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REVIEW

Epigenomics in stress tolerance of plants under the climate change

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Abstract

Background Climate change has had a tremendous impact on the environment in general as well as agricultural crops grown in these situations as time passed. Agricultural production of crops is less suited and of lower quality due to disturbances in plant metabolism brought on by sensitivity to environmental stresses, which are brought on by climate change. Abiotic stressors that are specific to climate change, including as drought, extremes in temperature, increasing CO_2, waterlogging from heavy rain, metal toxicity, and pH changes, are known to negatively affect an array of species. Plants adapt to these challenges by undergoing genome-wide epigenetic changes, which are frequently accompanied by differences in transcriptional gene expression. The sum of a cell's biochemical modifications to its nuclear DNA, post-translational modifications to histones, and variations in the synthesis of non-coding RNAs is called an epigenome. These modifications frequently lead to variations in gene expression that occur without any alteration in the underlying base sequence.

Epigenetic mechanisms and marks The methylation of homologous loci by three different modifications—genomic (DNA methylation), chromatin (histone modifications), and RNA-directed DNA methylation (RdDM)-could be regarded as epigenetic mechanisms that control the regulation of differential gene expression. Stresses from the environment cause chromatin remodelling, which enables plant cells to adjust their expression patterns temporarily or permanently.

Epigenomics' consequences for genome stability and gene expression DNA methylation affects gene expression in response to abiotic stressors by blocking or suppressing transcription. Environmental stimuli cause changes in DNA methylation levels, either upward in the case of hypermethylation or downward in the case of hypomethylation. The type of stress response that occurs as a result also affects the degree of DNA methylation alterations. Stress is also influenced by DRM2 and CMT3 methylating CNN, CNG, and CG. Both plant development and stress reactions depend on histone changes. Gene up-regulation is associated with histone tail phosphorylation, ubiquitination, and acetylation, while gene down-regulation is associated with de-acetylation and biotinylation. Plants undergo a variety of dynamic changes to histone tails in response to abiotic stressors. The relevance of these transcripts against stress is highlighted by the accumulation of numerous additional antisense transcripts, a source of siRNAs, caused by abiotic stresses. The study highlights the finding that plants can be protected from a range of abiotic stresses by epigenetic mechanisms such DNA methylation, histone modification, and RNA-directed DNA methylation.

Transgenerational inheritance and sources of epigenetic variation Stress results in the formation of epialleles, which are either transient or enduring epigenetic stress memory in plants. After the stress is gone, the stable memory is kept for the duration of the plant's remaining developmental cycles or passed on to the next generations, leading to plant evolution and adaptability. The bulk of epigenetic changes brought on by stress are temporary and return to normal after the stress has passed. Some of the modifications, however, might be long-lasting and transmitted across mitotic or even meiotic cell divisions. Epialleles often have genetic or non-genetic causes. Epialleles can arise spontaneously due to improper methylation state maintenance, short RNA off-target effects, or other non-genetic causes. Developmental or environmental variables that influence the stability of epigenetic states or direct chromatin modifications may also be non-genetic drivers of epigenetic variation. Transposon insertions that change local chromatin and structural rearrangements, such copy number changes that are genetically related or unrelated, are two genetic sources of epialleles.

Epigenomics in crop improvement To include epigenetics into crop breeding, it is necessary to create epigenetic variation as well as to identify and evaluate epialleles. Epigenome editing or epi-genomic selection may be required for epiallele creation and identification. In order to combat the challenges given by changing environments, these epigenetic mechanisms

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have generated novel epialleles that can be exploited to develop new crop types that are more climate-resilient. Numerous techniques can be used to alter the epigenome generally or at specific target loci in order to induce the epigenetic alterations necessary for crop development. Technologies like CRISPR/Cas9 and dCas, which have recently advanced, have opened up new avenues for the study of epigenetics. Epialleles could be employed in epigenomics-assisted breeding in addition to sequence-based markers for crop breeding.

Conclusions and future prospectus A few of the exciting questions that still need to be resolved in the area of heritable epigenetic variation include a better understanding of the epigenetic foundation of characteristics, the stability and heritability of epialleles, and the sources of epigenetic variation in crops. Investigating long intergenic non-coding RNAs (lincRNAs) as an epigenetic process might open up a new path to understanding crop plant's ability to withstand abiotic stress. For many of these technologies and approaches to be more applicable and deployable at a lower cost, technological breakthroughs will also be necessary. Breeders will probably need to pay closer attention to crop epialleles and how they can affect future responses to climate changes. The development of epialleles suitable for particular environmental circumstances may be made possible by creating targeted epigenetic changes in pertinent genes and by comprehending the molecular underpinnings of trans generational epigenetic inheritance. More research on a wider variety of plant species is required in order to fully comprehend the mechanisms that produce and stabilise epigenetic variation in crops. In addition to a collaborative and multidisciplinary effort by researchers in many fields of plant science, this will require a greater integration of the epigenomic data gathered in many crops. Before it may be applied generally, more study is required.

Keywords Epigenetics · Transcriptional gene expression · DNA methylation · Acetylation · Nucleosome · Non-coding RNA · Chromatin remodelling · Histone proteins · Climate resilience

Introduction

The environment in general and agricultural crops grown in these conditions has been significantly impacted by climate change over time. The Intergovernmental Panel on Climate Change (IPCC) has stated that the most notable factor adversely affecting agricultural output in lowlands primarily tenanted by developing nations is stress, which is faced by crops as a result of shift in climatic conditions [1]. Both the environmental temperature and the quantity of carbon dioxide in the air increase due to switch in climatic conditions [2]. Due to these considerable constraints on the availability of food and a healthy environment, the majority of researchers are looking for effective plant adaptation strategies [3], such as establishing plant varieties and smart crops that are hardy to the consequence of climate change [4]. Due to disruptions in plant metabolism caused by vulnerability to these stresses, which are brought on by climate change, agricultural crop production is less suitable and of poor quality [5]. Individual climate change stressors are abiotic in nature [6], and they stress out various species: these abiotic stressors include drought, low and high temperature, elevated CO2 [7], waterlogging, heavy rainfall, metal toxicity, and pH alterations. To cope up these stresses, however, is complicated due to their interdependence [8], with the main problem being to understand how these plants respond to diverse stressors, the diverse response pathways activated by them, and their genetic determination [9].

