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Plant Epigenetics: Mechanisms and Applications

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A B S T R A C T

Plant epigenetic has become one of the key research topics not only as the subject of basic research but also as a new source of useful traits for plant breeding. Epigenetic regulation is necessary for the production of differentiated cells throughout plant development, as well as maintaining the stability and integrity of the gene expression profiles. Although epigenetic processes are essential for natural growth, they can become misdirected led to abnormal phenotypes and diseases. Epigenetics is the study of heritable phenotype changes that do not involve alterations in the DNA sequence. The microstructure (not code) of DNA itself or the associated chromatin proteins may be modified, causing activation or silencing. This mechanism enables differentiated cells in a multicellular organism to express only the genes which are necessary for their own activity. In this review, our goal is to introduce epigenetics and its different applications in plants, especially in the production of transgenic plants, plants tolerate to biotic and abiotic stresses and understanding the mechanisms of gene silencing. Also, in this review, we have referred to the role of transposons in epigenetic, epigenetic engineering methods, epigenetic fingerprinting and ultimately methods for epigenetic data analysis and related databases.

Introduction

Plants are considered to be masters of epigenetic regulation because of their ability to rapidly and reversibly modification of their epigenetic state, and also preserve a stable memory of it. Under different conditions, plants grow under severe environmental situations that reduce total production and maybe not survive, thus they have developed complex mechanisms at the molecular level to survive under critical conditions which can resist environmental stresses throughout their life cycle (Abobatta, 2018).

The transcriptomic activity of an organism is determined not only by its genetic combination but also by its epigenetic regulations. Reprogramming by epigenetic modification is created through various environmental challenges that contribute to the phenotypic diversity and defense against these challenges (Saraswat et al., 2017).

Many of the environmentally induced epigenetic changes in plants are reset during gametogenesis, and some persist through gametogenesis and can be stable through many generations (Alis et al., 2014).

There are two factors that indicate the plants have more potential for epigenetic regulation than animals. First, there is the late differentiation of the germline. This does not occur in embryogenesis such as animals but occurs in somatic tissues after flowering in male and female reproductive organs (Pikaard & Mittelsten Scheid, 2014).

Therefore, the plant germline cells are isolated from somatic cells and they carry epigenetic marks as persistent remnants of earlier environmental stimuli. The second factor to differentiate transgenerational inheritance in plants and animals are related to epigenetic erasure during embryogenesis, which is more complete in animals than in plants (Gutierrez-Marcos & Dickinson 2012).

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The aim of this review is the study of epigenetic application in agricultural biotechnology and also provide methods for epigenetic breeding of plants.

Mechanisms of epigenetic

In eukaryotes, the chromatin structure plays an important role in gene expression. Chromatin is a compact genome structure. Gene expression can be controlled by altering the chromatin structure without changing the DNA sequence, which calls this phenomenon “epigenetic” (Fujimoto et al., 2012). Epigenetic modifications have a role in various aspects of plant life, including transgenic silencing, genome integrity, nuclear domination, nucleosome arrangement, flowering, paramutation, and etc. (Wollmann & Berger, 2012).

Three main epigenetics mechanisms in plants and higher organisms are; DNA methylation, histone modification, and RNA interference (Munshi et al., 2015).

DNA Methylation

DNA methylation involves the addition of a methyl group (-CH3) covalently to the base cytosine (C) in the dinucleotide 5´-CpG-3´. The term "CpG" refers to the cytosine base, which linked to the guanine base through the phosphate bond (Lim and Maher, 2010). In plants, cytosines are methylated in two ways symmetrical (CG or CHG) or asymmetrical (CHH, where H is A, T, or C) (Lister et al., 2009). DNA methylation is catalyzed by a family of conserved enzymes called DNA methyltransferases (MTases). Different types of DNA MTases include

1. Maintenance methylases, that maintain stable cytosine methylation patterns by consecutive cell generations.

2. De novo methylases, those are able to transfer methyl groups to unmethylated DNA cytosines.

3. domain-rearranged methylases (DRMs) which are directed from short RNAs and specifically methylate homologous genes in a process termed as RNA-directed DNA methylation (RdDM) (Munshi et al., 2015) (Fig1).

