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Epigenetic Regulation of Abiotic Stress Memory in Plants: Mechanisms and Potential for Crop Improvement

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Abstract

Abiotic stress memory in plants provides the potential to circumvent some of the damaging effects of different stresses. Different abiotic stressors can trigger various physiological changes in the plant, including alterations to growth and development, that may adopt distinct epigenetic signatures depending on the underlying stress cue and plant species. Epigenetic changes, such as reversible modifications in DNA and histones, can regulate the expression of stress-related genes, thereby enabling drought or salinity memory. In this review, we focus on epigenomic changes induced by various stresses in various plant species and stress modalities, emphasizing the crucial roles of epigenic regulatory mechanisms in both stress-memory recall and transgenerational stress memory, as summarized in this paper.

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1. Introduction

Plants encounter abiotic stresses such as drought, salinity, and extreme temperatures, which impact their growth and development [1]. Abiotic stress can negatively impact plant growth and development, causing it to reduce the yield lost in agricultural-based crops. Epigenetic regulation of abiotic stress memory in plants is yet to robustly explored [2]. Abiotic stress memory in plants provides the potential to circumvent some of the damaging effects of different stresses. Stresses that induce memory, the duration of memory, and how plants retain a memory of abiotic stress are also not fully understood [3]. Biotechnologies exist enabling the introduction of epigenetic changes and monitoring of epigenetic marks. Since epigenetic changes are heritable, it has the potential to create stress tolerant crops that does not require further exposure to abiotic stress [4, 5].

2. Abiotic Stress Memory

Biotic and abiotic stresses such as drought, salinity, extreme temperature, and pathogen attack can cause millions of dollars in yield losses globally [6]. Such environmental events lead to stunted growth, wilting of leaves, and eventual death when severely prolonged [7]. Interestingly, upon exposure to these environmental events, plants acquire memory traits that enable them to respond positively to subsequent stimuli of the same type, a phenomenon referred to as stress memory [8]. Tree species show evidence of long-term stress memory even after shedding leaves, whereas legumes can recall past infection by pathogens through systemic acquired resistance [9]. Upon exposure to abiotic events, plants conserve memory in a temporal and developmental setting, thus retaining the capability for a primed response for long durations. Drought- and salinity-induced stress memory is encased within plant tissues and developmental stages, such as the vegetative, flowering, and reproductive phases [2].

Current evidence indicates that upon initial drought or salinity exposure, plants develop a drought- or salt-responsive transcriptome along with epigenetic alterations such as alterations in histone modifications and DNA methylation that regulate memory genes, thereby enabling drought or salinity memory. Salt harassment significantly alters both DNA methylation and histone marks associated with stress-responsive genes [10].

Continuous illumination and drought stress permit plants to retain a drought memory and safeguard further dehydration events. Transcription of DREBs, PREBs, RD–COR, and ABF genes is markedly preserved in plants after drought stress, enabling subsequent desiccation tolerance. Moreover, drought and dehydration stress can sharpen salinity endurance by reinforcing expression of several salt-responsive genes, indicating that these markup transformations are sustained post-signal cessation. Most agricultural investigations on priming and acclimatization are performed on model species such as Arabidopsis and rice, yet these conclusions can be translated to other crops [11]. Therefore, it is crucial to bridge existing knowledge in model research to undisclosed species and non-model cultivars [12].

3. Epigenetic Mechanisms in Plants

Plants possess sophisticated mechanisms for coping with diverse environmental challenges, such as drought, salinity, flooding, heavy metals, heat, and freezing. These factors broadly fall under the umbrella of abiotic stresses, which cause severe damage at the physiological, biochemical, and molecular levels [13]. In the face of abiotic stress, agricultural crop production remains vulnerable. Plants have evolved a stress adaptive strategy termed stress memory, allowing them to copiously allocate energy toward tackling imminent threats [14, 15]. Stress memory also establishes a sequence of biosynthetic changes that facilitate swifter responses to recurring stresses [15]. Consequently, investigation of stress memory and the underlying epigenetic circuitry offers tremendous promise to enhance crop tolerance to abiotic threats [12].