Due to their sessile nature, plants must have evolved specific adaptation strategies to cope up with shifting environmental conditions, especially when resources are scarce. Plant breeders typically use trait variation caused by changes in DNA sequence brought on by mutations to quantify heritability and enhance trait performance in plant populations. Studies have shown that changes in chromatin states can explain plants' reactions to stress in addition to variations in DNA sequence [10]. The addition of methyl groups can modify chromatin architecture quickly and reversibly [11]. The term epigenetics derives from Aristotle's ancient notion of epigenesis, which he created in order to refute the preformation theory which was proposed by Jan Swammerdam and Charles Bonnet (1720–1794). The contemporary idea of epigenetics, on the other hand, was established in the twentieth century by Waddington (1942) [12] in the proposed model of "Epigenetics Landscape" [13]. Today, there are two different categories of widely accepted epigenetic definitions. One set of concepts is based on genetic inheritance and behavior. In these definitions, epigenetics is defined as inherited (meiotic or mitotic) changes in gene expression without alterations in the DNA sequence [14]. The alternative description type considers any change in chromatin to be epigenetic and is based on the biochemical properties of chromatin. Here, the terms "epigenetics" and "chromatin alterations" are used to refer to the genetic behavior of a system and changes in the biochemical characteristics of chromatin respectively. The term "epigenomics" describes genome-wide maps of chromatin that may include genome profiles of chromatin accessibility, DNA methylation, and variations in histone proteins. The epigenome is an

Table 1 Epigenetic mechanisms in response to different abiotic stresses in plants

Plant	Abiotic stress	Epigenetic mechanism (s)	Reference
Maize	Drought	Enrichment in H3K36me3, H3K9ac, and H3K4me3	[24]
		Modifications of H3K4me3 and H3K9ac dynamics	[25]
	Heat	Increased histone acetylation and decreased H3K9me3	[26]
		H3K4me2 and H3K9ac alterations	[27]
	Cold	Demethylation of gene *ZmMI1*	[28]
		DNA demethylation	[29]
		Enrichment in H3K9ac and decrease in DNA methylation and H3K9me2	[30]
		Reduction in histone acetylation in euchromatin-associated gene regions	[31]
Wheat	Heat	Increased histone demethylation of the various genes	[32]
	Salinity	5-methylcytosine depletion	[33]
		Hypermethylation of cytosines at *HKT* genes	[34]
Barley	Drought	Accumulation of miR408 transcripts	[35]
		H3K4 methyltransferase of gene *HvTX1*	[36]
		Hc-siRNA-mediated hyper-methylation at *CYTOKININ-OXIDASE 2.1* promoter	[37]
		Increase in H3 and loss in H3K9me2	[38]
Rice	Drought	Site-specific DNA methylation	[39, 40]
		Hypomethylation	[41]
		Up-regulation of miR408 expression	[42]
	Salinity	DNA methylation	[43]
		Demethylation at promoter region of *OsMYB91* gene and rapid histone modifications at *OsMYB9* locus	[44]
		DNA methylation	[45]
Soybean	Drought	Up-regulation of isomiRNAs	[46]
		miR1514a modulation of a NAC transcription factor transcript	[47]
	Heat	Hypomethylation of cytosine	[48]
Pea	Drought	Hypermethylation of cytosine residues	[49]
Chickpea	Drought	Accumulation of miR408 transcripts	[50]
	Drought and salinity	Accumulation of miRNAs at root apex	[51]
Cowpea	Drought	Increase of *P5CS* transcripts and very low expression of vun-miR5021 and vun-miR156b-3p	[52]
Bean	Drought	Dicistronic arrangement of miR398a and miR2119	[53]
Fababean	Drought	Increased DNA demethylation *LOX*, *CDPK*, *ABC*, *GH* and *PEPC* genes	[54]
Alfalfa	Drought	Overexpression of miR156	[55]
Rapeseed	Heat	Increased DNA demethylation	[56]
	Salinity	Increased DNA demethylation	[57]
Chinese cabbage	Cold	Long noncoding RNA (LncRNA) leads to epigenetic modification at *BrFLC2as* locus	[58]
Tomato	Drought	RNA-dependent DNA methylation	[59]
		Increased *Asr1* and *Asr2* expression due to demethylation of putative regulatory and transcribed regions	[60]
	Salinity and drought	*SlAGO4 A*, an ortholog of *AtAGO4* plays negative role through modulation of DNA methylation and RNAi pathway	[61]
	Cold	Increased DNA methylation	[62]
Beta vulgaris	Salinity	Elevated acetylation of H3K9 and H3K27 led to activation of *POX* gene	[63]
Arabidopsis	Salinity and drought	Higher histone acetylation (H3K9) in promoter regions of 14 genes	[64]
	Salinity	Loss in cytosine methylation in a putative small RNA gene *AtHKT1*	[65]
		Increased acetylation of histone H4 at *AtSOS1* due to inhibition of deacetylase	[66]
	Cold	Non-CG hypermethylation under cold and low light stress	[67]

Table 1 (continued)

Plant	Abiotic stress	Epigenetic mechanism (s)	Reference
	Drought	Histone methylation (H4R3sme2) in the promoter region of *ANACo55* gene	[68]
		Demethylation of H3K4me2 and H3K4me3 of the gene *JMJ17*	[69]
	Salinity and abscisic acid	Hypomethylation at *DRM2* gene under salinity conditions	[70]
	Affects UV-B absorption, oxidative stress	Acetylation of H3K56ac, H4K5ac of gene *HAG3*	[71]
	Heat, cold, and salinity	Acetylation of H3K9ac, H3K14ac; dimethylation and trimethylation of H3K4me2, H3K4me3 of gene *HAC1*	[72]
	ABA and salt stress responses by interacting with HDA6, adaptation to heat stress	Deacetylation of H3K9ac/K14ac; dimethylation and trimethylation of H3K9me2 and K3K4me3 of *HD2C* gene	[73, 74]
Hydrilla verticillata	Copper stress	Hypermethylation caused over-expression of *DRM*, *CMT* and *SUVH6* genes	[75]
Mangrove tree (*Bruguiera gymnorhiza*)	Salinity	Methylation level was highest in the CG context, followed by CHG and then CHH in each gene region	[76]
Populus trichocarpa	Drought	Hypermethylation of CG and CHG higher than CHH region	[77]
Eucalyptus grandis × *E. urophylla* and *E. urophylla*	Water stress	Clone/genotype-specific DNA methylation changes at specific sites	[78]
Populus tremula × *Populus alba*	Drought	Downregulation of the chromatin remodeler *Decreased in DNA METHYLATION1(DDM1)* in RNAi lines	[79]
Hydrocotyle vulgaris	Flood	Variability contributed by unmethylated and CHG-hemimethylated epigenetic states	[80]
Fragaria vesca	High/low temperature	Changes in DNA methylation pattern	[81]
Trifolium pratense	Drought and high pH	Changes of methylation in the CG context (m-subepiloci) may play a more important role for habitat adjustment than regulation of gene function in the CHG context (h-subepiloci)	[82]