Histone Modifications

Histones have many post-translational modifications, including acetylation and methylation of lysines (k) and arginines (R), phosphorylation of serine (S) and threonines (T), ubiquitination, sumoylation, and biotinylation of lysines as well as ADP ribosylation (Munshi et al., 2015).

Two important targets for epigenetic modifications in plants are histone H3 lysine 9 (H3K9) and H3 lysine 27 (H3K27). H3K9 methylation has been associated with heterochromatin formation or gene repression, while H3K27 methylation is related to gene expression required for developmental decisions (Zhou, 2009). Methylation H3K9 marks silent DNA and is found throughout heterochromatic regions including centromeres and telomeres. Lysine methylation can be monomeric, dimeric, or trimeric. These observations have led to the idea of the histone code, the degree of specificity of these codes varies so that a certain combination of histone symptoms does not always dictate the same biological function (Strahl & Allis, 2000) (Fig1).

RNA Interference (RNAi)

In many organisms, intergenic transcription or anti-senes transcription provide several classes of small RNAs and long non-coding RNAs that appear as key regulators of the chromatin structure in eukaryotic cells (Cech & Steitz, 2014). In addition to their roles in RNA degradation and suppressing the translation, small RNAs modified chromatin and gene expression of the target through RNA interference (RNAi) pathways (Reinhart & Bartel, 2002).

In many cases, nuclear RNAi pathways cause histones or DNA methylation events that suppress transcription (Holoch & Moazed, 2015). Therefore, the effector protein complex down-regulates the expression of the targeted RNA or DNA. Small RNA-directed gene regulation systems have been discovered in plants, fungi, worms, flies, and mammalian cells (Lindbo, 2012) (Fig1).

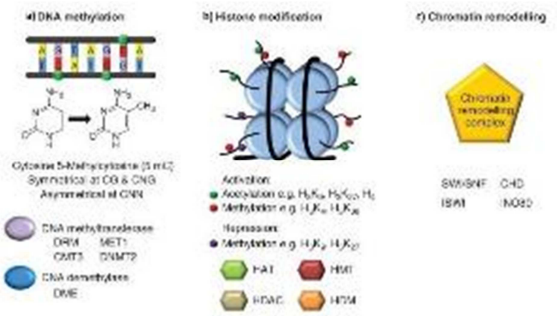

Fig. 1- Mechanisms of epigenetics. a) DNA methylation b) Histone modification c) Chromatin remodeling. (Temel et al. 2015)

Genomic Imprinting

Genomic Imprinting is an epigenetic mechanism that creates functional differences between the parent genomes and plays an important role in the growth and development of organisms (Munshi et al., 2015).

Application of epigenetic in plants

1. Epigenetic in transgenic plants

In genetically modified plants, sometimes transgenes are not expressed, which may be due to their silencing (Doerfler, 1995). Various factors can play a role in gene silencing including DNA methylation, transgene copy number and the repeat of the transgene insert, transgene expression level, possible

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production of aberrant RNAs, and ectopic DNA-DNA interactions (Stam et al, 1997).

The silencing of transgene locus can result in the silence of homologous transgenes in ectopic loci (Matzke et al., 1994). Also, the methylation of silencing locus causes the methylation of the target locus. In the homologous promoters, this methylation transfer can lead to inactivation of transcription. For example, for a potent silencer locus, the 271 transgene locus, which contains antisense nitrite reductase genes driven by a strong CaMV-35S promoter (Park et al., 1996). Gene activity is determined not only by the strength of the promoter that controls the transcription, but also epigenetic effects influence expression levels. This sometimes leads to gene inactivation either by blocking transcription or by inhibiting mRNA accumulation (Stem et al. 1997). If the transgene is inserted into the transcriptional active region (euchromatin), expression may be influenced by the regulatory sequences of nearby host genes (Kertbundit et al., 1991). If they integrate into or near repetitive DNA or heterochromatin, they can be inactivated (Prols & Meyer, 1992).