Abiotic stress memory enables a plant previously exposed to stress to mount a more efficient and robust response to subsequent exposures, even if the primary elicitor is removed [16]. After the shared or similar primary signal of stress exposure dissipates, plants trigger signal transduction pathways and gene expression programs that exhibit parallels with those observed during the initial exposure [2]. Supporting the role of abiotic stress memory, drought-primed Arabidopsis seedlings show transcriptional priming of drought-induced genes after a second challenging drought treatment; many of these genes demonstrate persistent enhancement of stress-induced expression after stress application [17].

Induction, retention, and retrieval of memory can occur over various timescales, from seconds to millennia. Memory can be stored in different organs and be functionally operative at different developmental stages; so-called inter-organ or inter-stage memory [18]. Transgenerational epigenetic inheritance represents the longest lasting memory, during which an epigenetic state or phenotype is stably passed down through multiple cell divisions and generations [19, 20]. Stress-induced alterations enabling memory persist beyond the initial exposure and facilitate more efficient retrieval and a more pronounced response upon repeat exposure [21]. Many important crop species are recalcitrant to genetic transformation or the transgenic approach is prohibited. Two frequently employed priming treatments in Arabidopsis that typify drought and salinity also exert their influence on non-programmable species with equally pronounced memory phenomena [22].

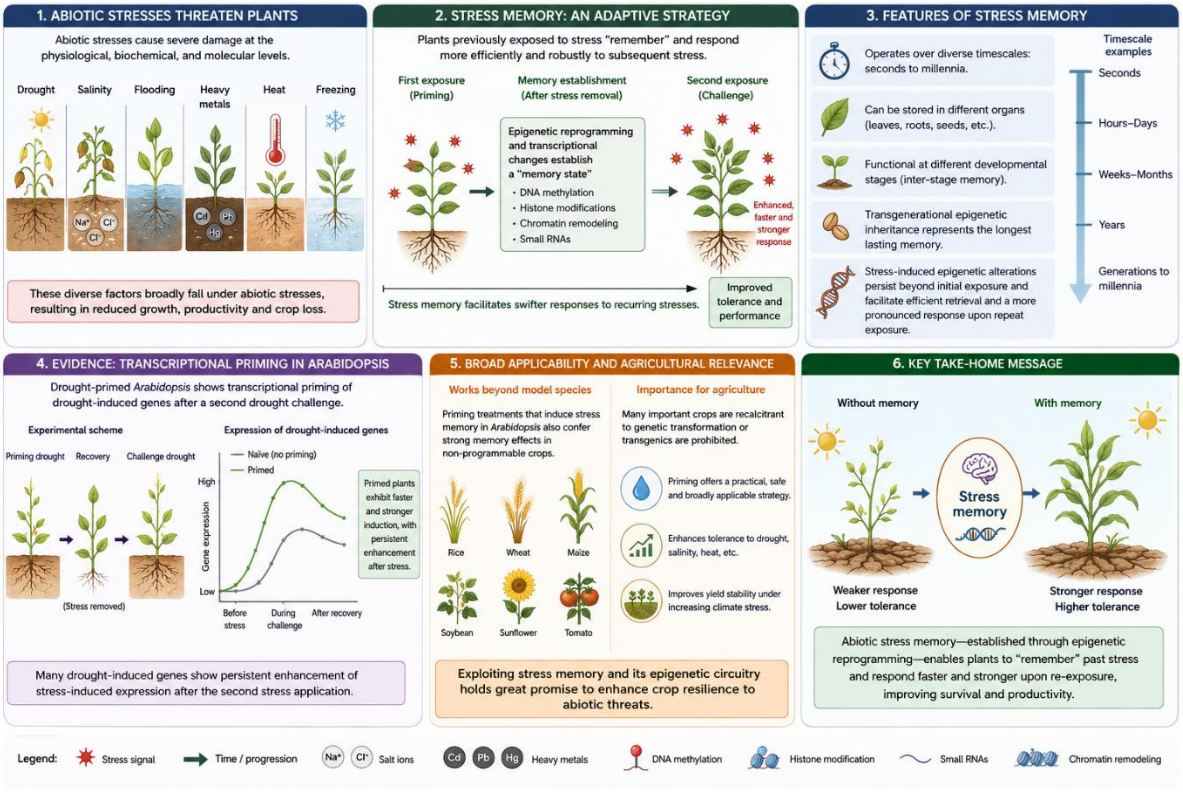

Fig 1:

3.1. DNA Methylation and Demethylation

Plants are exposed to various abiotic stresses that evoke responses allowing them to adapt and survive. Memory of previous exposure to stresses modulates subsequent developmental processes [16]. Interactions of various regulatory mechanisms initiate and maintain stress memory, and epigenetic mechanisms play central roles. Stress triggered reprogramming of the epigenome occurs, leading to changes in gene transcription and stress responses [23]. Stress priming of gene expression allows for faster and more robust induction of stress response gene expression during subsequent exposures [24]. Stress responsive genes and transposable elements are targets of reprogramming by drought, salinity, heat and chilling and provide distinct transcriptional timing during subsequent exposure to the same stress [23]. Accessory factors participate to promote appropriate temporal expression of stress response genes during multiple exposures to the same stress, ensuring robust and rapid response [12]. Across diverse plant species, non-coding RNAs, DNA methylation, histone modification, and chromatin remodeling are implicated in stress adaptation and memory [5].

DNA methylation involves the transfer of a methyl group to the cytosine base producing 5-methylcytosine, and constitutes a basic mechanism regulating expression of genes, transposable elements, and genomic imprinting [25]. Among higher plants DNA methylation occurs broadly and at CG and non-CG contexts in gene regions [26]. During DNA replication maintenance of methylation at CG context is performed by MET1 and at non-CG by CMT2 and CMT3 [27]. DNA methylation within regulatory regions that govern transcription initiation and elongation is associated with transcriptional silence and molecular memory [28]. De novo methylation is mediated via the RdDM pathway executed by DRM1 or DRM2 [29]. Active demethylation is catalyzed by ROS1 family proteins and DME and supports diversity of the epigenome, also contributing to memory. Drought, salinity, heavy metal, extreme temperature, and nutrient deprivation induce DNA methylation fluctuations on a variety of gene and transposable element targets that effect adaptation [30]. Yet some of these DNAm patterns endure and are inherited across generations, granting progeny improved capacity to withstand parental stresses [31].

3.2. Histone Modifications

In response to heat, drought, or high salinity, plants adopt a series of adjustment programs enabling them to cope with such abiotic stresses; plant responses vary within time and communicate to many developmental and physiological programs [32, 33]. Following a stress event, plants can retain a "memory" of the stress history, enabling them to adapt efficiently to the next round of stresses [15].

Transcriptional memory is integrated into programs of adjustment at subsequent rounds of those stresses [2]. Chemical reagents and stress treatments have been applied to perturb wild types or mutants to investigate stress memory for improvement of crops [5]. Responses, including osmotic response to salinity stress, unfolded protein response to heat stress, and jasmonate response to drought treatment can emerge quickly and develop persistence during stress-off periods, demonstrating the conservation and significance of stress memory on adjustment program in various species [34]. Under natural conditions, successive drought treatment and watering cycles can enlarge the duration of stress memory [35]. Some folk knowledge and slogans also claim that "plant memory" exists. Both genotype and environment have invoked interests in screen of climate-smart phenotypes.

To adapt to stress such as low temperature, repeated application of drought, salinity or pathogen treatment can take advantages of stress memory that exist in crop species [16]. By understanding the mechanism of stress memory, it will help to elucidate knowledge of plant response and further cross-breed crop species for enhancement of survival rate under stress, thus improving gross productivity [12].

3.3. Chromatin Remodeling and Nucleosome Dynamics

ATP-dependent chromatin-remodeling complexes change histone-nucleosome interactions and alter the local accessibility of DNA [36]. They either slide or reposition histones on the genome to maintain, establish or reset epigenetic states across cells and generations [20, 37]. Genome-wide DNA-methylation and histone-modification patterns can be maintained by dynamic nucleosome positioning 38. Transcription-priming marks are established at the loci and associated with a time-dependent reallocation of RNA polymerase II [39].