assembly of chromatin patterns in a cell that can hold both heritable and transitory details [15]. Genetic and biochemical methods have recently increased our understanding of various epigenetic mechanisms, including histone modification, DNA methylation, and RNA-mediated gene silencing. These mechanisms are inter-linked as DNA methylation is required for chromatin modifications and vice versa, and both these processes are controlled by RNAi-based mechanisms [16].

Epigenetic mechanisms and marks

There are three modifications at various levels i.e. genomic (DNA methylation), chromatin (histone modifications), and RNA-directed DNA methylation (RdDM), which lead to the methylation of homologous loci could be considered as epigenetic mechanisms that affect the regulation of differential gene expression. The environmental stresses lead to chromatin remodeling which allows plant cells to fine-tune the expression profiles to adapt transiently or permanently [16].

DNA methylation

Symmetrical (CNG/CG) and non-symmetrical (CNN where N = C/A/T) DNA methylation pattern has been found in plants. Symmetrical methylation is easily copied followed by DNA replication, while non-symmetrical methylation is created de novo after each cycle of DNA replication [17]. Enzymes METHYL TRANSFERASE1 (MET1) and CHROMOMETHYLASE3 (CMT3), carries out CG and CHG methylation in plants respectively [18]. There are two mechanisms operated for de novo CHH methylation in crop plants. The creation of 24-nt siRNAs (small interfering RNAs) that are targeted to pertinent genomic loci by members of the ARGONAUTE (AGO) family and methylated via DOMAINS REARRANGED METHYL TRANSFERASE2 (DRM2) constitutes the first mechanism of RNA-dependent DNA methylation. In chromatic regions where histone H1 is abundant, CHROMOMETHYLASE2 (CMT2) must interact with DECREASE IN DNA METHYLATION1 (DDM1) in order for a second mechanism to work [19]. Cytosine demethylation is also necessary because it regains changed sites to their original state, which again affects

gene expression. Either a passive or active technique can be used to remove the methyl group from cytosines. Passive mechanism refers to the incorporation of unmodified cytosines during the process of DNA replication, which may be caused by the decrease of activity of maintenance DNA methylases, including MET1 and CMT3 [20]. The inactivity of the enzyme causes a progressive decline in DNA methylation in succeeding generations [21]. Additionally, a family of bifunctional methyl-cytosine glycosylases-apyrimidinic/apuriniclyases can actively draw out DNA methylation through a nucleotide excision repair mechanism [22]. DNA methylation may control gene expression, regulate imprinting, and activate transposable elements (TEs) and TEs associated genes, particularly in response to environmental signals against several abiotic stresses in plants [23] (Table 1).

Histone modification

DNA accessibility for transcription process is modulated by nucleosome positioning [83]. Each nucleosome core is made up of a histone octamer with two copies each of histone H_4, H_3, H_{2A} and H_{2B} with nearly 146 base pairs positioned in two turns.Depending on the degree of compaction of nucleosome, H_1, the linker histone, connects unpackaged DNA to nucleosomes of variable length. Post transcriptional modifications of histone tails lead to alterations in interactions between histone and DNA. Moreover, similar phenomena called as histone code controls chromatin condensations and accessibility of DNA [84]. Well intended reversible changes *i.e.* histone methylation and demethylation as well as histone acetylation and deacetylation were reported in plants [85]. Transcriptional activation is associated with acetylation of H3K9ac (histone 3 lysine 9 acetylation), H3K14ac (histone 3 lysine 14 acetylation), and H3K36ac (histone 3 lysine 36 acetylation) whereas repression linked with the deacetylation of histones at similar positions.

Depending on where it happens, histone methylation can either suppress or activate genes for instance H3K4 (histone H3 lysine4) and H3K36 methylation are associated with gene activation, whilst H3K9 and H3K27 methylation are associated with gene repression. Histone H3 lysine9 monomethylation (H3K9me1) and dimethylation (H3K9me2) designate transposable elements (TEs) and repetitive base sequence-enriched heterochromatic areas in plants, that conserve the repressive transcriptional state. H3K27me1 is also associated with heterochromatin regions, whereas the trimethylated form of H3K27 i.e., H3K27me3 is repressive in euchromatin regions. Throughout the entirety of the transcribed region of dormant genes, H3K27me3 is especially prevalent [86]. Histone alterations require a large amount of enzymatic machinery, including important enzymes such as histone methyltransferase (HMT), histone acetyltransferase (HAT), histone de-methylase (HDM), and histone de-acetylase (HDAC) [87]. The transfer of up to three methyl groups (-CH3) to the lysine and arginine residues of H_3 and H_4 is catalysed by the enzyme histone methyltransferase (HMT). Different genes are silenced and expressed in response to various abiotic stimuli in plants, which is a crucial survival tactic in plants (Table 1).

RNA-directed DNA methylation

RNA-directed DNA methylation (RdDM) is caused by double-stranded RNA (ds-RNA) molecules inducing sequence-specific methylation. Given that RdDM and RNA interference (RNAi) are related, it is likely that short RNAs play a part in activating and directing cytosine methylation [88]. MicroRNAs are non- coding RNA structures that play a role in RNA silencing and post-transcriptional regulation of gene expression in plants. They are encoded by eukaryotic nuclear DNA [89]. Double-stranded small interfering RNAs (siRNAs) have the ability to silence genes during both the transcriptional (RNA silencing) and post-transcriptional stages of gene expression.