Transcriptional gene silencing (TGS) is often associated with heavily methylated and inactive promoter sequences (Park et al., 1996). The effect of methylation on gene expression in the promoter is more than the other parts. Methylation of the coding regions does not have a detectable effect on transcription (English et al., 1996), in some cases, it appears to be involved in post-transcriptional gene silencing (PTGS). Methylation of foreign DNA appears to be a cellular defense response against the potentially harmful activity of this DNA (Doerfler, 1995). Transgene of T-DNA that is inserted as a DR (Direct Repeat) or an IR (Inverse Repeat) has a tendency to become inactivated (Vaucheret, 1993; Matzke et al., 1994). In the case of IRs, it might be the ability to create a cruciform which is a good substrate for DNA methyltransferases (Laayoun & Smith, 1995). In Post-transcriptional silencing of transgenes, promoters are active and the genes transcribed, but mRNA fails to accumulate. The transgene-induced PTGS mechanism affects the expression of the transgenes and endogenous genes with which they share a considerable degree of sequence identity (Stem et al., 1997).

2. Epigenetic in crop improvement

Under stress conditions, DNA methylation, histone post-translational modifications (PTMs), chromatin 26ehaviour26g and mechanisms such as RNA-interference can rapidly regulate gene expression (Bocchini et al., 2015; Liu et al., 2015). After stress, this type of modification can be 'memorized' by plant somatic cells and can be utilized as an epigenetic mark that can be inherited transgenerationally, thus, the same epigenetic modification will occur when the progenies will face stressful conditions (Migicovsky et al., 2014; Tricker et al., 2013). This process appears to function mainly through the female gamete (Wibowo et al., 2016).

This epigenetic plasticity that is transmitted through generations is a key factor in the plant immediate response to stress and its long-term adaptation and can have a great impact on breeding programs (Fortes and Gallusci, 2017; Mirouze & Paszkowski, 2011). Reprogramming of epigenomes have been demonstrated in several plant species [Arabidopsis, rice, maize, poplar (Populus), moss (Physcomitrella patens), and tomato (Solanum lycopersicum)] in response to several abiotic and biotic stresses, including drought (González, 2013), salt (Al-Lawati, 2016), temperature (Dai, 2015), and mineral stresses (Yong-Villalobos, 2015), and pathogen and herbivory attacks (Dowen, 2012). Epigenetic mechanisms affect crop improvement:

2-1. Histone Modification

Histone undergoes several covalent modifications like acetylation, methylation, phosphorylation, ubiquitination, and biotinylation in response to various environmental stresses and regulates the transcription of DNA sequence. These modifications alter the packaging structure which either activates the DNA for the transcription or makes the structure even condensed so that transcription machinery is unable to bind to it (Saraswat et al., 2017).

2-2. DNA Methylation

DNA methylation shows different 26ehaviour according to the location of methylation but mostly is related to the repression of the gene. Methylation in transposable elements and promoter region of a gene leads to the silencing (Li et al., 2012) and methylation inside of gene sequence causes to regulate gene expression (Lu et al., 2015).

Increasing genome DNA methylation may reduce the expression of the transcriptome, which leads to a reduction in the rate of plant metabolism that enables the plant to maintain its energy for biotic and abiotic stresses and help the plant to overcome temporary challenges like sleeping (Saraswat et al., 2017).

2-3. MicroRNAs

MiRNA plays a role in processes including cell proliferation, cell death, immunity, and control of leaf and flower development and in the abiotic and biotic stresses as well (Ragupathy et al., 2016).

Recent studies indicated that epigenetic mechanisms such as DNA methylation, histone post-translational modifications, and small non-coding RNAs are involved in almost all aspects of plant life including flowering time, fruit development, responses to environmental factors, and plant immunity. Epigenetic modifications control gene expression by

regulating the access of regulatory complexes to the genome (Álvarez-Venegas & De-la-Peña, 2016). Epigenetic mechanisms affect crop biotechnology. Histone methylation has an active role in the regulation of plant hormones (Barraza et al., 2008).

