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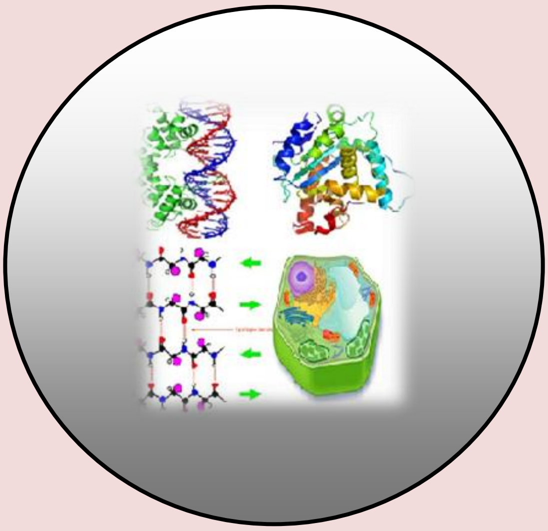

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Epigenomics Projects in Crop Plants: An Ocean of Possibilities

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ABSTRACT

Epigenomics is the study of the molecular changes that occurs in DNA and alters the expression of genes, without altering the nucleotide sequences. Such molecular modifications are also called as epigenetic modifications. The study of these epigenetic modifications in plants can help understating of various physiological mechanisms like flowering, biotic & abiotic stress resistance, growth, yield etc. Hence, these mechanisms may be regulated at genome level to develop enhanced varieties of different crops.

Keywords: Epigenetics, epigenomics, DNA modifications, plant projects and DNA silencing.

Significant Statement: This review covers all the different types of epigenomics studies in plants, application of epigenomics for crop improvement, a detail of some ongoing epigenomics projects and future prospects of epigenomics based research in crop plants.

INTRODUCTION

The term "epigenetics" has emerged from the Greek word "epigenesis" which means "extra growth". It was first coined by Conrad Waddington in 1942 to describe the impact of environment over the gene expression (Murrel et al, 2005). Epigenetics is the study of DNA changes that alter the expression of genes without any alteration in the gene sequences (Riggs et al, 1996). These changes are can be reversible or non-reversible and hence, can be heritable or non-heritable (Berger et al, 2009). Currently, this area of research is being widely elaborated to know the insights of DNA expressions and extend their applications like human health, environmental aspects and plant or crop improvement. The cellular mechanisms that lead to epigenetic modifications generally include DNA methylation (by DNA methyl transferase enzyme), Histone modifications (acetylation, deacetylation, phosphoylation, deamination and ubiquitylation) and non-coding RNA (micro-RNA, small-interfering RNA, piwi-interacting RNA, long non-coding RNA etc).

These epigenetic modifications play a significant role in the process of cell development, differentiation and cancer (Zhu et al, 2013). Chromatin modifications influence gene expression during development and in response to environmental cues. Such differentially expressed genes among plant varieties are given the term "epialleles", which refers to the genes with identical nucleotide sequence but altered expression abilities due to epigenetic events (Weigel and Colot, 2012). Epigenomics is the study of the all the epigenetic changes in a genome of a cell, such genome is also called as epigenome (Russell, 2010). The understanding of epigenomics can be valuable for various crop improvement approaches (Rival et al, 2010). However, the epigenomics has been well characterized on aspects of human health and medicine as compared to plant based studies. This review is mainly focused on the epigenetic events that widely affect the gene expression and phenotype of crop plants and their applications in crop improvements.

Development of epigenomics in crop research

Initially, the epigenomics based researches were mostly contributed towards the understanding the phenomena of various human diseases, mainly cancer (Thakur et al, 2013). The conceptual idea of epigenomics research for crop improvement has well emerged in the past decade when whole genome data of various crop plants (*Arabidopsis*, wheat, rice, maize etc) became available. The epigenetic modifications occur in response to various environmental pressures and it has been determined that such modifications play a crucial role in mediating productivity and stability in plant populations (Wang et al, 2014). Now, there are various techniques available for detecting the epigenetic modifications in plant genome. For example, tools like methylation-sensitive restriction endonucleases, affinity enrichment, bisulfite conversion and array & sequence based detection methods are available to detect DNA methylation events in plant genome (Kim et al, 2014).