Endogenous siRNAs in plants are classified into three types: trans-acting siRNAs, natural antisense siRNAs, and heterochromatic-siRNAs [90]. Through RdDM and histone methylation, these siRNAs are responsible for mediating gene silencing [91]. These RdDM pathways govern development, maintain genomic stability, and regulate adaptive responses to a variety of stress circumstances mostly abiotic [92]. Asymmetric methylation is lost in the absence of RdDM, but CHG methylation is adeptly maintained by the maintenance methyltransferase1 (MET1) and chromomethyltransferase3 (CMT3) [93]. Long non-coding RNAs (lncRNAs), which differ from short RNAs in that they are transcripts longer than 200 nucleotides and can interact with both proteins and nucleic acids, serve as scaffolding for the formation of specialized functional complexes in the nucleus. Long non-coding RNAs and small RNAs (miRNAs and siRNAs) have a substantial impact on how well organisms tolerate abiotic stressors. Additionally, the gene regulation mediated by these RNAs may be inherited and contribute significantly to the epigenetic processes involved in the plant's stress tolerance system. (Table 1).

Role of epigenomics in gene expression and genome stability in response to abiotic stresses

By preventing or suppressing transcription, DNA methylation modifies gene expression in response to abiotic stresses [94]. Environmental stimuli lead to changes in extent of DNA methylation either upward in case of hypermethylation

or downward in hypomethylation and consequent changes in degree of DNA methylation also depends upon the type of stress response prevalent [14]. Under saline conditions hypermethylation was reported in mangrove and rice plants [43]. While drought-tolerant rice genotypes were hypomethylated, rice genotypes cultivated under drought conditions tended to be hypermethylated [41].

The methylation of CNN, CNG, and CG by DRM2 and CMT3 also play a role in stress. In rice, CG methylation is found primarily in genic regions, whereas non-CG methylation (CHH and CHG) is mostly found in TEs [95]. As a result, tobacco plants exposed to cold and salt stress in the presence of paraquat and aluminium have shown CG demethylation in the coding area of the *NtGPDL* (*glycerophosphodiesterase-like protein*) gene [96]. Hypermethylation of CG and CHG islands of pea genome and satellite DNA of halophytes respectively due to osmotic stress leads to shift in C_3 pathway to CAM (crassulacean acid metabolism) [97]. Moreover, after the withdrawal of stress, hypermethylation reverts back to its original state. In this context, Kovarik et al. [98] delineated CHG hypermethylation under the saline and osmotic stress of tobacco suspension culture and subsequently reversion occurs under the normal conditions. In contrast to it, demethylation does not revert back when chilling stress is removed in maize [29]. There are several different ways that methylation and demethylation at genic or non-genic regions might affect the transcript that is produced. It has been demonstrated that methylating the gene's flanking sequence, 3′ region, and promoter suppresses gene expression. Methylation in the promoter region is associated with gene down regulation, but methylation in the genic region has a parabolic connection with transcription. Genes with low expression levels are more likely to be methylated, whereas genes with high expression levels are less likely to be methylated [95, 99]. Transposable elements' distinctive methylation patterns contribute to the way that plants acquire different adaptations [100]. A retrotransposon-like sequence (ZmMI1) revealed demethylation patterns in maize roots under cold stress [28]. Severe cold stress in *Antirrhinum majus* reduced methylation status and elevated the excision rate of a specific transposon, *Tam3* [101]. Stress-mediated induction of transposons has been observed for *Tos17* (rice) [102], *Tnt1* (tobacco) [103], and BARE-1 (barley) [104]. Recent research has also revealed that some retrotransposons (ONSEN, an LTR-copia type retrotransposon in *Arabidopsis*) use demethylation to activate themselves under heat stress [105]. Histone alterations are important for both plant growth and stress responses. While histone tail phosphorylation, ubiquitination and acetylation, are related to gene up-regulation, de- acetylation and biotinylation are connected with down-regulation of genes [106]. In response to abiotic stresses, plants experience a variety of dynamic alterations to histone tails. Cold, salt stress, and abscisic acid (ABA) all caused H3 Ser10, H3 Ser10, and H4 lys14 to be phosphorylated, phospho-acetylated, and acetylated, respectively, in tobacco plant cells [107]. This histone modification causes an upregulation of stress-related genes. Increased acetylation of H3K9 and H3K4 in the coding areas of dehydration sensitive genes *i.e.,* Rd29A, RD29B, RD20, and RAP2.4 of *Arabidopsis* results in their upregulation [108]. In *Arabidopsis* and wheat, UV-B exposure increased acetylation of H3K9/K14 in the promoter area of *ELIP1* [109]. Chen et al. [106] discovered that ABA and salt stress-induced gene activation is related with the elevation of marks such as H3K9/K14ac and H3K4me3, as well as the reduction of gene repression marks such as H3K9me2 at ABA and other abiotic stress-responsive genes. The offsprings of stressed plants displayed hypermethylation after being exposed to varied levels of salt stress in *Arabidopsis* plants [110].

The accumulation of multiple new antisense transcripts, a source of siRNAs, induced by abiotic stressors highlights the importance of these transcripts against stress [111]. Hc-siRNAs, siR441 and siR446 were discovered to be downregulated in response to abiotic challenges but show a surge in the synthesis of their precursors, signaling that the processing of siRNA precursors is hindered, which seems to be a stress responsive mechanism [112]. Furthermore, nat-siRNAs (Natural antisense short interfering RNA) and ta-siRNAs (*Trans*- acting siRNA) have been known to have direct implications against stress response. Under salt stress, *Arabidopsis* forms nat-siRNAs by double-stranded overlapping antisense transcription of the gene *P5CDH (DELTA1-PYRROLINE-5-CARBOXYLATE DEHYDROGENASE*), which results in buildup of proline in cell [113]. One crucial metabolite thought to be involved in salt tolerance is proline. Plant development is regulated by the presence of Ta-siRNAs in stressful conditions [114]. Furthermore, siRNA can affect one-third of the methylation of chromosomal sites since they are associated with RdDM [115]. SlAGO4, a substantial orthologue of AGO4 (the main factor of RdDM), performs a crucial role in tomato under drought and salt stress [61]. RdDM is crucial to the tobacco plant's defense against Gemini virus infection, according to iTRAQ study on the plant [116]. Twenty six new miRNAs that were either up- or down-regulated by abiotic stresses were discovered in a study of *Arabidopsis* seedlings [117]. Cold stress was discovered to downregulate miR319 in rice [118], but multiple families of miRNAs were found to be over expressed in *Brachypodium* [119]. In these plants that respond to stress tolerance, these variations in miRNA concentration are associated with an important modulation of miRNA targets. Table 1 lists report that epigenetic mechanisms, such as DNA methylation, histone modification, and RNA-directed DNA methylation, can protect plants from a variety of abiotic stresses.