Mechanisms of epigenetic regulation in somatic embryogenesis (SE) could help to increase plant productivity and improve agronomical breeding practices (De-la-Peña et al., 2012). Methylation signatures affect in vitro propagation and optimization of in vitro meristem propagation protocols and diagnosis of the origin of clonal stocks (Kitimu et al., 2015). Most of the miRNA examined increase upon hormone depletion, whereas the expression of miRNA target genes is effectively regulated by the photoperiod exposure. MiRNA roles in macro/micro-nutrients deficiencies in plants, regulation of nutrients transporters and other metabolic enzymes (Paul et al., 2015). Abiotic conditions affect epigenetics and therefore plant behavior, also biotic challenges are an important topic of study (Loza-Muller et al., 2015). Molecular mechanisms of histone modifications and chromatin remodeling contribute to plant immunity against pathogens (Ding & Wang, 2015).

Su et al., (2012) find, in Arachis hypogaea, an RPD3/HDA1-like superfamily histone deacetylase (HDAC), termed AhHDA1, which is seemingly involved in the epigenetic regulation of stress resistance genes in response to osmotic stress and ABA treatment.

3. Epigenetic and transposons

Transposable genetic elements (TEs) includes a wide range of DNA sequences, all of them have the ability to move to new locations in the genome, or directly by the transposons or indirectly via the RNA middle mediate (retrotransposons)(Fedoroff, 2012). Transposable elements make up an essential part of the genome in most plants. Transposons are controlled by mechanisms that detect their function and silence them epigenetically. In most cases, the transposons are inactive, but under different conditions, they are activated. There are many different kinds of transposons, each of which employs a distinct strategy to increase its copy number. They can cycle between these states during the development of an individual plant and these patterns can replicate themselves in subsequent generations (Lisch, 2009). Active TEs are highly mutagenic and often target the protein-encoding genes, they also causing chromosome breakage, illegitimate recombination, and genome rearrangement. TEs can also influence neighboring genes by altering splicing and polyadenylation patterns, or by functioning as enhancers or promoters (Girard & Freeling, 1999) (Fig2). To combat the harmful effects of active TEs, the genome has developed epigenetic defense mechanisms to suppress their activity. An epigenetically inactive TE maintains the coding potential for its mobility but does not produce the proteins required because of the suppressor chromatin environment (Slotkin & Martienssen, 2007). They can sometimes provide selective benefit to their hosts (Jordan et al., 2003). TEs have the ability to mutate genes, alter gene regulation and generate new genes, each providing fuel for evolution (Hickey, 1982; Doolittle & Sapienza, 1980). For example, Pack-MULEs, are Mutator-like TEs that carry fragments of genes in different plants and were proposed as important mediators of gene evolution in plants (Jiang et al., 2004). TEs also have a major role in generating intraspecies variation (Wang & Dooner, 2006).

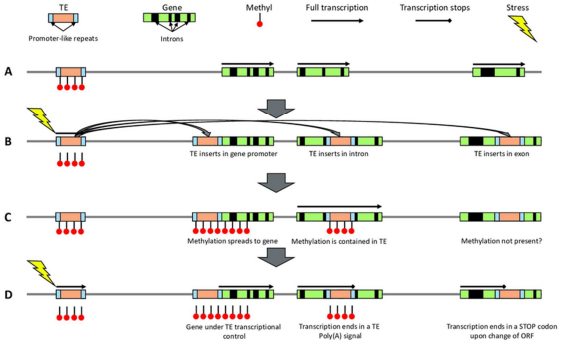

Fig. 2- Epigenetic control of transposable elements TEs through methylation (Galindo-González et al. 2018).

