3K9ac H3K9me2 H3	Drought	Increase in H3K4me3, H3K9ac, H3 and loss in H3K9me2 activity was observed	Temel et al. 2017 [123]	
	RNA interference	miR408		Accumulation of miR408 transcripts was observed		Kantar et al. 2010 [161]
	Wheat	Histone acetylation	TaGCN5 H3K9 and H3K14	Heat	Under heat stress, the TaGCN5 gene in wheat is upregulated, and acetylation levels of H3K9 and H3K14 in the promoters of TaHSF1, TaHSF4, TaMBF1c, TaHSP17.4, and TaHSP101 were significantly increased.	Ni et al. 2018 [136]
Histone demethylation		H3K4me1/2	Heat	Gene encoding lysine-specific histone demethylase 1, involved in histone demethylation, was up-regulated	Wang et al. 2016 [162]	

	DNA methylation	TaGAPC1	Salinity	Promoter methylation of TaGAPC1 and its expression analysis under osmotic and salinity stress	Fei et al. 2017 [163]
		High-affinity potassium transporters (HKTs)		Tolerance to salt stress was conferred by differential expression of HKTs such that DMRs (differentially methylated regions) were also identified.	Kumar et al 2017 [139]
		Genomewide		Differential status of hypomethylation of the CCGG sequence analysed by MSAP technique	Zhong 2009 [164]
		TaFLS1		Methylation level at the promoter of stress-responsive gene TaFLS1 was lesser in salinity tolerant cultivar	Kong et al 2020 [165]
		Genome wide	Drought stress	Increased water deficiency led to increased tissue specificity of 5mC content and methylation level of wheat seedling, increasing significantly in leaf	Duan et al. 2020 [166]
		TaABCCs, TaHMA2	Heavy metal	DNA methylation levels at the promoter of TaABCCs and TaHMA2 were lower in heavy metal-resistant varieties than in heavy metal-sensitive varieties	Shafiq et al. 2019 [155]
Maize	DNA methylation	Genome-wide	Cold	Global methylation shift	Tan, 2010 [167]
		ZmMII		Root-specific hypomethylation	Steward et al. 2002 [129]
		ZIP transporters	Heavy metal	Heavy metals alter the DNA methylation and histone acetylation levels through the activity of DNA methyltransferases and histone deacetylases, mainly at ZIP transporters	Shafiq et al. 2020 [155]
	Histone modification	H3K9ac H3K9me2	Cold	Decreasing trend in histone acetylation in euchromatin associated gene regions Accumulation of H3K9ac and decrease in H3K9me2	Hu et al. 2011[128] Hu et al. 2012[130]
		H3K4me3 H3K9ac		Drought	Modifications of H3K4me3 and H3K9ac dynamics
		H3K36me3	Enrichment in H3K36me3, H3K9ac and H3K4me3		Xu et al. 2017 [113]

		H3K9ac H3K4me3			
		H3K4me2 H3K9ac	Heat	H3K4me2 and H3K9ac alterations	Hou et al. 2019 [142]
		H3K9me3		Increased histone acetylation and decreased H3K9me3	Wang et al. 2015 [169]
		Zm HDACs		HDAC genes were downregulated while levels of H3K9ac and H4K5ac increased under heat stress	Zhang et al. 2020 [143]
	RNA interference	PDH POK MAPK PLD	Drought	11 different miRNA were up-regulated under exposure to drought	Wei et al. 2009 [170] Kantar et al. 2011 [171]
		MEDIATOR OF PARA MUTATION1 (MOP 1)	Abiotic stress response	In response to ABA, some genotypes expressed MOP1-RdDM loci, suggesting environmentally-induced transcriptional responses being influenced by epigenetic variation	Vendramin et al. 2020 [172]