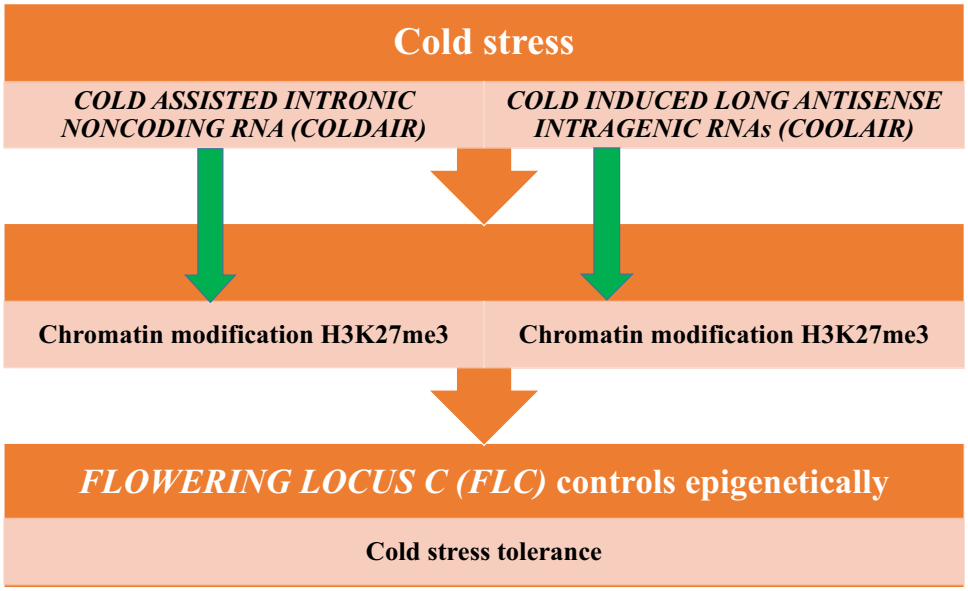

Fig. 1 Long non-coding mediated epigenetic silencing in plants

In cold-climate adapted plant species, vernalization is a well-known process that suppresses flowering during vegetative growth in winter and, under favorable circumstances in spring, enables flowering during the reproductive phase [120]. *FLOWERING LOCUS C (FLC)* is a well-studied regulatory locus in *Arabidopsis* that regulates flowering period epigenetically [121]. Additionally, *FLC* prevents *Arabidopsis* from blossoming in a cold climate [122]. In this context, Polycomb-mediated epigenetic regulation, which involves lncRNAs in lowering *FLC* locus expression through the vernalization mechanism, is a well-established technique for altering cold acclimation in *Arabidopsis*. As a result of chromatin alteration at the *FLC* locus during vernalization (decreasing active histone mark H3K36me3 and augmenting repressive histone mark H3K27me3), COLD INDUCED LONG ANTISENSE INTRAGENIC RNAs (COOLAIR), an alternatively, spliced NAT lncRNA, are responsible for *FLC* locus repression [123]. It has been discovered that in the species *Arabidopsis thaliana*, *A. alpina*, and *A. lyrata*, the class I antisense COOLAIR regulates *FLC* repression during vernalization [124]. Similar to this, the *FLC* gene intron1-coded COLD ASSISTED INTRONIC NONCODING RNA (COLDAIR) draws the Polycomb Repressive Complex2 (PRC2), which assists in *FLC* locus chromatin modification (increase H3K27me3) and represses *FLC* expression (Fig. 1) [125]. After that, Kim et al. [120] suggested that "Polycomb-binding lncRNA, COLDWRAP" may be involved in the ongoing control of the *FLC* gene in *Arabidopsis* during vernalization.

To adapt to climate change and the rise in unexpected climatic conditions, plants have developed genetic and epigenetic systems that enable them to bear single or combination stresses and their interactions [126]. Knowing the genetic and epigenetic underpinnings of these reactions is necessary in order to comprehend the complexity of crop responses to environmental alterations. In order to identify genes that are specifically required for heat stress memory but not for the initial reactions to heat, Brzezinka et al. in 2016 [127] employed a heat stress priming model to delineate the memory of abiotic stresses in *Arabidopsis*. In order to ensure that the heat-inducible genes are always accessible and active, it has been found that the *FORGETTER1* (*FGT1*) gene produces the FGT1 protein, which binds directly to a specific class of heat-inducible genes. This is accomplished by changing the way the DNA containing these genes is packed. Because it is crucial for breeding applications to comprehend the stability and heredity of epigenetic marks and epigenetic regulatory systems, their discoveries may result in fresh strategies for crop breeding programmes to increase resilience to abiotic stress [128]. A few crop-related cases were covered in more detail in this review (Table 1).

Transgenerational inheritance of epigenetic variation in plants

Understanding the process through which epigenetic changes are inherit across generations is necessary for developing crops that are climate-smart. Priming or memory is widely accepted as a crucial component of these epigenetic changes since it plays a role in an improved ability to withstand stress in the future, even when not primed by the same stress. Priming, however, is not often noticed because it has the capacity to affect plant growth and development. Plants use systems to decide whether they should forget or retain [129]. Epi-alleles, which are either temporary or permanent epigenetic stress memories