3.4. Non-coding RNAs in Epigenetic Regulation

Abiotic stress induces persistent transcriptional and epigenetic alterations across diverse plant species, hence qualifying as imprinting stress. Stress-induced epigenetic changes substantially correlate with transcriptional modification and organ-dependent memory retention [23]. Epigenetic states previously shaped by drought stress remain intact even after prolonged non-stress periods [40]. Epigenetic traits represent primed states enabling enhanced stress responsiveness upon re-exposure to the same stressor [41]. Epigenetic modifications such as DNA methylation, histone modification, and chromatin accessibility directly influence memory duration [42]. Drought stress initially activates an abscisic acid signalling network, leading to cumulative DNA methylation modifications, which subsequently preserve the stress-responsive chromatin configuration [43].

4. Epigenetic Regulation of Abiotic Stress Memory

Plants face various physically, chemically, or biologically detrimental external factors [44]. These include drought, pre- and post-emergence flooding, salinity, freezing, and intense heat from multiple sources including temperature variations, water crises, and soil nutrient imbalance due to urbanisation and desertification [45]. Stress-inducing environmental and abiotic conditions, accentuated by external chemical pollutants such as phosphorus, sulphur, nitrogen, and, in particular, heavy metal Toxicants influence crop productivity globally [46]. Abiotic stress memory (ASM) refers to the ability of plants to form "a memory" of abiotic stress conditions to survive and improve tolerance to subsequent episode(s) of the same abiotic stress [47].

Abiotic stress memory in plants begins with an initial physiological stress and produces defined, "all-round" alterations to multiple physiological characteristics enabling the organism to endure that specific abiotic stress more effectively [2]. The memory of the initial abiotic stress persists for days and even weeks after the cue ends and exerts a beneficial effect on a later, even more severe, stress event [16]. A form of epigenetic regulation termed "epigenetic crosstalk" assists plants in their abiotic stress memory processes [48]. The abiotic stress risk alleviation tactics that certain crops initiate and regulate via epigenetic mechanisms help scientists to mitigate abiotic stress-related poverty, malnutrition, and starvation [12].

4.1. Memory Induction by Drought Stress

Environmental stresses affecting growth, yield and quality of crops are common in agricultural systems today [49]. Apart from genetic variability, acquisition of stress memory through chromatin remodelling and selective gene expression reprogramming forms the basis for abiotic stress tolerance [16]. Exposure of Arabidopsis seedlings to drought stress at early stages generated long-term drought stress memory resulting in upregulation of drought-inducible genes and/or downregulation of drought-repressed genes upon subsequent drought exposure [50]. Drought stress triggers MAPK signalling cascade, activating both ABA-dependent and ABA-independent pathways where MYC transcription factors and/or their mediators such as ANAC019, ANAC055 and ANAC072 initiate early drought-responsive gene expression [51]. Primed drought memory responses are dictated by an increase in nucleosome-remodelling factor HOT-A and elevated histone-acteylation levels on the associated gene regulatory regions. Thirteen drought-responsive transcription factor encoding genes remain in a transcriptionally primed state, amenable to drought-enhanced expression during subsequent drought stress [52]. Drought-induced transcription factors binding to gene regulatory regions is associated with the gain of H3K4me3 and H2A.Z deposition, while transcription factors controlling stress-responsive genes also deposited H3K27me3 in the same gene regulatory regions, predicting indefinite persistent memory signalling 23. Exposure of 6-week-old tomato plants to Gibberellic acid, Abscisic acid or drought left 103 epigenetic changes, in gene expression and CHG/CHH-methylation which persist up to 21 days. The epigenetic changes post-drought associated with enhanced tolerance for later drought exposure supports dryland agriculture and can be applied to the improvement of drought tolerance in important crops by breeding [53].

4.2. Memory Induction by Salinity Stress

Salt stress leads to substantial global crop loss due to salinity of irrigation and rainfall [54]. Consequently, elucidating its underlying mechanisms holds great significance [53]. Stress memory is among various adaptive responses triggered by salinity [55]. Under salinity, epigenetic changes perpetuate signalling cascades that bolster stress tolerance and growth when first exposure occurs during seedling or reproductive stages [56].