4. Epi-fingerprinting

Epigenetic fingerprinting is understanding the relationship between various epigenetic states and responses of the crop to specific aspects of the growing environment (Rodríguez López & Wilkinson, 2015). Epi-fingerprinting has common uses in agriculture, including detects and creates epigenetic variation under in vitro conditions. In vitro plant cell and tissue culture techniques is the basis of many micropropagation and breeding programs for scientific research (Us-Camas et al., 2014). During in vitro culture, plants are affected by a variety of conditions such as components in the culture media, exogenous addition of plant growth regulators, humidity in the vessels, etc (Vanstraelen & Benkova, 2012). Epigenetic variation at several levels has been reported during and after being exposed to in vitro culture conditions (De-la-Pena et al., 2012). The loss of epigenetic fidelity during micropropagation has been a major source of economic damage in several crops (Matthes et al., 2001). Many studies have reported global changes to the distribution of cytosine methylation can be induced by in vitro culture in various species such as tobacco (Schmitt et al., 1997). In addition to economic damage, ‘somaclonal variation’ may offer a source of valuable new variation that has potential applications in plant breeding (Henry, 1998). Epigenetic theories primarily emphasize the

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interaction between genes and the environment. According to these theories, the environment plays an important role in determining the epigenetic changes in the individual genome, which ultimately affects the growth of the organism and the process of inheritance (Brautigam et al., 2013; Springer, 2013; Yakovlev et al., 2011).

Another application of Epi-fingerprinting is plant breeding and selection of economical varieties. Some plants with a same genetic origin, despite being cultured under the same controlled conditions, exhibit a variety of morphological and developmental changes that can be explained by epigenetic variation (Hauben et al., 2009). These epigenetic changes may even be larger than genetic variations (Hirsch et al., 2013; Schmitz et al., 2013). These epigenetic changes may lead to the production of desirable agronomic traits (Gourcilleau et al., 2010; Alonso et al., 2014) or potentially economic features (Zhang et al., 2012). It has also been suggested that deliberate manipulation of specific aspects of growth environment can lead to desirable changes in drought tolerance (Tricker et al., 2013b), but the distinction between these types of epigenetic variation from the genetic background that has the capacity to produce new variations, is difficult and disturbs in their commercial production (Cortijo et al., 2014).

Epi-fingerprinting can also be used as a plant health indicator. Plants have developed mechanisms for identifying stress and then responding to them, including substantial amendments to key metabolic pathways (Madlung & Comai, 2004). These responses can be activated in a variety of ways, including the transcriptional regulation of genes through differential cytosine methylation (Aceituno et al., 2008). Large numbers of biotic and abiotic stresses induce global changes to the methylation patterns of plants (Boyko & Kovalchuk, 2011). It is also possible to use the C-methylation profile to better understand the relationship between stress and the physiological response of the plant to this stress. Sequence characterization of these differentially methylated loci may ultimately provide a useful route to discover the candidate genes involved in these responses (Sha et al., 2005). The apparent stability of some C-methylation sites after induction allows for stress detection long after initial exposure. This ‘memory of stress’ is not limited to cells and cell lineages but can persist through progeny generations (Rodríguez López & Wilkinson, 2015).

Epi-fingerprinting also plays a role in product quality. Confirm the authenticity and origin of products is a legal requirement in many jurisdictions to prevent unfair competition and to ensure consumers protection against fraudulent practices (Reid et al., 2006). Qualitative characteristics of plant products, in addition to plant species and varieties, are affected by components of harvest (Srancikova et al., 2013), climate, location, the age of the product, and management systems used to cultivate the products (Posner et al., 2008). Measurement of these components often requires the development of a set of independent tests for detecting fraudulent labeling. The use of methylation profiles as a diagnostic tool relating to several different aspects of crop quality is therefore appealing because it provides a ‘plant’s perspective of the growing environment.’ Such markers could not only have potential value in identifying the cultivating system and product composition but also to other factors affecting quality such as storage, transport and processing conditions (Rodríguez López & Wilkinson, 2015).

Epigenetic engineering

The goal of epigenetic engineering is to change the epigenetic information at specific regulatory loci, such as enhancers and promoters, in order to inactive or activate single genes (Magnani, 2014). Locus-specific DNA methylation and histone modification changes can now be induced using epigenetic engineering technologies. These technologies regulate enzymes that create specific epigenetic changes in the genes desired (Day, 2014). DNA methyltransferase (DNMT) and histone deacetylase (HDAC) inhibitors are two most commonly used tools for probing epigenetic function that operates globally at their target enzymes (Szyf, 2009).