4.2 Epigenetic modifications for adaptation to biotic stress tolerance

Compared to abiotic stresses, there are fewer reports on epigenetic modifications for adaptation to biotic stresses. Few of these examples are enumerated in Table 2. In rice, one such example is the association of monoubiquitinated H2A and H2B histones with promoter regions targeted by the gene BRHIS1 (encoding SNF2 ATPase), which results in the suppression of immunity against the fungal pathogen that causes blast [173]. Rice has inheritable DNA methylation changes in response to salt and nitrogen deficiency stress. Notably, demethylation of the Xa21G promoter region was induced artificially to confer resistance to *Xanthomonas oryzae* pv. *Oryzae* overcomes the constitutive silence of the gene, which is caused by hypermethylation, resulting in the host developing resistance to infection. [174]. Deng et al. discovered that the rice Pigm locus contains a cluster of genes encoding nucleotide-binding leucine-rich repeat (NLR) receptors that impart long-lasting resistance to the fungus *Magnaporthe Oryzae* without jeopardising yield. This study elucidates a mechanism for balancing disease resistance and yield via epigenetic regulation of paired antagonistic NLR receptors, thereby paving the way for the development of elite crop varieties [175]. According to Li et al. DNA methylation of the promoter region of *Pib* gene plays a significant role in configuring high levels of its induced expression during *Magnaporthe grisea* infection [176] and JM705, a biotic stress-responsive H3K27me2/3 demethylase [177].

JM704 enhances rice resistance to *XanthomonasOryzae*pv. *Oryzae* infection by lowering H3K4me2/3, associated with negative disease resistance regulators [178]. A research by Demetriou et al. identified that the HD2 genes in barley have been linked to plant resistance to biotic stress conditions by enhancing Abscisic acid (ABA), Salicylic acid (SA), and Jasmonic acid (JA) levels, implying that they are involved in stress resistance. HD2 genes' expression pattern suggests they could play a role in epigenetic control of seed development and stress response, according to the information [179, 180]. Few reports showed that fungal pathogens account for 15% to 20% of annual yield losses in wheat [181,182]. Differences in the expression of genes encoding methyltransferases, non-coding RNAs, and histone acetylases/methyltransferases mediated by Lr28 related to *Pucciniatriticinaleaf* rust resistance.were discovered in previous transcriptome results [183]. With the development of high-throughput sequencing technology and computational methods, the research of ncRNA has been carried out gradually in wheat and barley [184-186]. Non-coding RNAs (ncRNAs), such as microRNAs (miRNAs), target mimics (TM), and other long non-coding RNAs (lncRNAs), have been implicated in the response to spot blotch disease and should be investigated in the same way that yellow rust and other abiotic stressors have been in wheat [187, 188].

In wheat diploid progenitor *Aegilopstauschii*, DNA methylation, specifically CHH methylation, is involved in the regulation of defence responses to Bgt (*Blumeria graminis* f. sp. *tritici*), the causal agent of wheat powdery mildew, according to a recent study. Differentially methylated regions (DMRs) were found to be associated with hypomethylation of CHH after Bgt infection [189]. qRfg1 is a causal gene in maize that is encoded by the ZmCCT gene, which is a CCT domain-containing gene that also contains a polymorphic CACTA-like transposable element (TE1) c. It is located 2.4 kilobases upstream of the ZmCCT gene, which is involved in human allelic variation. The non-TE1 ZmCCT allele appears to be poised, with both repressive (H3K27me3/H3K9me3) and active (H3K4me3) histone marks present in the anticipated bivalent chromatin of the non-TE1 ZmCCT allele. In this non-TE1 ZmCCT allele, there was a rapid but transient decrease in H3K27me3/H3K9me3 and a progressive decrease in

H3K4me3, resulting in disease resistance to *Fusarium graminearum*'s Gibberella stalk rot, a maize-deadly disease [190]. Therefore, there was ample studies available on biotic stress tolerance through epigenetic means especially in poaceae family.

Table 1. Examples of biotic Stress tolerance through epigenetic regulation crop plants of family Poaceae.