The diversity of genome structures and organization in crop plants is largely due to variation in transposable elements (TEs) and whole-genome duplication (WGD) events. It has been evident that epigenomics regulations are highly influenced by the pattern of TEs and WGDs in the genome and many crop species have likely evolved chromatin-based mechanisms to tolerate silenced TEs near actively expressed genes (Springer et al, 2016). Many model plant species have been studied to evaluate the changes in expression profile due to epigenetic events and it has been found that such changes may lead to either silencing or over expression of genes (Sarma et al, 2015). These interactions have important roles in modulating gene expression and variability within species.

Epigenetics plays most important role in the process of vernalization (flowering in plants after a prolonged period of cold). The plants have evolved the ability to memorize the cold of winters and initiates flowering in spring season. The molecular basis of this event was studied on *Arabidopsis* and it was found that the cold treatment induces the synthesis of Vernalization Insensitive 3 (VIN3) protein which stimulates chromatin structure modifications in plant genome at flowering repressor gene *i.e. Flowering Locus* C *(FLC)*, that switch the gene in repressed state, inducing flowering (Fu et al, 2007). Further, Song *et al* (2015) studied the role of methylation of miRNA in the development of flowering in monoecious plants (Song et al, 2014).

Shitusukawa *et al* (2007), reported that both genetic and epigenetic alterations have occurred in the homologs of a wheat class 'E' MADS box gene (Shitsukawa et al, 2007). These MADS box genes comprise A, B, C, D and E genes that are concerned with stimulating flowering in the wheat. Two class 'E' genes were identified in wheat, wheat SEPALLATA (WSEP) and wheat LEAFY HULL STERILE1 (WLHS1), which are homologs of Os MADS45 and Os MADS1 in rice (*Oryza sativa*), respectively. The three wheat homoeologs of WSEP showed similar genomic structures and expression profiles. By contrast, the three homoeologs of WLHS1 showed genetic and epigenetic alterations.

The epigenetic events occur at greater frequency during the plant cell differentiation and development process *in vitro*. The chromatin remodeling during the developing stage of plants *in vitro*, leads to formation of various somaclonal variants that could be of interest to the researcher or breeder (Miguel and Marum, 2011). It is also evident now that epigenomic modifications can be heritable. In one of the studies on recombinant inbred lines (RILs) of soybean, it was found that the differentially methylated regions (DMRs) were heritable and contributed to the phenotype of the plant (Schmitz et al, 2017).

However, the possible extent of heritability of these modifications is variable and cannot be significantly determined by currently available techniques (Hirsch et al, 2013), which provides scope for future research.

Epigenomics research aspects for crop improvement: case studies

The availability of whole genome sequence information of various crop plants has encouraged the researchers to discover the insights of epigenomics and their possible effects on crop improvement programs. However, as plant epigenomics is still not very illustratively defined and hence, majority of projects are still much focused on understanding the phenomenon of epigenetic events in crop plants. The major crop plants *viz* wheat, rice, maize etc have been well studied for the determination of various aspects of epigenomics. Here, some epigenomics case studies have been discussed, which are promising to develop better crop varieties in near future:

Wheat (*Triticum sp*)

- Bottley *et al* (2008) have demonstrated that polyploids are affected by homoeologous gene silencing and suggested that much of the homoeologous silencing observed in differentiated tissues during wheat callus development, is probably under epigenetic control, rather than being linked to genomic instability.
- Yao *et al* (2010) analyzed the expression of small RNAs in seedling of wheat by northern blot, which indicated that some small RNAs were responsive to abiotic stress treatments including heat, cold, salt and dehydration. It may be proved to be a promising approach to develop abiotic stress resistance in wheat crops.
- Gardiner *et al* (2015) studied the pattern of genome wide DNA methylations in three sub-genomes of hexaploid wheat (AABBDD) by using the techniques sodium bisulphate treatment and targeted gene enrichment and found that majorly the methylation pattern is conserved throughout the genome of the three sub-genomes; however, some unique methylations were also present in the genomes.