Three methods for editing the epigenome included zinc finger nucleases (ZFNs), transcriptional-activator like effectors (TALEs), and clustered regularly interspaced short palindromic repeats (CRISPR), which interact with Cas9 nucleases (Day, 2014).

Development of epigenome modification through CRISPR/Cas9 tool is a talented technology to change gene expression directly to cell phenotype and to scrutinize the fundamental epigenetic mechanism of gene regulation (Thakore et al., 2015).

Targeting of DNA methylation enzymes is done for specific DNA sequences using TALE or CRISPR based tools, which results in the methylation and demethylation of specific DNA sequences (Jurkowska & Jeltsch, 2010) (Fig3). Targeted DNA demethylation has also been accomplished by fusing thymine deglycosylase (TDG) to the DNA binding domain of a transcription factor (Gregory et al., 2012).

Recently TALE-based strategies to target histone methyltransferases, histone demethylases, histone acetyltransferases, and histone deacetylases directly to endogenous DNA sequences have been used (Konermann et al., 2013). These manipulations lead to a significant increase in histone methylation and a decrease in histone acetylation, each of which led to 1.5-3 fold decrease in mRNA levels. Histone

demethylation resulted in reduced enhancer RNA and decreased transcription of nearby gene targets, and was thus critical for revealing the actual function (Mendenhall et al., 2013).

Researchers identify differentially methylated genes between wild and cultivated cotton that have potentially contributed to domestication traits, including flowering-time and seed dormancy, opening new opportunities for breeding of polyploid crops by epigenetic engineering (Song et al. 2017).

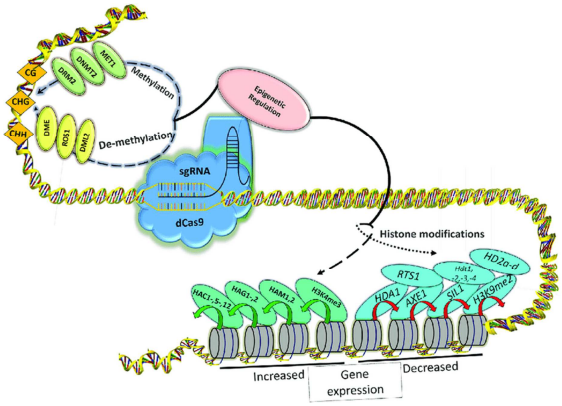

Fig. 3- Engineering dCas9 for Epigenetic Modifications (Shrestha et al. 2018).

Analysis of epigenetic data

The development of accurate computational methods for the analysis of complex epigenetic profiles is essential for discovering the mechanisms of cellular development, complex interaction networks, and for the determination of chromatin changes and DNA methylation to control gene expression. The characteristics of the computational method used to analyze the epigenetic data depend considerably on the characteristics of the experimental techniques used to perform epigenomic profiles (Angarica & Del Sol, 2017).

The most commonly used experimental methods to profile histone posttranslational modifications are ChIP-on-chip (Barski et al., 2007), ChIP-seq (Furey, 2012), and mass spectrometry (Bartke et al., 2013). ChIP-on-chip: histone modification-specific antibodies, bound to chromatin regions bearing the corresponding modification, are cross-linked to DNA by treatment with formaldehyde. ChIP-seq: Its early stages are like ChIP-on-chip, but unlike that, it relies on HTS DNA sequencing rather than on microarrays for identifying the sequences enriched in histone marks. Proteomic profiling using mass spectrometry (MS) allows the detailed characterization of histone tail posttranslational modifications.

Moreover, different approaches for analyzing this data have been developed, comprising RRBSMAP (Xi et al., 2012), RMAP (Smith et al., 2009), GSNAP (Wu et al., 2010), and Segemehl (Otto et al., 2012).

a. Bioinformatics methods for Analyzing Methylation Profiling

DNA methylation can be profiled experimentally with bisulfite sequencing (Booth et al., 2012), bisulfite microarrays (Bibikova et al. 2011), and enrichment methods, such as MeDIP-seq and MethylCap-seq (Down et al., 2008).