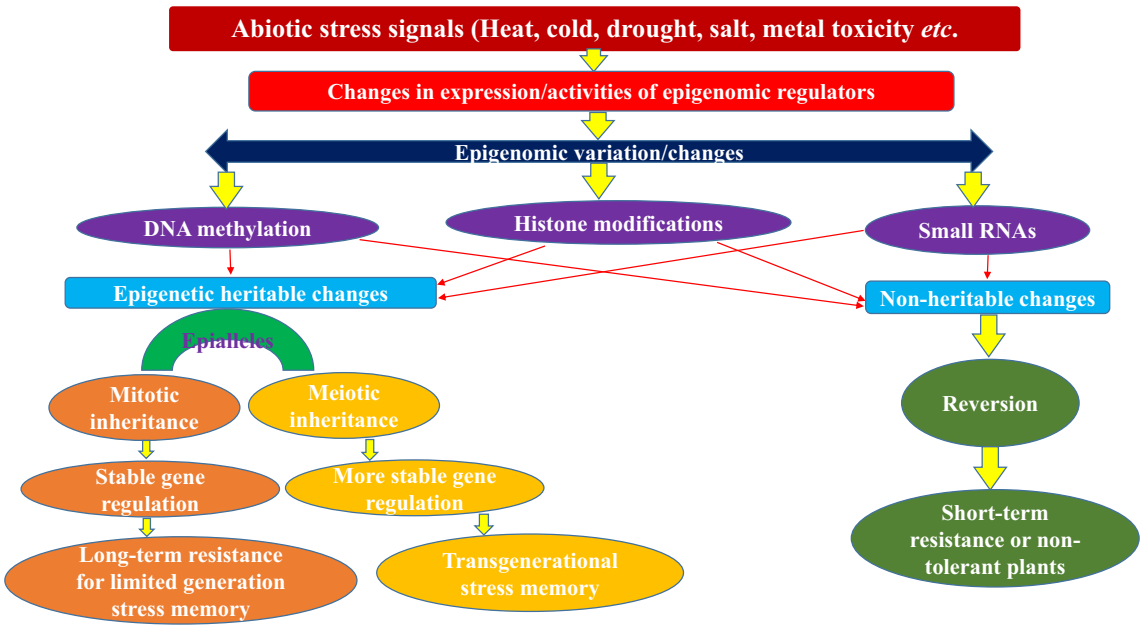

Fig. 2 Epigenetic variation in response to abiotic stress tolerance in plants

in plants, are formed as a result of stress [130]. The stable memory after the stress has been removed is preserved during the remaining cycles of plant development or handed on to the next generations, resulting in plant adaptability and evolution. However, transitory memory can be reversed if the stress is removed (Fig. 2). Plants develop their germ-line late during development, they remember challenges they encounter throughout their lives and memorize them, probably through epigenetic mechanisms in cell lineages that constitute germ-line and pass them on to their descendants [131]. There is still disagreement on how long stress memories last and how much and how long it takes for heritable epialleles to form. The coding region of submergence inducible genes

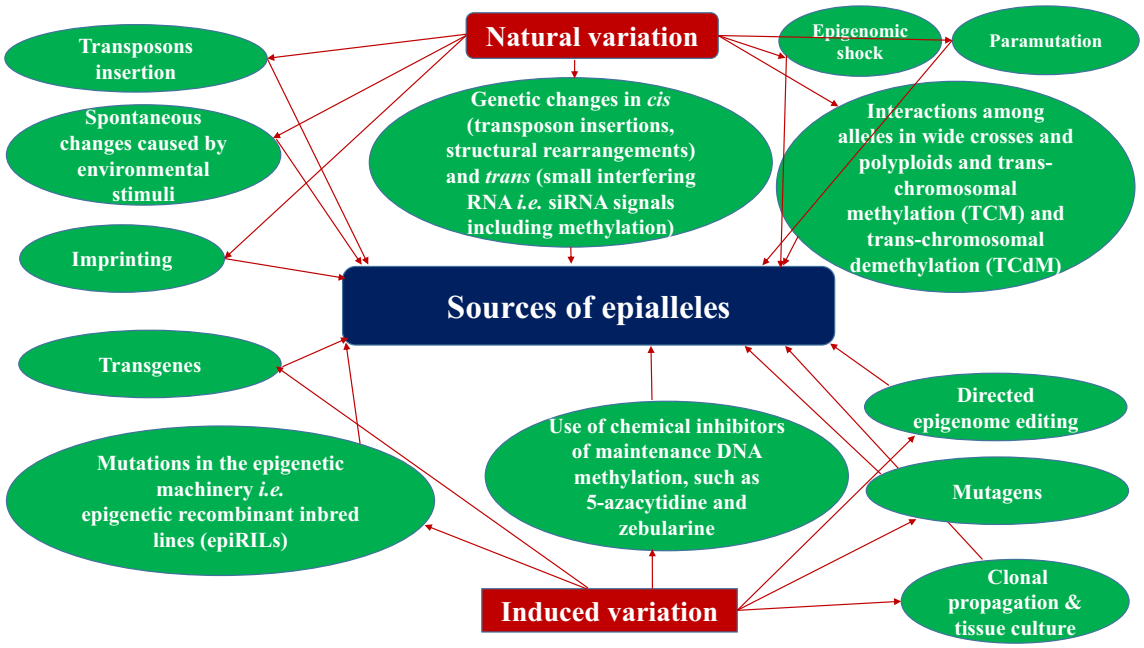

Fig. 3 Sources of epigenetic variation

in rice plants grown under water submergence conditions displayed H3K4me3 enrichment and a decrease in H3K4me2. Upon re-aeration, these histone modifications were temporarily returned to normal levels [85]. When *Arabidopsis* was exposed to cold stress, the enrichment level of the H3K27me3 mark decreased. Even when the temperature had returned to normal, this drop persisted for up to three days [132]. Since these histone modifications seem to produce transient epi-alleles that lessen their impact after the stress is removed, they might not be passed on to subsequent generations. Another study discovered that subjecting *Arabidopsis* plants to temperature stress resulted in the release of transcriptional gene silencing at numerous heterochromatin locations. Transcriptome analysis validated this condition at the genome level [133]. This transcriptional activation was transitory, and silencing was restored after a few days of stress removal. Pecinka et al. [133] found an association between transient changes in nucleosome density and the temporary release of silencing and its restoration. Recently, it was shown that DNA replication-coupled alteration of the H3.1 histone variant can restore the transcriptional inhibitory mark H3K27me3 in daughter plant cells [134]. Because of this, the majority of stress-induced epigenetic alterations is transient and goes back to normal when the stress is removed. However, some of the changes may be permanent and passed down via mitotic or even meiotic cell divisions (Fig. 2).

Epigenetic variation sources

Epialleles can develop through a number of different methods (Fig. 3). Epialleles typically result from either non-genetic or genetic origins [135]. Non-genetic origins include spontaneous origin of epialleles caused by a failure to appropriately maintain methylation states or through short RNA off-target effects. Non-genetic causes of epigenetic variation may also include developmental or environmental factors that affect the stability of epigenetic states or direct chromatin changes. Two genetic sources of epialleles are transposon insertions that alter local chromatin and structural rearrangements, such as copy number variations that are genetically related or unrelated [136]. Whether in *cis* or *trans*, exposure to these loci can alter the methylation of a locus by a number of different mechanisms, such as the production of siRNAs that result in RdDM or the recruitment of heterochromatin. Paramutation, or directed allelic interactions that promote epiallele development, can also occur in individuals who are heterozygous for various epigenetic states [137]. Our ability to use epigenetic information for crop improvement depends on our ability to comprehend the durability of epigenomic patterns in an organism. If DNA methylation patterns are typically stable throughout development; it may be possible to accurately reflect an individual's epigenetic profile and predict characteristics using the methylome from any one tissue. If, on the other hand, DNA methylation is strongly modified by development and differentiation, or by environmental factors, then the profiles most likely reflect the state of a specific organism rather than the predictive capabilities of a genotype across space and time.

