



Epigenetic Memory of Stress Responses in Plants Kumar S^{*}

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Plants being sessile organisms are constantly challenged by environmental perturbations. They have evolved several strategies to cope with environmental stresses through biochemical and molecular changes including epigenetic regulation of gene expression [1]. Over the past few decades, our understanding about stress signaling in plants has increased considerably. Plants use a range of sensing and signaling mechanisms to induce stress responses when exposed to environmental stresses [2]. Growing evidence suggests that DNA methylation, chromatin modifications, and siRNA are involved in epigenetic regulation of the genes critical for stress responses [3]. Epigenetic mechanisms have been implicated in the regulation of stress-associated genes [4,5]. Evidence also suggests that DNA not only provide genetic information for a trait but also as chromatin modulator to contribute to the expression of the trait. Thus, DNA methylation, post-translational histone modifications, and regulatory/non-coding RNAs determine epigenetic state of the genome (epigenome), which may vary due to environmental perturbations [6]. Since the epigenetic state of chromatin is variable, transfer of a trait from one species to another would not only require the transfer of the gene(s) associated with a trait of interest but also the epigenetic status so that the trait can express optimally. Therefore, it is essential to understand the epigenetic state of the donor plant to ensure proper re-establishment of the epigenetic status in the recipient plant for gene expression. It has been demonstrated that plant can remember previous stress, and can use the memory to respond promptly to the stress when it reoccurs [7]. The memories are inherited through mitotic cell divisions and can be transmitted to the next generation. Transgenerational stability of the epigenetic marks requires their passage through the germline without being erased by the mechanisms which ensure the establishment of cellular totipotency at the time of ontogenesis. Plants do not sequester germline cells, as animals do, but develop their germ cells from meristematic cells relatively late in their life cycle. Therefore, any epigenetic change acquired during vegetative growth could be inherited to the next generation [7]. Recent studies provide evidence for the epigenetic mechanisms necessary for stress memory and adaptation in plants. Ding et al. [8] reported that repeated exposures to drought stress enabled the plant to respond to a new stress by quick adaptive changes compared with the plant not previously exposed to the stress. They reported downregulated expression of genes and suggested that higher level of histone modification might function as stress memory. However, there is limited evidence for natural epialleles, and yet we know only a little about phenotypic and ecological consequences of the epigenetic variations. Since epiRILs are identical for DNA sequence but carry differences in the epigenetic marks due to recombination, they might be a powerful tool for epigenetic studies in plants. Molecular analyses have demonstrated that variation in methylation pattern in epiRILs is stable over the generations.

Advances in high throughput methylome analysis allow generation of single-base resolution methylome maps describing DNA methylation landscape of a genome. However, challenges are still there to compile methylome maps of a specific cell, tissue, and organ under varying environmental conditions in addition to collecting the equivalent information for histone marks and siRNA biogenesis. The challenges ahead include improving our understanding of the stability, reversibility, and heritability of epialleles. We would require devising strategies to ensure stable retention of the desirable epialleles within breeding materials, and to develop techniques for targeted epigenetic manipulation [1]. Genomes of many crop plants are complex due to repetitive elements and their polyploid nature which makes gene interaction networks complicated, and difficult to modulate for improved plasticity [9]. How epigenetic changes are superimposed on the multiple gene copies to confer plasticity may provide a clue towards developing desirable crop variety tailored to cope up with the multiplestresses due to the global climate change. Epigenetic engineering may provide a way to achieve the desired variability and adaptive advantages without altering the underlying DNA sequence. Stable inheritance of such adaptive epialleles may provide increased fitness/adaptability to the plant for climate resilient agriculture.

Though we are still trying to understand the interplay between DNA methylation and other epigenetic features, further studies are needed to identify more developmental processes regulated through epigenetic mechanisms [6]. Assessing the contribution of transgenerational epimarks to heritable phenotypic variation has been a major challenge as many of the epigenetic changes and gene expression variants co-segregate with DNA sequence polymorphisms. Nonetheless, there is evidence that plants possess heritable epiallelic variations that can be associated with the trait of interest and utilized for crop improvement. Although it had been difficult to manipulate DNA methylation/chromatin state in a locus-specific manner, the situation is improving with the advances in genome-editing tools like CRISPR-Cas9 [10]. However, it would require a deeper understanding of the interactions between the genome and the regulatory networks to manipulate phenotypic plasticity. Many of stress-induced chromatin modifications do not persist post-gametogenesis, others are faithfully re-acquired at least in a few subsequent generations not exposed to the stress [11]. Epigenetic and genetic variations co-evolve, which is needed so that epigenetic plasticity does not completely buffer the evolutionary process and reduce the correlation between fitness and genotype. Though rapid accumulation of epigenetic variations in response to the environment can be seen in the first generation, transgenerational epigenetic memory ensures plasticity and adaptability. The dual

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inheritance of genetic and epigenetic variation ensures adaptation and evolution of the plant. Future studies in plants will undoubtedly provide insights into transgenerational epigenetic stress memory and adaptation in the plant.

While biochemical and physiological effects of stresses on crop yield are relatively understood, further research on epigenetics of stress tolerance needs to be undertaken. Global climate change is likely to further deteriorate the climatic conditions which will not only affect the productivity of crops but the quality of the produces also. Providing food to burgeon global population is only a preliminary challenge, a major challenge would be to produce ample food under the increasingly unfavorable environmental conditions [12]. Therefore, comprehensive ecological-epigenetic studies would be required to unravel the role of epigenetic memory in plant's adaptation to the changing environment.

The views expressed herein are those of the author only, and these may not necessarily be the views of the institution/organization the author is associated with.

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