Species	Type of Epigenetic mechanism	Locus/Loci involved	Nature of involved locus/loci	Biological Evidence	Reference
Rice	Epigenetic regulation	PigmR PigmS	Antagonistic receptors	Through epigenetic regulation of paired antagonistic NLR receptors, a technique has been developed that balances disease resistance and yield.	Deng et al. 2017 [175]
	DNA methylation	<i>Pib</i>	CpG islands; cytosine methylated	Promoter DNA methylation played an enhancing role in high-level expression of <i>Pib</i> gene during infection by <i>Magnaporthe grisea</i>	Li et al. 2011 [177]
	Histone deacetylation	HDT701	HD2 subfamily of HDACs	After infection with <i>Magnaporthe Oryzae</i> , transcription of HDT701 increased in compatible reactions and decreased in incompatible reactions.	Ding et al. 2012 [191]
	Histone demethylation	JMJ704 H3K4me2/3	Demethylation; di- and tri- methylation	JMJ704 suppressed the transcription of rice defense negative regulator genes <i>NRR</i> , <i>OsWRKY62</i> and <i>Os-11N3</i> by activating H3K4me2/3, imposing tolerance to bacterial blight	Hou et al 2015 [178]
	Histone methylation	JMJ705	lysine 27 (H3K27me2/3)	Expression of MJM705 is induced by stress signals during pathogen infection	Li et al 2013[176]

Barley	Histone Deacetylation	HvHDAC2-1 HvHDAC2-2	Histone deacetylase	Significant differences were observed in plants under biotic and abiotic stress	Demetriou et al. 2009 [179]
Wheat	Histone deacetylation	TaHDA6		TaHDA6 represses histone acetylation at promoters of defence-related genes, thus negatively regulating their expressions as well as plant defense responses to wheat PM (Bgt; <i>Blumeriagraminisf.sp. tritici</i>)	Liu et al. 2019 [192]
	Histone acetylation	TaGCN5	Histone acetyltransferase	Expression of wheat geneTaGCN5 in Arabidopsis gcn5 mutant for salt tolerance	Zheng et al. 2019 [193] Hu et al. 2015 [194]
	Chromatin remodeling	TaCHR729	Chromatin remodeling factor	TaCHR729 promotes H3K4me3 at TaKCS6 Promoter sites, positively regulating TaKCS6 expression; cuticular wax biosynthesis thus affects wheat-Bgt interaction	Wang et al 2019 [195]
	Non-coding RNA	TalncRNA18 TalncRNA73 TalncRNA106 TalncRNA108	Lnc RNA	They exhibit differential expression and target wheat defence-related genes in response to pest infections	Zhang et al. 2018 [196]
Maize	Chromatin remodeling	ZmCCT is the causal gene at the qRfg1 locus	Chromatin remodeling factor	Gibberella stalk rot resistance in maize	Wang et al 2017 [190]

5. Conclusion and Future Prospects

As climate change is expected to increase the prevalence of extreme weather conditions, crops will become more vulnerable to various biotic and abiotic stresses. Therefore, enhanced stress tolerance becomes a significant breeding objective. Understanding of mechanisms that lead to one or more concurrently occurring stresses becomes important for their improvement. Evidence in favour of epigenetic mechanisms playing a role in increasing crop resilience to specific stresses is mounting by the day. An insight into the epigenetic mechanisms leading to stable, heritable phenotypic variation without changes in the underlying DNA sequence can potentially help plant breeders generate flexible varieties by exploiting such phenomena, providing an environment buffer under a rapidly changing climate. The recognition of epialleles and epigenetic regulatory systems with functional impacts on agronomic traits can lead to a range of epigenetic breeding strategies for crop plants, including the use of mutant lines, recurrent epi-selection, hybrid mimics, epigenomic selection and epigenome editing, along with exploitation of stress priming pathways to induce a constitutively primed state and increase the ability of the crop to tolerate stress without the undesired reduction in biomass accumulation and yield. Thus, epigenetics, together with functional genomics, has multiple implications in plant breeding. Traditional breeding methods for improving crop varieties are tedious, time-consuming, and expensive, and are unable to meet today's pragmatic demands. Epigenetics holds a great promise for improving plant varieties in terms of yield and nutritional quality through the creation of novel epialleles and through transgenic RNAi approaches.

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