There is solid proof that tissue culture, a highly artificial environment that is widely used in crop improvement programmes, causes a multitude of DNA methylation changes. Somaclonal variation is the term for the occurrence wherein plants grown from tissue culture exhibit a significant level of phenotypic diversity from the donor material [138]. Early studies found evidence that tissue culture might reactivate transposons that were epigenetically silenced, leading to unique allelic variants in plants produced through tissue culture [102]. There is also evidence for direct epigenetic modifications resulting from tissue culture that influences gene expression [139] or splicing [140]. The hypermethylation of CHH sites in *A. thaliana* cell suspension cultures [141] and rice callus tissue have been discovered using genome-wide profiling [142]. In maize or rice plants grown from tissue culture, there is little evidence for substantial changes in CHH methylation, although several hundred loci show reduced levels of CG and/or CHG methylation that can be inherited [142, 143]. These researches have provided compelling evidence that tissue culture can alter epigenetic variation in plants.

A source of unique phenotypic variation may arise during population generation if the parental epigenomes are sufficiently diverse. Classical genetic investigations have given evidence for paramutation [144], the directed interactions between alleles that result in changed epigenetic states, at a few loci. Crosses between different *A. thaliana* accessions with different epigenomes have revealed paramutation-like phenomena known as *trans*- chromosomal methylation (TCM) and *trans*-chromosomal demethylation (TCdM) (Fig. 3), in which the chromatin status of one allele influences the status of the other allele [145]. These occurrences occur at a subset of loci in which the two parents have different epigenetic states. Although the frequency of such occurrences may vary depending on how different the epigenomes were, in general, the genomic regions changed by TCdM, TCM, or hypermethylation constitute a small proportion of methylated regions among genotypes.

After studying the DNA methylome of hybrids from a wild-type parent and a MET1-deficient parent, an extreme example that resulted in a high frequency of epigenomic variation, termed as 'epigenomic shock,' was demonstrated in *A. thaliana* [146, 147]. Additional instances of increased epigenome variation have been observed as a result of polyploidization [148]. Plant genome evolution has been greatly aided by whole-genome duplication. Effective genome

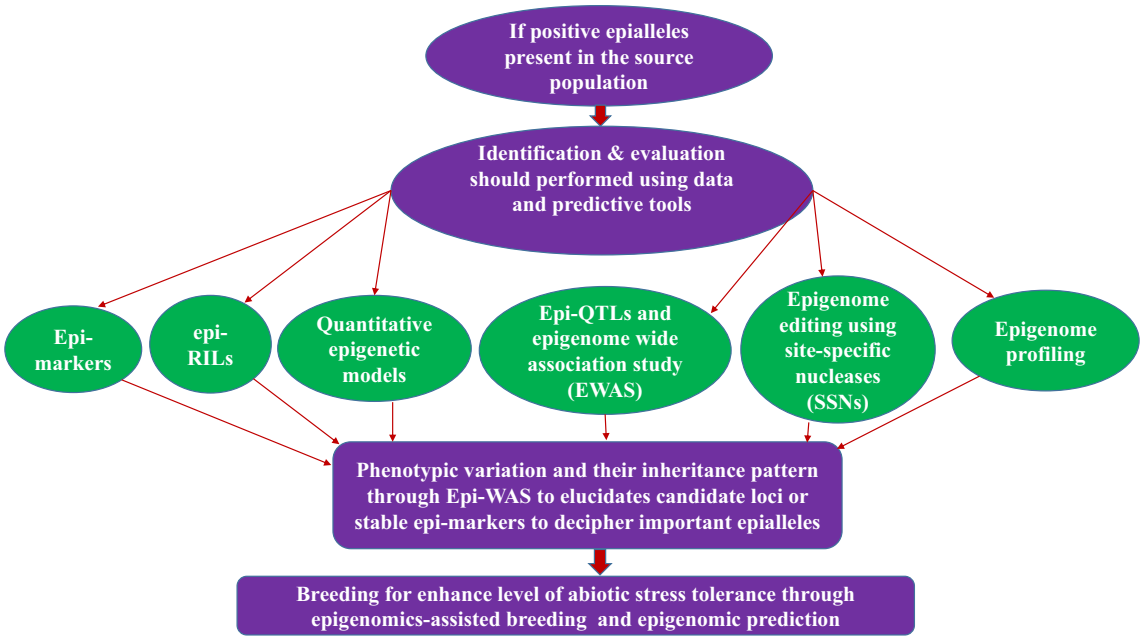

Fig. 4 Uses of epialleles in crop improvement

doubling requires the proper reinforcement of silenced regions within each set of chromosomes. There is a lot of possibility for establishing epigenetic diversity at particular loci using hybrids and/or crossing among parents with remarkably varied epigenomes. Utilizing the techniques shown in Fig. 3, it is possible to create unique populations that are tolerant of abiotic stresses in plants.

Role of epigenomics in crop improvement

The creation of epigenetic variation as well as the identification and assessment of epialleles are required for integrating epigenetics into crop breeding. For epiallele generation and identification, epigenome editing or epi-genomic selection may be needed. Through a breeding effort, the validated epialleles could then be introduced into elite cultivars (Fig. 4). An important step in applying epigenetics to crop breeding is the discovery and assessment of epialleles linked to economic traits. Since the influence of the underlying genetic variation must be eliminated, it can be challenging to identify and form associations between epigenetic changes and associated plant phenotypes. It is now possible to analyse epigenetic events at the whole genome level in ways that were previously not possible when modern sequencing technology is paired with conventional plant breeding techniques. The application of epigenome analysis and engineering may create new opportunities for maximizing the contribution of epigenetics to crop development. This could allow for the creation of novel epiallelic variations through changes in DNA methylation or other chromatin modifications, as well as crop improvement through epigenome engineering, in combination with the new epigenome editing tools [15]. Genome-wide epigenetic mark mapping and epigenetic target identification are two current key methodologies in major crops [15]. In order to choose novel crop varieties that are more tolerant to environmental changes, breeders will have new tools to increase and manipulate epigenomic variability. The discovery of numerous cellular products, including RNAs, chromatin modifications, DNA–protein interactions, and chromatin accessibility, resulted in the development of epigenomics, an emerging field that is enhancing our capacity to explain observed phenotypic variation. Genome annotation, cross-species comparisons, and a better understanding of the function of epigenomic processes in crop response to stress will all be made possible by gathering and standardizing epigenomic data for a range of plant species [149].