Rice (*Oryza sativa*)

- Miura *et al* (2009) studied the effect of epigenetic changes on the rice plant height. They identified a spontaneous rice mutant, *Epi-d1*, showing a metastable dwarf phenotype. The phenotype is mitotically and meiotically inheritable and corresponds to the metastable epigenetic silencing of the *DWARF1* (*D1*) gene. The study postulated the epigenetic control of plant height, which can be further elaborated for crop improvement programs in future.
- Wen *et al* (2016) studied the expression pattern of mRNA and miRNA in six accessions of two rice varieties *Oryza sativa* L. ssp. indica and *Oryza sativa* L. ssp. Japonica. They found about 11% differentially expressing miRNA among accessions of sub-species and genes involved in various metabolic processes and stress responses are enriched in the differentially expressed genes between rice indica and japonica subspecies. A similar study was done previously by He *et al* (2010), where they studied the differential expression of mRNA and siRNA.

Maize (*Zea mays*)

- Lunardon *et al* (2016) performed siRNA and total RNA sequencing from control and abiotically stressed B73 wild-type plants and rmr6-1 mutants of maize and identified novel miRNA loci and verified miR399 target conservation in maize. They demonstrated correlation in long-term drought tolerance with changes of miRNA and sRNA accumulation in the wild-type maize.
- Bousios *et al* (2017) studied 6456 carefully annotated; full-length Sirevirus LTR retrotransposons in maize and showed that their silencing is associated with underlying characteristics of the TE sequences. They also uncovered features of the host–TE interactions in host epigenetic response against pathogen.

Future prospects

Plant epigenomics is still in its budding state and needs high throughput research and development for its application in crop improvement programs. Most of the currently ongoing epigenomics projects are contributed towards understanding all the possible epigenetic events that occur in plant genome. Following questions need to be answered in near future:

1. How many different epigenetic modifications occur in the plant genome?
2. At what stage of development, these changes occur?
3.

4. How these changes affect the physiology of plants?
5. How can these modifications be explored to be applicable in crop improvement programs?
6. What are the techniques which need to develop to facilitate epigenomics research?

Lane *et al* (2014) enforced the development of pENCODE (Plant Encyclopedia of DNA Elements). The goal of such a project would be, to coordinate the ongoing work in individual laboratories across the globe, to focus community efforts on a set of high priorities and to standardize sample/data preparation, acquisition, and dissemination. Such encyclopedia (ENCODE) already exists for human genome some other model animal and microbial genome. A major goal of pENCODE would be to facilitate decoding the manner in which plant genomes are expressed [27]. Various online epigenomics resource databases have been developed (Table 1), which can contribute for such a project.

Table 1. List of epigenomics resource databases.

S. No.	Database Resource	URL	Plant Species	Reference
1	Gramene	http://www.gramene.org	*Arabidopsis*, Maize, Wheat, Rice	Mochida and Shinozaki, 2011
2	EPIC	https://www.plant-epigenome.org	All the sequenced plant genomes	Mochida and Shinozaki, 2011
3	Yale Plant Genomics	http://plantgenomics.biology.yale.edu	Rice, Maize	Mochida and Shinozaki, 2011
4	NCBI Epigenomics	www.ncbi.nlm.nih.gov/epigenomics	All the sequenced plant genomes	Fingerman *et al*, 2011
5	Expression Atlas	http://www.ebi.ac.uk/gxa	All the sequenced plant genomes	Petryszak *et al*, 2016

With the availability of plant genome information and recent technologies, the future of epigenomics is promising to apply this area of research for the crop improvement programs.

Summary

- Epigenetics is the study of DNA changes that alter the expression of genes without any alteration in the gene sequences. Epigenomics is the study of the all the epigenetic changes in a genome of a cell *viz* chromatin modifications, DNA methylation, RNAs (coding and noncoding) etc.
- Epigenomics research in plants emerged after discovery of impact of epigenetic events in plant physiology *viz* vernalization, DNA repair, response to abiotic and biotic stresses etc.
- Various epigenomics studies have been done on crop plants to improve abiotic and biotic stress resistance. Currently, various research projects are in progress worldwide; to better understand the plant epigenomics, so that it can be applied for crop improvement programs in near future.
- Various researchers have encouraged the development of epigenomics databases like pENCODE, Esembl, EPIC and many others; to enhance collaboration and collect the information of various epigenomics projects being conducted worldwide.

CONCLUSION

The epigenomics research in plants is in a phase where most of the researches are based on understanding the impact of epigenetic modifications on various physiological events of plants. Great research is still required to apply the epigenomics for the crop improvement programs. However, the newly developed technology in plant sciences and availability of nucleotide sequence information of various crop plants is promising a great significance of epigenomics for crop improvement programs.

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