Consequently, plants prefer brood size to further fertilising capacity when first exposure occurs during the seedling stage. Stress memory influences progeny growth and resistance to related cues. Pre-exposure to salinity advances early flowering, proline accumulation, and carbon assimilation [57].

4.3. Memory Induction by Heat and Cold Stress

Heat and cold are the most common environmental stresses faced by plants [53]. Increasing temperatures caused by climate change alter plant growth and developmental stages [58]. This might affect availability of food resources, and provoke adverse conditions such as droughts, hence endangering the survival of plants [59]. Exposure to temperatures exceeding 38 °C elicits heat stress and a wide array of defensive responses. Enhancing heat tolerance can improve crop yield in heat-prone areas [60]. Young plants exposed to high-temperature stress before flowering exhibit increased seed formation and population sustainability. During seed maturity, heat stress maintains a warm temperature favoring high crop yield. Cold temperatures below 0 °C restrict growth and productivity [61]. Plants exposed to low temperatures exhibit increased germination capacity after overcoming a dormancy phase. Low temperatures stimulate seedling growth and increase seed production at moderate developmental stages. Cold acclimation enables plant survival at temperatures below zero [62].

5. Transgenerational Epigenetic Inheritance and Stress Memory

Stressed plants exhibit an increased ability to tolerate a subsequent stress event—an effect that can persist for multiple generations—and the underlying molecular mechanisms have been actively investigated [12]. Stress-induced alterations to the epigenetic landscape, including reversible modifications to DNA and histones, can regulate the expression of stress-related genes and thus represent a key aspect of abiotic stress memory in plants. Evidence indicates that epigenetic changes induced by drought, salinity, heat, and cold alter the ability of plants to cope with similar or different stressors, underscoring the potential of epigenetic marks to serve as molecular memory elements [63]. Stressed plants can therefore exhibit an increased ability to tolerate a subsequent stress event—an effect that can persist for multiple generations [64].

Epigenetic marks are known to be reprogrammed following fertilization in flowering plants, yet the epigenome remains partly inherited after stress exposure, allowing offspring to benefit from acquired information [65]. Only a few plant species, such as Arabidopsis, wheat, and maize, have been examined in this context, and several questions concerning the specificity, heritability, and ecological significance of transgenerational epigenetic phenomena remain open [66]. Under transgenerational conditions, marked genes as well as the design and signature of stress-related epialleles can differ from those found under the corresponding parental stress. The potential ecological and evolutionary implications are profound, because information acquired during a stressful parental environment can be transmitted to the next generation [67].

6. Technologies and Methodologies for Studying Epigenetic Regulation

High-throughput sequencing technologies and bioinformatics tools have enabled the comprehensive, genome-wide profiling of epigenetic changes in plants [12]. A combination of three techniques provides an overview of the plant epigenome (DNA methylation, histone modification, and chromatin structure) [63]. Bisulfite sequencing is the first method for DNA methylation profiling; in this technique, nonmethylated C is converted to U via bisulfite treatment, and subsequently the treated DNA is amplified and sequenced [68]. ChIP-seq is a method employed to profile histone modifications or transcription factors; chromatin obtained from cross-linked nuclei is subjected to immunoprecipitation with specific antibodies, and the protein–DNA complex is sequenced to obtain the location of the binding [69]. ATAC-seq measures chromatin accessibility; a Tn5 transposase is employed to tag open chromatin, and the region is further amplified and sequenced. Data from these three assays can be integrated using epigenetic orientation or worm-holes to identify genomic regulatory elements [70].

Targeted epigenome editing using CRISPR-dCas systems is attracting wide attention; dCas9, dCpf1, and dCas9-cripSR FokI, fused with effector domains such as chromatin-remodeling166 or DNA-methylation166 effector proteins, enable targeted modification of the epigenome [71]. Precise design of constructing gRNAs in CRISPR-mediated genome editing determines the editing efficiency and target specificity, so higher efficiency and specificity can be obtained with multiplexing and connection of gRNA with sequences affecting transcription [72]. To investigate epigenetic mechanisms of stress memory at the genome-wide scale in plants, the following experiments can be designed: epigenome profiling of plants exposed to stress treatments followed by stress-free recovery to identify long-lasting epigenomic changes; conventional transgenic approaches accompanied with relevant phenotypic assays; and time-course analyses of epigenetic modifications for priming memory [63].