Stress exposure initiates a response signalling cycle in plants that, along with genetic alterations, causes numerous epigenetic changes through mechanisms like chromatin remodeling, DNA methylation, histone modification, and non-coding RNAs [150]. These epigenetic mechanisms have produced novel epialleles that can be used to create new crop varieties that are more climate-resilient in order to overcome the difficulties posed by changing environments [151]. It's possible that stress-induced epimutations inherited through generations and play an important role in the way plants adapt to challenging conditions. Using the methylation-sensitive amplified polymorphism (MSAP)

technique, research has been done to examine the effects of epigenetic differentiation between upland and lowland rice ecotypes on their drought tolerance in 180 rice landraces under both normal and osmotic conditions. When rice is exposed to osmotic stress, significant changes in DNA methylation are observed (52.9–54.3% of all individual-locus combinations). In upland rice, the highly divergent epiloci (HDE) that were found under normal conditions tended to remain at low levels, especially those that were de-methylated in response to osmotic stress. Under normal or stressful circumstances, there were differences in the expression of three of the four chosen HDE genes between upland and lowland rice. Additionally, when a gene at HDE was up- or down-regulated in response to osmotic stress, its expression in upland rice under normal circumstances was higher or lower [152]. Increased DNA methylation reduced the effects of cold, heat, and salinity stress on tomatoes, drought on faba beans, and rice's ability to photosynthesis [74, 153]. In the same way, changes in H3K4me2 in maize assisted in reducing biotic and abiotic challenges [153], while histone acetylation was found to control drought stress in tomato and *Arabidopsis* [64]. It has been shown that the histone deacetylase HDA9 is essential for controlling the effects of drought stress on plants [150]. Because of altered DNA methylation patterns of the *Tos17* retrotransposon and several protein-coding genes, heavy metal treatment of rice seedlings impeded the growth of the shoot and roots [154, 155].

To induce epigenetic modifications crucial for crop production, a variety of methods can be utilized to modify the epigenome broadly or at specific target loci. Recent advancements in CRISPR/Cas9 and dCas technologies have created new opportunities in the study of epigenetics [156, 157, 158, 159]. The emergence of epigenome editing techniques that specifically target a genome region to change epigenetic changes (cytosine de/methylation or histone tail de/methylation, de/acetylation, etc.) has made it possible to precisely manufacture artificial epialleles. These techniques were developed by integrating nuclease-free genome editing tools with epigenetic modifiers or an interactive platform that may attract epimodifiers, guiding the combined functional module to a preset place, and then producing precise epigenome modifications [160]. This innovative method allows for the controlled manipulation of epigenetic features, which can be used to alter plant phenotypes or clarify how the epigenome and transcriptional regulation interact [161]. Recent progress in the synthesis of synthetic DNA binding domains may enhance the precision of locus-specific epigenetic breeding methods. The acquired knowledge could be used to long-term activate or repress a specific gene or pathway for trait improvement in crops, in conjunction with the use of epigenetic techniques like epigenetic QTLs, epigenetic SNPs, or single nucleotide polymorphisms. This might lead to the development of a novel, efficient, and transgene-free breeding technique [162].

In addition to using sequence-based markers for crop breeding, epialleles could also be used in epigenomics-assisted breeding and epigenomic prediction [163]. One of the chromatin markers that are most readily adapted to extensive research is 5-methylcytosine (5mC). It has even been used to build "epigenotype" maps of plant genomes, which reveal recombination even in the absence of genetic diversity [164]. These DNA methylation alterations can be used as markers for QTL mapping, enabling the mapping of phenotypic variation to genomic regions with altered methylation [165]. Epigenetic marker discovery is still in its infancy, and more investigation is required to find these markers. Markers that can offer vital information on biotic and abiotic pressures as well as desired agronomic characteristics will be a great help to agricultural biology and can be used as epi-biomarkers [83]. However, the discovery of interesting epibiomarkers has only occurred in a few studies [140, 166, 167].

Conclusions and future prospectus of epigenomics studies

Crop development methods can be aided by epigenomics, which studies the combinatorial coding of chromatin modifications. Epigenomics also provides a better understanding of crop genomes and the molecular underpinnings of phenotypes. A deeper knowledge of the epigenetic basis of traits, the stability and heritability of epialleles, and the origins of epigenetic variation in crops are just a few of the fascinating issues that lie ahead in the field of heritable epigenetic variation [168]. Exploration of long intergenic non-coding RNAs (lincRNAs) might be a new avenue as an epigenetic mechanism to understand the abiotic stress tolerance in crop plants [169]. The utilization of epigenetic variation in crop breeding as well as the quicker and more effective creation of climate-smart crop varieties have all been made possible by recent technological advances. To better comprehend the relationship between stress-induced gene expression changes and variations in DNA methylation and histone modifications, the method of inheritance of these modifications, and their adaptive relevance, additional research for particular traits and crops is necessary [11]. However, more research is needed before it can be generalized. It will be crucial to have a better knowledge of the interactions between various chromatin alterations and regulatory pathways, as well as how these functions differently in different cell types. This will be required in order to perform epigenomic/epigenetic modelling and engineering. Many of these technologies and methodologies will also require technological advancements to make them more relevant and cost-effective for

deployment. Breeders will likely need to focus more on crop epialleles and their potential role in future responses to climatic changes. By making targeted epigenetic alterations in relevant genes, and understanding the molecular underpinnings of transgenerational epigenetic inheritance may enable the creation of epialleles suited to specific environmental situations. To gain a more thorough understanding of the mechanisms that generate and stabilize epigenetic variation in crops, greater study on a wider range of plant species is necessary. This will need for increased integration of the epigenomic information acquired in many crops, as well as a collaborative and multidisciplinary effort by researchers in many domains of plant science.

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Declarations

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