In order to measure the levels of methylation, first bisulfite sequence reads are aligned to the reference genome, the methylation levels of specific genomic regions can be estimated by using variant caller algorithms, which allow the quantitation of the frequency of Cs and Ts (Angarica & Del Sol, 2017).

b. Analysis of Chromatin Data

The chromatin of genomic regions can be profiled with methods such as DNase-seq (Song & Crawford, 2010), FAIRE-seq (Giresi et al., 2007), and ATAC-seq (Buenrostro et al., 2013), which rely on different experimental principles and produce different data outputs.

c. Epigenomic Databases and Epigenome Mapping projects

The great developments of high-throughput sequencing technologies have allowed the steady generation of great quantities of epigenomic data in different cell types/ lines and multiple organisms (Angarica & Del Sol, 2017). Some epigenome mapping projects are the ENCODE project (Consortium, 2012), the NIH Roadmap Epigenomics (Bernstein et al., 2010), and the HEROIC European project (http://cordis.europa.eu/project/rcn/78439_en.html). The MethBase database (http://smithlabresearch.org/software/methbase/, (Song et al., 2013), encompassing hundreds of methylomes from different organisms allow comparing the methylation profiles of genomic regions in different animal and plant genomes.

Conclusion

Epigenetic is one of the most important topics in the field of plant genetics. Plants play an important role in food security. Malnutrition is a significant public issue in most of the developing world. Plant biotechnology could play a major role in combating malnutrition through the engineering of high nutritional value crops. From the past few years, there was an increase in the breeding of crops with transgenes which express desirable traits and using epigenetic we can produce plants with desirable and appropriate traits in short time.

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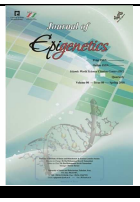

اپی ژنتیک گیاهی: مکانیسم ها و کاربردها

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چکیده

اپی‌ژنتیک گیاهی به یکی از موضوعات کلیدی تحقیق، نه تنها به عنوان موضوع پایه پـژوهش بلکـه همچنـین بعنـوان منبـع جدیـد صفات مفید برای اصلاح گیاهان تبدیل شده است. تنظیم اپی‌ژنتیکی برای تولید سلول‌های تمایزیافته در طول نمو سلول و همچنین حفظ ثبات و یکپارچگی پروفایل‌های بیان ژن ضروری است. اگرچه، فرآیندهای اپی‌ژنتیک برای رشد طبیعی ضـروری هسـتند آنهـا می توانند به اشتباه هدایت شده و منجر به فنوتیپ‌های غیرطبیعی و بیماری‌ها شوند. اپی‌ژنتیـک، مطالعـه تغییـرات فنـوتیپی قابـل توارث است که شامل تغییرات در توالی DNA نمی‌شود. ریزساختار خود DNA (بدون کد) یا پروتئینهای کروماتین مربوطـه ممکـن است تغییر کند که باعث فعالسازی یا خاموشی می‌شود. این مکانیسم سلول‌های تمایزیافته را قادر می‌سازد تا تنها ژن‌هـایی را بیـان کند که برای فعالیت خودشان مورد نیاز است. در این بررسی، هدف ما معرفی اپی ژنتیک و کاربردهـای مختلـف آن در گیاهـان، بـه ویژه در تولید گیاهان تراریخته، گیاهان متحمل بـه تـنش هـای زنـده و غیرزنـده و درک مکانیسـم هـای خاموشـی ژن مـی باشـد. همچنین، در این بررسی، ما به نقش ترانسپوزون ها در اپی ژنتیک، روش های مهندسی اپی ژنتیک، انگشت نگاری اپی ژنتیکی و در نهایت روش های آنالیز داده های اپی ژنتیک و پایگاه های داده مربوطه اشاره کرده ایم.

واژگان کلیدی: اپی ژنتیک، گیاهان، کاربرد، مهندسی اپی‌ژنتیک، انگشت نگاری اپی ژنتیکی.

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