6.1. Genome-wide Epigenomic Profiling

Following exposure to abiotic stress, plants exhibit altered physiological and molecular responses upon subsequent encounters [73]. This phenomenon is termed abiotic stress memory [2]. It can be induced by osmotic or salt stress, extreme temperature, drought, or desiccation [74]. The duration of such memory varies with the plant species considered [75]. In Arabidopsis, memory induced by parental high salinity stress lasts over five generations, while in rice and barley, it persists for three generations [76]. The underlying mechanisms remain incompletely resolved, and the expression of memory-inducing stress as well as the timing of the second stress can significantly influence the nature and strength of the acquired memory [77]. The research area of abiotic stress memory is in its infancy, with most studies conducted using model species. Information regarding memory induced by various stresses in diverse plant species has been collated with a view to facilitating further research on abiotic stress memory, particularly into the phenomena of memory retention and transgenerational epigenetic inheritance [16].

Plants possess sophisticated adaptations to cope with environmental changes [78]. A major factor contributing to the capacity of plants to survive such changes is memory of past experiences, which induces an enhanced and accelerated response to either the same or a different stress [15]. Research on abiotic stress memory has revealed that transient exposure to drought, salinity, freezing, or heat can initiate a second more vigorous response as well as a primed transcriptional response [16]. The involvement of epigenetic changes in the establishment of abiotic stress memory is increasingly recognized [23]. Experimental evidence in several plant species indicates that abiotic stress-induced epigenetic changes can moderate the expression of many genes, establishing a transcriptional memory of the prior exposure and providing epigenetic information to the progeny [5]. The involvement of the epigenome and epigenetic changes in abiotic stress memory in Arabidopsis and other plant species is summarized [23]. Experimental datasets indicate that abiotic stress reprograms hundreds of genes, with oligonucleotide mapping providing direct evidence for stress-responsive active and inactive chromatin states [79]. The critical importance of epigenetic memory in the adaptation of plants to abiotic stress during environmental alterations, climate change, and crop improvement underscores the relevance of this topic [12].

6.2. Targeted Epigenome Editing

Novel targeted epigenome-editing systems based on dead Cas9 (dCas9) fused with distinct effector domains have been developed to study the epigenetic regulation of abiotic stress memory in plants [12]. Although most of the dCas9-based epigenome-editing systems harness the catalytic activity of DNA methyltransferases or demethylases to modify targeted cytosine methylation, some systems also allow the targeted modulation of histone acetylation and mono-methylation at histone H3 lysine [27, 80].

Along with transient dCas9-derivatives, modular and easily customizable dCas9 vectors facilitate the combinatorial modulation of multiple epigenetic marks simultaneously to investigate cross talk and interactions between various epigenetic landscapes, chromatin states, and transcriptional regulation [81]. Continuous development of these systems enables the highly efficient targeted epigenome editing of a variety of crops and serves as a powerful tool for functional genomic studies, guiding the determination of regulatory networks, and the improvement of other agronomically important traits [82].

6.3. Functional Genomics and Phenotypic Assays

Diverse abiotic stressors can trigger various physiological changes in the plant, including alterations to growth and development, that may adopt distinct epigenetic signatures depending on the abiotic cue and plant species. Drought, salinity, and extreme temperatures are among the most detrimental abiotic stressors and these perturbations affect the plants even after the stress imposition is relieved [83]. Nevertheless, in plants, chromatin modifications are highly dynamic and epigenetic genes undergo extensive reprogramming during development in the absence of external stimuli 84. Consequently, during stress-related priming and subsequently the memory phase, these chromatin alterations could be reshuffled by other environmental cues affecting not only the measured transcriptome response but also the very stability and visibility of the “memory” [12].

7. Implications for Crop Improvement

The topic of abiotic stress memory, a form of biological memory acquired by plants when exposed to non-living environmental conditions, has not gained traction until recently [85]. Etymologically, the term "memory" refers to the process of storing, retaining, and recalling information, and, therefore, describes the maintenance of a stress-induced state that enhances a plant’s ability to respond to the same stress [12]. Such reinforcement positions the plant favourably on the stress tolerance continuum, thereby increasing its chances of survival [86].

Despite similar memory phenomena being documented in other organisms, most notably in animal species, certain aspects of these phenomena make plant systems unique [87]. The most common abiotic stress stimuli that leave a long-lasting—generally defined as occurring over three or more days—memory are drought, salinity, and extreme temperature (heat and cold) [16]. Also, in both a developmental and a spatial context, plants are known to take a “whole-body” approach to memory retention. For example, the memory can be retained and recalled at vegetative stages following yet another stress cycle applied at the mature stage [88]. The memory is even able to traverse from developmental stages and to other tissues: plants subjected to drought stress at the seedling stage continue to retain the imprint and capable of recalling it when exposed to heat stress at the flowering stage [89].

7.1. Epigenetic Breeding and Selection Strategies

Epigenetic breeding aims to establish heritable traits through breeding selection [90]. Several biotechnological and breeding procedures enhance the transferability of induced traits [91]. Markers linked to memory, preferably with a two- or three-generation stability, could accelerate allele introgression before magnitude and duration fluctuate or revert [12]. Knowledge regarding candidate memories is essential for such approaches. Field-pruning protocols that circumvent memory loss could increase input efficiency if such traits are habitually monitored in breeding pipelines [92].

7.2. Epigenetic Engineering for Stress Resilience

Transgenerational stress memory phenomena govern stress acclimatization within a wide array of species and stress modalities, emphasizing the crucial roles of epigenetic regulatory mechanisms in both stress-memory recall and epigenetic regulation of transgenerational stress memory, as summarized in [12]. The occurrence of transgenerational stress memory (specially called ‘episodic memory’) has been demonstrated for 1 prediction of flowering time and phase transition under variable temperature conditions in hydroponically grown Arabidopsis thaliana (Li *et al.*, 2023) [93]. The modulation of transgenerational stress memory establishes a time-window prevention of flowering in progeny under unfavorable stress conditions. It has been shown that targeting epigenetic regulators involved in stress-memory regulation would make interesting targets for crop stress-resilience improvement [94].

7.3. Risks, Trade-offs, and Ethical Considerations

Genetic engineering, although promising, brings several risks and trade-offs [95]. The primary concern centers on the potential for unintended, pleiotropic effects [96]. For example, targeting a single locus could trigger widespread changes in chromatin accessibility or increased transposon activity. Even with targeted editing, large chromosomal rearrangements could arise [97]. Such unwanted alterations might not pose serious health hazards when modifying single crops for local use; however, international distribution and commercial sale could invoke a more proactive regulatory response [98]. Consequently, attention should be diverted to fundamental research elucidating epigenetic networks, which themselves present a safer mechanism for germplasm enhancement [12]. In addition to regulatory scrutiny, other considerations arise. Global atmospheric CO2 levels are expected to double within the next century [99]. While few studies predict how this scenario will impact crop productivity, many plants experience reduced growth in low-CO2 environments [100]. Such projections underscore the need for fundamental research on epigenetic memory as a universal, long-term strategy for enhancing production in vital food species without large expenditure, potential choking-up of entire markets, or further dependence on agrochemicals. Finally, perturbing epigenetic allocation may have unforeseen societal consequences, inadvertently compromising individuals holding sensitive information about their history [101].

9. Conclusion

Normal plant development is invariably chronicled by genome-wide transcriptional reprogramming, which reflects both temporal and spatial cues. Epigenetic marks govern the differential activation of genes involved in diverse physiological processes in response to abiotic stimuli. In some plant species, expression levels of stress-responsive genes display a sustained increase after a stress event, resulting in heightened performance compared to non-stressed individuals. This is accompanied by substantial alterations in both DNA methylation and histone modifications associated with chromatin remodelling and gene accessibility.

Terrestrial plants are subjected to various types of abiotic stress, including drought, salinity, extreme temperature, flooding, heavy metals, radiation, and UV exposure. Such stresses have substantial and detrimental effects on normal plant growth. Because of climate changes and human activities, the incidence of abiotic stress has increased dramatically, resulting in significant losses to agricultural yield and the productivity of natural ecosystems.

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